

THE PATRIARCH HYPOTHESIS

An Alternative Explanation of Menopause

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Menopause is puzzling because life-history theory predicts there should be no selection for outliving one's reproductive capacity. Adaptive explanations of menopause offered thus far turn on women's long-term investment in offspring and grandoffspring, all variations on the grandmother hypothesis. Here, I offer a very different explanation. The patriarch hypothesis proposes that once males became capable of maintaining high status and reproductive access beyond their peak physical condition, selection favored the extension of maximum life span in males. Because the relevant genes were not on the Y chromosome, life span increased in females as well. However, the female reproductive span was constrained by the depletion of viable oocytes, which resulted in menopause.

KEY WORDS: Grandmother hypothesis; Hadza; Life history theory; Male-male competition; Menopause; Oocyte depletion; Pair-bond; Patriarch hypothesis

Menopause has recently received much attention from evolutionary theorists because it presents a riddle: since natural selection only favors that which enhances reproductive success, why should a female outlive her ability to reproduce? In captivity, females of several species live slightly beyond their reproductive capacity (vom Saal et al. 1988), but for a female to live well beyond her reproductive career in a natural habitat is almost uniquely human. Women spend about one third of their lives post-

Received: May 2, 1999; accepted: August 16, 1999.

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Human Nature, Vol. 11, No. 1, pp. 27-42.

1045-6767/99/\$1.00+.10

reproductive, a trait that appears to be shared only by the short-finned pilot whale (Austad 1994; Marsh and Kasuya 1986). What explains this puzzling life history trait?

One non-adaptive explanation of menopause is that life span was only recently extended and there has not been time for selection to extend the female reproductive span (Symons 1979; Washburn 1981). This seems unlikely if the extension of life span is attributed to a recent drop in mortality since senescence appears to be programmed; for example, even the most well cared for dog is not going to live to be 50 years old. Often this non-adaptive explanation is favored simply because life expectancies are misunderstood. Average life expectancy *at birth* for contemporary foragers is about 30–35 years. This leads many to conclude that few individuals live past that age, hence menopause needs no adaptive explanation. However, these low life expectancies are due to high infant and juvenile mortality rates. Life expectancy *at age 20* for women among contemporary foragers is 20–30 years past the age of menopause (Blurton Jones et al. 1992; Hill and Hurtado 1996; Howell 1979). Still, based on skeletal remains, some maintain few of our recent ancestors lived past age 45 (Lovejoy et al. 1977; Trinkaus 1995; Vallois 1961). Many of us who work with contemporary foragers are dubious since up to 20% of living women can be post-menopausal. Furthermore, maximum life span appears to have changed little with the adoption of agriculture (Weiss 1981).

Others question the need for an adaptive explanation of menopause, noting simply the constraint on the female reproductive span set by the depletion of viable oocytes (Austad 1994, 1997; Gosden 1985; Wood et al. 1994). In mammals and birds, with low fecundity and high offspring investment, females produce their whole supply of gametes during embryonic development, rather than continuously throughout life as males do. Limiting oocyte production to the early phase of embryonic development has likely evolved to minimize the accumulation of mutations (Ellison n.d.). The problem with the constraint argument is that it simply does not explain menopause, it only explains why the reproductive span ends. It leaves unexplained why the rest of the body senesces at a slower rate than ova. If women died when their oocytes were depleted, menopause would not exist. Since they do not, one must explain why they keep living.

Adaptive explanations of menopause have focused on female investment in offspring and grandoffspring, all variations on the grandmother hypothesis (Alexander 1990; Gaulin 1980; Hamilton 1966; Lancaster and King 1992; Peccei 1995; Williams 1957). As originally proposed, the grandmother hypothesis suggested that older women increased their fitness more by caring for their children or grandchildren than by continuing to reproduce, so selection favored stopping reproduction early. Stopping early is not essential, however (Hawkes et al. 1997, 1998). Assuming the re-

productive span was unchanged, one must still explain why it paid to live beyond that span. The grandmother hypothesis offers an answer: it paid to keep living because a female could continue to add to her inclusive fitness by caring for her children, grandchildren, and other kin. Furthermore, she might lose her last-born offspring if she died soon after giving birth. One problem with the grandmother hypothesis, as Gurven and Hill note (1997), is that it does not tell us why males live so long.

I propose an alternative explanation of menopause, which I call the patriarch hypothesis in order to emphasize the elderly, high status male (not to imply patrilocal residence, patrilineal descent, or anything else associated with patriarchy). The patriarch hypothesis proposes that menopause is a by-product in females of an adaptation in males. Because hominid males became successful reproducers beyond their peak vigor, selection favored males who lived longer. Genes that extended male life span were selected for. Since these genes were not located on the Y chromosome they promoted female longevity as well. Once hominid females began to live beyond age 45, they experienced menopause simply because their ovarian follicles were depleted. Female longevity was "dragged along" with male longevity even though females gained no direct reproductive benefit. Once females outlived their reproductive careers, they could enhance their inclusive fitness by helping kin, but the gains from such help need not exceed the theoretical gains from continued reproduction. More important, the gains from such kin-directed help, in this view, were not the cause of the extended life span.

A TWO-STAGE SCENARIO

Stage 1: Tools, Male-Male Competition, and the Initial Extension of Life Span

I assume that, like chimpanzees (and bonobos), our early hominid ancestors, if they were lucky, lived to be 35–45 years old. Because they were bipedal and occupied less forested habitat than chimpanzees, they benefited more from using tools, and tool making put a premium on intelligence. As intelligence increased and tools/weapons became more effective, perhaps with early *Homo*, male-male competition became less contingent upon strength and more contingent upon coalition building—more Machiavelian. Tools/weapons initiated this shift because they tended to compensate for natural fighting ability, and because the more intelligent the inventor, the more effective the tool/weapon. They also increased food productivity and affected mortality rates from predