

Grandmothers' Longevity Negatively Affects Daughters' Fertility

Lorena Madrigal^{1*} and Mauricio Meléndez-Obando²

¹*Department of Anthropology, University of South Florida, Tampa, FL 33617*

²*Academia Costarricense de Ciencias Genealógicas y Asociación de Genealogía e Historia de Costa Rica*

KEY WORDS grandmother hypothesis; mother hypothesis; heritability of longevity

ABSTRACT The evolution of postmenopausal longevity in human females has been the subject of debate. Specifically, there is disagreement about whether the evolution of the trait should be understood as an adaptive or a neutral process, and if the former, what the selective mechanism is. There are two main adaptive proposals to explain the evolution of postreproductive longevity: the grandmother and the mother hypotheses. The grandmother hypothesis proposes that postreproductive longevity evolved because it is selectively advantageous for females to stop reproducing and to help raise their grandchildren. The mother hypothesis states that postmenopausal longevity evolved because it is advantageous for women to cease reproduction and concentrate their resources and energy in raising the children already produced. In this article, we test the mother

and the grandmother hypotheses with a historical data set from which we bootstrapped random samples of women from different families who lived from the 1500s to the 1900s in the central valley of Costa Rica. We also compute the heritability of longevity, which allows us to determine if genes involved in longevity are nearly fixed in this population. Here we show that although longevity positively affects a woman's fertility, it negatively affects her daughter's fertility; for this reason, the heritability of longevity is unexpectedly high. Our data provide strong grounds for questioning the universality of the grandmother hypothesis and for supporting the mother hypothesis as a likely explanation for the evolution of human postreproductive longevity. *Am J Phys Anthropol* 136:223–229, 2008. © 2008 Wiley-Liss, Inc.

Human evolutionary biologists and anthropologists have been interested in the evolution of postmenopausal longevity in human females. Most if not all workers on this subject recognize William's 1957 article as their original source. Referring to the human female, Williams writes: "A termination of increasingly hazardous pregnancies would enable her to devote her whole remaining energy to the care of her living children, and would remove childbirth mortality as a possible cause for failure to raise these children" (Williams, 1957; p 408).

Although menopause was the initial focus of study, there is wide agreement that the trait whose evolution needs explaining is not menopause itself, but postreproductive longevity (Peccei, 1995a,b, 2001a,b, 2005). In other words, why does somatic senescence "slow down" independently of the rate of reproductive senescence, so that postcycling women have many years of vigorous and healthy life after the onset of menopause.

Senescence itself has been explained evolutionarily with two major theories. The antagonistic pleiotropy theory (Williams, 1957) proposes that genes, which are beneficial in early life, may have deleterious effects in late life. Allen et al. (2005), note that the antagonistic pleiotropy theory is a refinement of the earlier, mutation accumulation theory. Secondly, the disposable soma theory proposes that there has been selection for investing energy in reproduction earlier in life as opposed to somatic maintenance in old age. Although female postreproductive longevity could be seen as an "evolutionary byproduct" explained by either the disposable soma or the antagonistic pleiotropy theory, there is wide agreement that the trait evolved as a result of natural selection (Peccei, 1995a,b, 2001a,b; Jamison et al., 2002; Allen et al., 2005; Voland et al., 2005; Hawkes, 2006). Suc-

cinctly, there are two adaptive proposals which seek to explain the evolution of female postcycling longevity: the grandmother and the mother hypotheses, the former receiving more attention than the latter.

According to the grandmother hypothesis, at some point in the evolutionary history of hominines (probably in the Plio-Pleistocene), reproductive-age females started needing support raising their still dependent offspring, while at the same time, maintaining new pregnancies. In this condition, older females whose fertility was declining increased their own fitness by assisting their reproductive-age offspring (primarily daughters) raise their young (Peccei, 2001b). Therefore, postreproductive longevity in human females evolved because these females assisted their daughters, who had a higher fertility than did others who did not have a postreproductive mother's assistance. The grandmother hypothesis explains not only postreproductive longevity in human females, but the evolution of other derived human life history traits such as high rates of birth and early ages at weaning (Hawkes and Jones, 2005).

Grant sponsor: National Institutes of Aging; Grant number: 1-R03-AG022616-01.

*Correspondence to: Lorena Madrigal, Department of Anthropology, University of South Florida, Tampa, FL 33617, USA.
E-mail: madrigal@cas.usf.edu

Received 24 April 2007; accepted 14 December 2007

DOI 10.1002/ajpa.20798

Published online 5 March 2008 in Wiley InterScience (www.interscience.wiley.com).

William's initial proposal, cited earlier, is currently referred to as the mother hypothesis. However, it has been previously called the altriciality-lifespan hypothesis and the prudent mother hypothesis (Jamison et al., 2002). According to this proposal, postmenopausal longevity evolved because a woman's fitness benefits from her cessation of reproduction and concentration of resources and energy in raising the children already produced (Peccei, 1995a,b, 2001a,b; Peccei, 2005). Since the mother hypothesis has received less attention, fewer studies support it, but none has rejected it.

In sum, there are several proposals which seem relevant to our understanding of the evolution of female postreproductive longevity, from general theories about senescence (the disposable soma and the antagonistic pleiotropy theory), to paleoanthropological ones (the trait was established sometime in the Plio/Pleistocene and it is related to the evolution of derived human life history traits). As varied as the theories involved are, so have been the approaches used to test them, resulting in conflicting results and interpretations of the results. This is certainly the case for paleoanthropological and skeletal studies. Thus, Caspari and Lee (2004) indicate that the fossil record shows that older individuals became frequent only in the modern humans of the Early Upper Paleolithic, much after the Plio-Pleistocene. Peccei (2001b), based on skeletal studies, also posits that postmenopausal longevity must have been rare as recently as 1,000 year ago. In contrast Hawkes (2003) and Allen et al., (2005) question the validity of paleodemographic and skeletal data concerning the question of whether postreproductive longevity in women evolved in the Plio-Pleistocene, in conjunction with other human life history traits.

In work with living or recently living humans, for the grandmother and mother hypotheses to be accepted, it must be shown that postreproductive longevity in females is fitness enhancing (Peccei, 2001b). For the grandmother hypothesis, the benefit should be seen in increased fertility of daughters (and perhaps nieces; Hawkes, 2003), whereas for the mother hypothesis, the benefit should be seen in increased survivorship of offspring. In previous work, fitness has been measured by various proxies, such as nutritional supplementation, probability of survival, and child height.

For example, in her classic work with the Hadza, Hawkes (2003; Hawkes et al., 1997) showed that maternal grandmothers make a substantial contribution to the nutritional welfare of their grandchildren. Gibson and Mace (2005) indicated that presence of maternal grandmothers had a positive effect on child survival and height, and Beise (2005) noted that maternal and paternal grandmothers reduce a child's probability of dying. Lahdenpera et al.'s work (2004) was able to measure completed fertility, as the authors reconstructed the reproductive careers of daughters until they themselves became nonreproductive. Lahdenpera et al. writes: "... the length of a woman's postreproductive lifespan has a significant positive effect on the number of grandchildren that she gives rise to..." In contrast, Jamison et al. (2002) and Hurtado et al. (1992) did not find any beneficial effect of grandmothers on grandchildren survival, and Volland and Beise (2002) and Jamison et al. (2002) actually report a detrimental effect of paternal grandmothers. Thus, only one article (Lahdenpera et al., 2004) has been able to measure completed fertility in daughters to determine if grandmother's postreproduc-

tive longevity positively affects daughters' fitness. Even the study always taken to illustrate the beneficial effect of grandmothers, that is, Hawkes' work with the Hadza, did not measure completed fertility.

A corollary of the grandmother and mother hypotheses is that long-lived females should have higher fitness, whether by producing greater number of grandchildren or children or both. Therefore, there should be selection for longevity genes, so that the heritability of longevity should be low (Alvarez, 2000). This is indeed, what is predicted of all life-history traits (Falconer, 1981).

In this article, we submit the grandmother and the mother hypotheses to test, where our proxy for fitness is the number of children produced by a woman, not the number of children who survived by the time she reached menopause. In addition, we compute the heritability of longevity to determine if additive genetic variance of longevity is available in this population.

Following the expectations generated by both hypotheses, we propose to test that:

1. If the data support the grandmother hypothesis, the length of a woman's postreproductive lifespan has a significant positive effect on the number of grandchildren that she produces through her daughter (Hawkes, 2003; Lahdenpera et al., 2004).
2. If the data support the mother hypothesis, the length of a woman's postreproductive lifespan has a significant positive effect on the number or children that she produces (Peccei, 2001b).

We should note that there is no reason to assume that both hypotheses are contradictory. Indeed, Volland and Beise (2005) note that the reproductive interest of grandmothers and their adult daughters may overlap.

MATERIALS AND METHODS

The data set

The data consist of maternal genealogies started from 152 living subjects, all of whom lived in Atenas, Costa Rica. The genealogies were reconstructed with records obtained from the Church Chancery, the local parish and the National Document Register. Only adults able to give informed consent were interviewed. The project was approved by the committee on bioethics of the University of South Florida and the Universidad de Costa Rica. Most genealogies are at least seven generations long, two are 17 and 13 generations long, and six are 16, 15, 12, and 11 generations long. Considering all individuals across all generations and all lineages, we have 1,172 individuals in our data set. Several families extend back to the 1500s, as shown in Figure 1.

Atenas is in the province of Alajuela, 21 km from Alajuela City, the capital of the province. Atenas was chosen over other towns in Costa Rica because its Church records (housed at the Chancery in San Jose and at the Church itself) of vital events are complete since the foundation of the Parish in 1846. In addition, because of the location of Atenas in the Central Valley of Costa Rica, it was feasible for us to continue tracing a genealogy, even if the family migrated out of the area, since such migration usually took place between Atenas and other areas within the valley. For the centuries before the creation of the Atenas Parish, we relied on the vital event records held at the national register and the central church chancery (Meléndez-Obando, 2004).

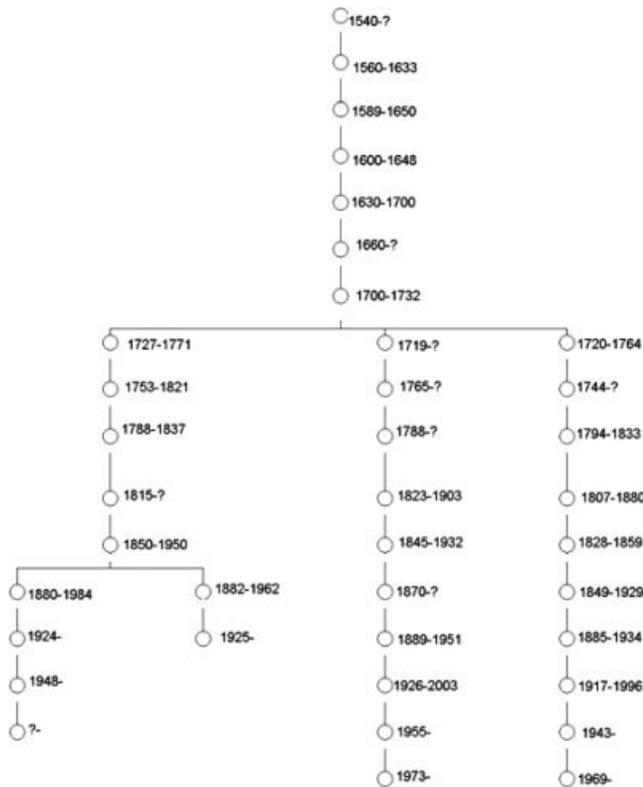


Fig. 1. A lineage started with living subjects going back to the 1500s. Shown are each person's birth and death years.

At the time of the Spanish invasion in the 1500s, the region of Atenas had a large indigenous population now called the *Huetares*. This indigenous group offered strong resistance to the invaders under the leadership of their Cacique Garabito, but was subjugated in 1569, at which point the remaining Amerindians were given out to Spaniards in slave-like conditions under the system of *encomiendas*.

After the decimation of the indigenous population, the entire region of Atenas grew in size, being peopled by migrants from areas within the central valley. These early settlers initially cultivated tobacco, coffee, sugar cane, and beans, and later on turned to cattle raising (López-Guzmán, 1968). Most of these farmers had a small family operated farm, which had been obtained through the mechanism of *denuncia*: if a family declared an area to be its own, and no one contested this claim, the government ceded the land to the claimant. Thus, throughout the history of Costa Rica, including up to the 1900s, land could be acquired by anyone who desired it, resulting in a land tenure system which allowed young couples to establish their own neolocal home stead (Fox, 1967; Cardoso, 1989).

In the decade of 1830, local families petitioned the Catholic Church to establish a Parish because there were more than 1,000 inhabitants in the area. Their petition was heard, and the parish was established in 1846. Atenas has continued to grow, with 11,878 inhabitants in 1966. Currently, its population is becoming involved in the tourism industry, although it still maintains its agricultural and cattle economic activities (López-Guzmán, 1968; Meléndez-Obando, 2004).

Statistical methodology

This data set presented the problem that the women in one lineage were not independent from each other. Therefore, we bootstrapped 2,000 random samples which included one randomly selected woman from each of the lineages, so that no lineage was represented more often than others were. A woman's datum includes her longevity, number of children produced, her daughter's longevity, and the number of children produced by this daughter. We computed the correlation between a woman's longevity and the number of children she produced or the number of grandchildren she had through her daughter, to test the mother and grandmother hypotheses, respectively. The heritability of fertility was computed as indicated by Falconer (1981) by regressing a female's longevity on her mother's longevity, and multiplying the regression coefficient by 2. We did this by randomly choosing a mother-daughter dyad per lineage 2,000 times.

Given that bootstrapping generates large sample sizes, it is customary to draw 90% confidence intervals (CI) around the mean of a distribution and use these intervals for testing the hypothesis that the parametric mean is equal to 0 (Efron and Tibshiran, 1998). The 90% CI was computed according to Efron and Tibshiran's equation 12.7 (1998; p 154). The SAS macro language was used for the bootstrapping.

RESULTS

A histogram of the correlation between a woman's longevity and her fertility, with a normal curve superimposed, is displayed in Figure 2. Shown in the histogram are the two 90% CI around the mean correlation of $r = 0.1258$. Since values of 0 are found in the 90% acceptance region, we cannot reject the null hypothesis that the parametric correlation between longevity and fertility is 0. However, the great majority of the correlation coefficients were moderate and positive, whereas there are few negative coefficients. Therefore, the correlation between mother's longevity and her fertility indicates that as longevity increases, so does fertility.

Figure 3 shows a histogram of the bootstrapped correlations between grandmother's longevity and number of grandchildren produced. In direct contradiction of the expectation generated by the grandmother hypothesis, we find that the mean correlation is -0.106 , with 90% CI from -0.20 to -0.007 . These results clearly show that a very small proportion of the distribution (less than 2.5%) has a positive correlation between grand maternal longevity and number of grandchildren produced. Since the upper confidence limit is under 0 we can reject the null hypothesis that the parametric correlation between grand maternal longevity and number of children produced is 0. We do this acknowledging that -0.007 is very close to the value of 0.

Figure 4 illustrates the contradictory behavior of the correlation between maternal and grand maternal longevity and the number of children or grandchildren produced. The plot dramatically shows that whereas maternal longevity is positively correlated with number of children produced, grand maternal longevity is negatively correlated with number of grandchildren produced. Indeed, the 90% areas of the distributions of both correlations do not overlap, indicating that the correlations do not sample the same statistical population.

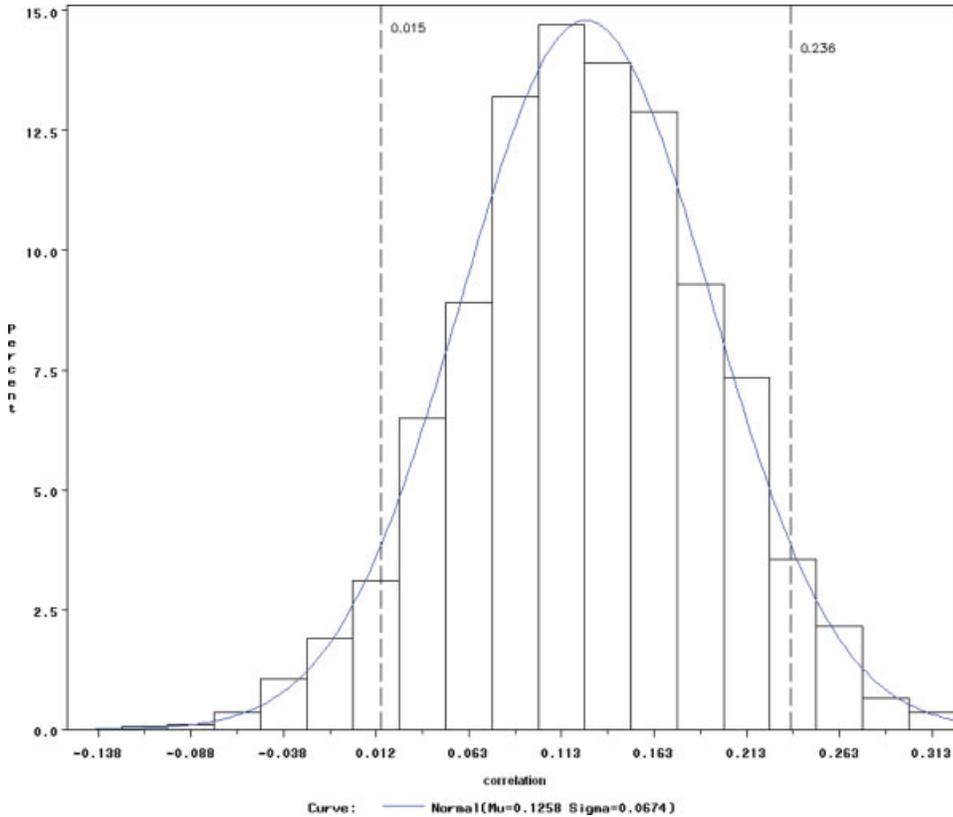


Fig. 2. A histogram of 2,000 correlations between maternal longevity and the number of children produced. Shown are the 90% confidence intervals around the mean of 0.1258. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

Therefore, there is no directional selection favoring women's longevity.

Lastly, we computed the heritability of longevity according to Falconer (1981). The distribution of these heritabilities is shown in Figure 5, which indicates that the lower CI (0.12) around the mean of 0.35 does not overlap with 0, allowing us to reject the null hypothesis that the heritability of longevity is equal to 0. Such high values of heritability are unexpected in traits connected with reproductive fitness, whose heritabilities should be low (Falconer, 1981). These high values indicate that there is opportunity for natural selection to operate through differential longevity, and that genes involved in the determination of longevity are not close to being fixed in this population. Clearly, the fact that longevity is selectively advantageous for mothers but not for mothers' mothers is reflected in such high heritability.

DISCUSSION

In this article, we tested the grandmother and mother hypotheses and computed the heritability of longevity with the same data set. We bootstrapped 2,000 random samples of women living across four centuries, from the 1500s to the 1900s. The conclusions obtained in most of our data sets, as defined by the normal curve superimposed on the bar graphs, were remarkably similar, suggesting that the sampling of a particular time period or lineage is unlikely to have biased the analysis.

Although female postreproductive longevity could be explained as a by-product of other, naturally selected life history traits, most authors see it as an adaptive, naturally selected trait in its own right. Of the adaptive evolutionary scenarios proposed to explain it, the grand-

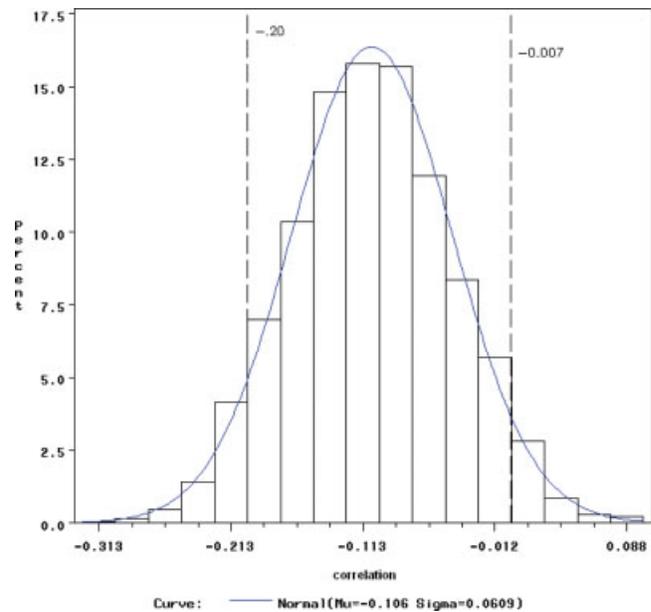


Fig. 3. A histogram of 2,000 correlations between grandmaternal longevity and the number of grandchildren produced. Shown are the 90% confidence intervals around the mean of -0.106 . [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

mother hypothesis has received much attention, whereas the mother hypothesis has received less. The grandmother hypothesis has been proposed to be a powerful explanatory model for the evolution of postreproductive

Fig. 4. Histograms of the correlation between maternal and grand maternal longevity and the number of children or grandchildren produced. Each histogram shows 2,000 correlations. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

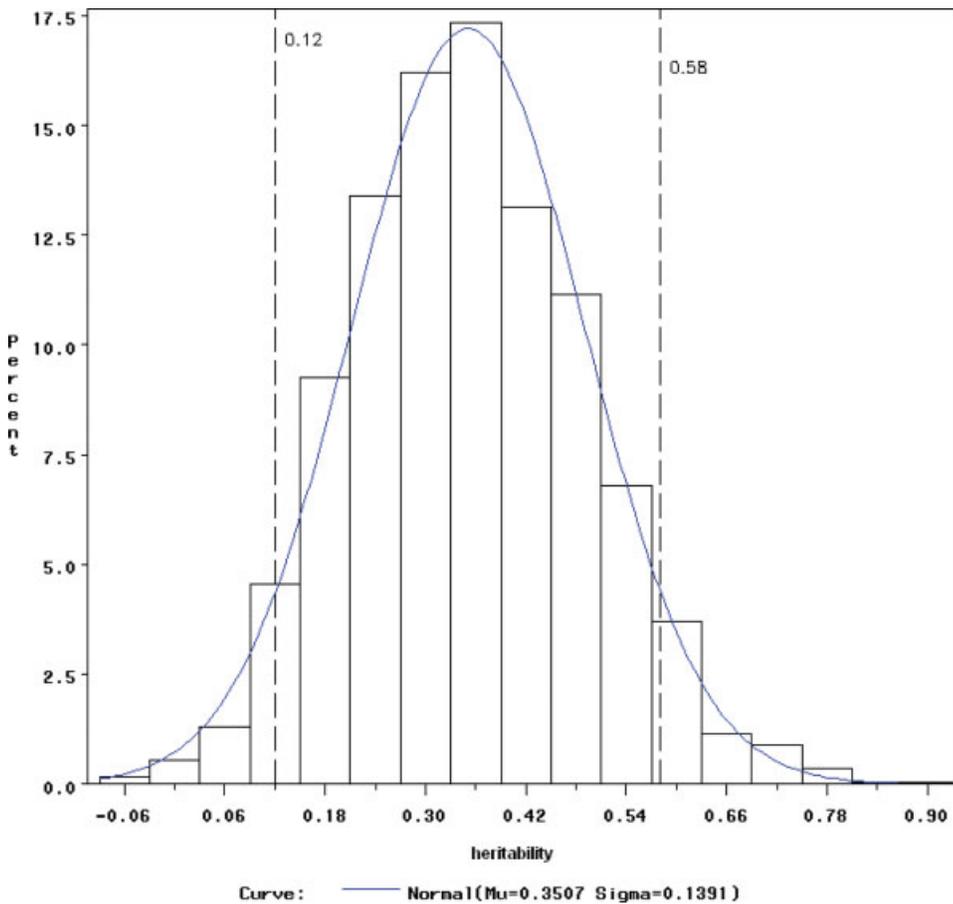
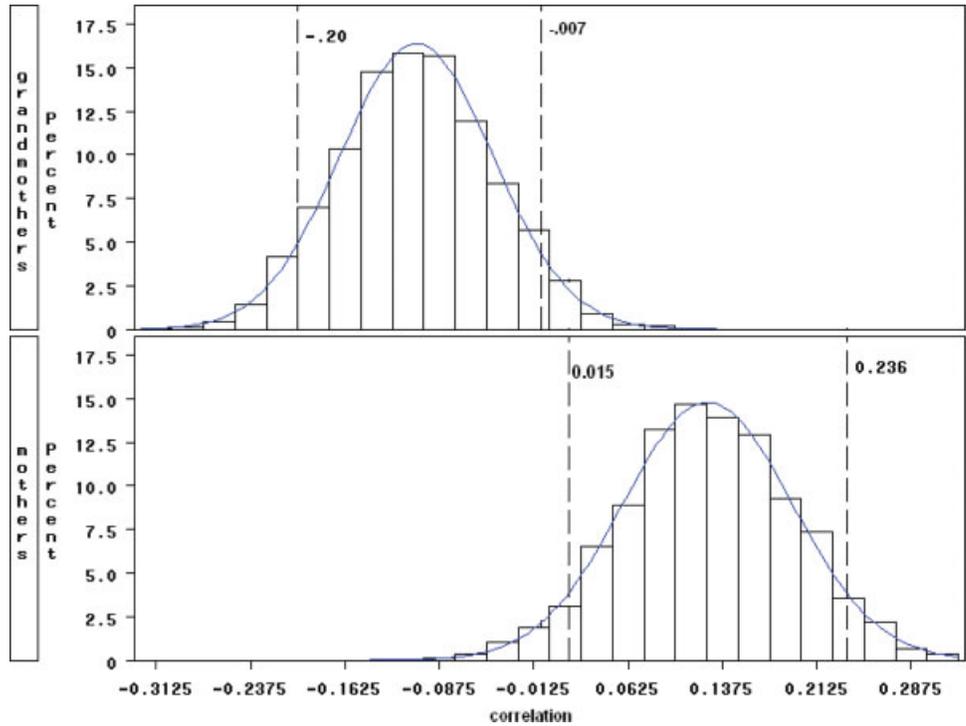


Fig. 5. The distribution of 2,000 heritabilities. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

longevity in women and other uniquely derived life history traits in our species, including high rates of birth and early ages of weaning (Alvarez, 2000). Indeed,

Hawkes and Jones (2005) state: “This hypothesis makes distinctive features of human life histories a consequence of the productivity of ancestral grandmothers.” The

grandmother hypothesis provides a strong challenge to the hunting hypothesis, which attempted to explain human life history traits based on increased reliance of hunting and meat sharing.

The value of evolutionary scenarios such as the hunting and the grandmother hypotheses is that they provide impetus for further work, which seeks to test predictions generated by the theories. But how should the grandmother be tested? There is ample debate about the validity of using paleoanthropological and skeletal data to test whether human longevity was present in preindustrial human groups (Hawkes, 2003). However, as they concern recent living human groups, both the grandmother and the mother hypotheses do offer testable predictions: postreproductive longevity should result in an increased number of grandchildren (grandmother hypothesis) or children (mother hypothesis). A close examination of the literature reveals that only one study has been able to measure the number of grandchildren produced by grandmothers when their daughters reach menopause: Lahdenpera et al. (2004) showed that longevity in grandmothers was significantly positively correlated with greater completed fertility of daughters. Given the long life span of humans, and the incompleteness of data sets, most other studies have measured the effect of grandmothers on children by using other proxies such as probability of survival, child height, and nutritional status. Although we can postulate that reproductive age daughters may achieve a higher fertility if they have a mother who helps her children have a better nutritional status or height, we do not know that for a fact unless we follow the children's progress until their mother achieves menopause. These studies however, have been important in that they provide a plausible mechanism for the beneficial effect of grandmothers on daughters' fertilities demonstrated by Lahdenpera et al. (2004).

In this study, we used the number of children produced by a woman as a proxy for the number of surviving children she had when she achieved menopause. Although it is not completed fertility, the number of children born to a woman is closer to completed fertility than is a child's height or nutritional status. We acknowledge that there may be a trade-off between increased number of children and the chance that the offspring will survive. We are simply not in a position to test this possibility, and must work with the data we do have. Missing from our data is comparable information on the possible effect (whether beneficial or not) of mothers on a sons' fertility. Although this is a regrettable missing piece of information in our data, the work of Jamison et al. (2002) and Volland and Beise (2002) shows that paternal grandmothers have a negative effect on grandchildren's wellbeing.

Our data clearly show that whereas maternal longevity was positively correlated with increased number of children, grand maternal longevity was negatively and significantly correlated with number of grandchildren. Previous studies (Jamison et al., 2002; Volland and Beise, 2002) described a negative impact of paternal grandparents on grandchildren survival. Our results differ from those in that in our data, the maternal grandmother is exerting the negative influence. Our data do not allow us to propose a precise mechanism by which grand maternal longevity decreases daughter's number of children. However, it is possible that the opposite of mechanisms demonstrated by others, such as a grand maternal

effect on grandchild's nutrition or height, are at play. The correlations between maternal longevity and number of children and grand maternal longevity and number of grandchildren do not overlap, allowing us to reject the null hypothesis that they sample the same parametric population of correlation coefficients. Thus, although it is theoretically possible that a grandmother's postreproductive longevity benefits both herself and her daughter, that is not the case here. We would like to emphasize that our results say nothing about the evolution of other human life history traits. Here we have only submitted to test proposals which stem from the grandmother and mother hypotheses that could be rejected or accepted by our data. Hopefully, other researchers will test predictions which emerge from large evolutionary scenarios such as the grandmother and the hunting hypotheses, and which we could not address with our data.

We found an unexpectedly high heritability of longevity in our data, indicating that the genes which lead to longevity are not fixed and that there is room for natural selection to operate in the population. These results can be explained by the fact that whereas a woman's longevity is advantageous for her fertility, it is disadvantageous for her inclusive fitness when we consider the number of grandchildren she produces. Since the selection for longevity is not consistent in its direction (always positive or negative), the heritability of longevity is high.

Previous studies which demonstrate that long-lived grandmothers exert a positive influence on grandchildren survival did not compute the heritability of longevity. Therefore, we do not know to what extent differential grand mothering had selected for postreproductive longevity and to what extent such selection had depleted additive genetic variance of the trait. In addition, with few exceptions (Volland and Beise, 2002), these studies encompassed a century or less so they were unable to show if there was a long-term effect of maternal or grand maternal longevity on fertility, whether measured through the number of children or grandchildren produced.

The relatively large number of studies on the grandmother hypothesis have overshadowed a simpler explanation for the evolution of postmenopausal longevity: postcycling females achieve higher fertility by supporting their own offspring, not their grandchildren. Alvarez (2000) suggests that if postmenopausal longevity were the result of a maternal (not grand maternal) effect, other species with extended maternal care would have evolved such longevity. Perhaps the fact that the human species is the only one which has evolved this trait indicates just how much more human offspring rely on their mothers.

The enormous variation in human household composition and postmarital residence is evidenced in the studies on differential grand mothering edited by Volland et al. (2005). The cultural specificity of human families is probably responsible for the fact that in some cultures maternal grandmothers favor grandchildren survival (Hawkes et al., 1997; Mace, 2000; Lahdenpera et al., 2004; Gibson and Mace, 2005), whereas in others (this study) they compromise it, and even in others they have a neutral influence (Hurtado et al., 1992; Jamison et al., 2002). Similarly, in some cultures the paternal grandmother has a negative effect on grandchildren survival (Jamison et al., 2002; Volland and Beise, 2002), whereas in others their effect is positive (Beise, 2005). Given such

different results, and the tremendous variation in the presence of grandparents in the household, it is difficult to think that grand mothering itself is the primary selective force behind the evolution of female postreproductive longevity. In contrast, a mother, even if she does not live with her grown children, is more likely to transfer some kind of benefit to them, whether labor, social prestige, or wealth. We argue, together with Peccei (1995a,b, 2001, 2005) for a more critical scrutiny of the grandmother hypothesis, and for renewed interest in evaluating the mother hypothesis.

CONCLUSIONS

Our data show that postreproductive longevity is associated with increased number of children, but decreased number of grandchildren. Thus, postreproductive longevity is beneficial to a woman's own fertility, but detrimental to her inclusive fitness. As a consequence of such positive and negative effects, there is no systematic selection for increased longevity, resulting in high heritability of longevity. Our data support the proposals generated by the mother hypothesis and reject those generated by the grandmother hypothesis.

ACKNOWLEDGMENTS

We thank Drs. G. Barbuji and H. Harpending for reading an earlier version of this article, and two anonymous reviewers for their comments. We thank the people of Atenas for their participation.

LITERATURE CITED

- Allen J, Bruss J, Damasio H. 2005. The aging brain: the cognitive reserve hypothesis and hominid evolution. *Am J Hum Biol* 17:673–689.
- Alvarez H. 2000. Grandmother hypothesis and primate life histories. *Am J Phys Anthropol* 133:435–450.
- Beise J. 2005. The helping and the helpful grandmother. The role of maternal and paternal grandmothers in child mortality in the seventeenth- and eighteenth-century population of French settlers in Quebec, Canada. In: Voland E, Chasiotis A, Schiefenhover W, editors. *Grandmotherhood: the evolutionary significance of the second half of female life*. New Brunswick: Rutgers University Press. p 215–238.
- Caspari H, Lee SH. 2004. Older age becomes common late in human evolution. *Proc Natl Acad Sci USA* 101:10895–10900.
- Cardoso C. 1989. La pequeña propiedad. In: Guillén D, editor. *Costa Rica: Universidad de Guadalajara Press*. p 73–81.
- Efron B, Tibshirani RJ. 1998. *An introduction to the bootstrap*. New York: Chapman and Hall.
- Falconer D. 1981. *Introduction to quantitative genetics*. New York: Longman.
- Fox R. 1967. *Kinship and marriage*. Middlesex: Penguin Books.
- Gibson MH, Mace R. 2005. Helpful grandmothers in rural Ethiopia: a study of the effect of kin on child survival and growth. *Evol Hum Behav* 26:469–482.
- Hawkes K. 2003. Grandmothers and the evolution of human longevity. *Am J Hum Biol* 15:380–400.
- Hawkes K. 2006. Life history theory and human evolution. A chronicle of ideas and findings. In: Hawkes K, Paine RR, editors. *The evolution of human life history*. Santa Fe: School of American Research Press. p 45–93.
- Hawkes K, Jones NB. 2005. Human age structures, paleodemography, and the grandmother hypothesis. In: Voland E, Chasiotis A, Schiefenhover W, editors. *Grandmotherhood: the evolutionary significance of the second half of female life*. New Brunswick: Rutgers University Press. p 118–140.
- Hawkes K, OConnell J, Jones N. 1997. Hadza women's time allocation, offspring provisioning, and the evolution of long postmenopausal life spans. *Curr Anthropol* 38:551–577.
- Hurtado A, Hill K, Kaplan H, Hurtado I. 1992. Trade-offs between females food acquisition and child care among Hiwi and Ache foragers. *Hum Nat* 3:185–216.
- Jamison C, Cornell L, Jamison P, Nakazato H. 2002. Are all grandmothers equal? A review and a preliminary test of the "grandmother hypothesis" in Tokugawa Japan. *Am J Phys Anthropol* 119:67–76.
- Lahdenpera M, Lummaa V, Helle S, Tremblay M, Russell A. 2004. Fitness benefits of prolonged post-reproductive lifespan in women. *Nature* 428:178–181.
- López-Guzmán L. 1968. *Primer centenario de la fundación del cantón de Atenas*. San Jose: Imprenta y litografía Lehmann.
- Mace R. 2000. Review. Evolutionary ecology of human life history. *Anim Behav* 59:1–10.
- Meléndez-Obando M. 2004. Importancia de la genealogía aplicada a estudios genéticos en Costa Rica. *Rev Biol Trop* 52:423–450.
- Peccei J. 1995a. A hypothesis for the origin and evolution of menopause. *Maturitas* 21:83–89.
- Peccei J. 1995b. The origin and evolution of menopause: the altriciality-lifespan hypothesis. *Ethol Sociobiol* 16:425–449.
- Peccei J. 2001a. Menopause: adaptation or epiphenomenon? *Evol Anthropol* 10:43–57.
- Peccei J. 2001b. A critique of the grandmother hypotheses: old and new. *Am J Hum Biol* 13:434–452.
- Peccei J. 2005. Menopause: adaptation and epiphenomenon. In: Voland E, Chasiotis A, Schiefenhover W, editors. *Grandmotherhood: the evolutionary significance of the second half of female life*. New Brunswick: Rutgers University Press. p 38–58.
- Voland E, Beise J. 2002. Opposite effects of maternal and paternal grandmothers on infant survival in historical Krummhorn. *Behav Ecol Sociobiol* 52:435–443.
- Voland E, Chasiotis A, Schiefenhover W. 2005. *Grandmotherhood: The evolutionary significance of the second half of female life*. New Brunswick: Rutgers University Press.
- Williams GC. 1957. Pleiotropy, natural selection, and the evolution of senescence. *Evolution* 11:398–411.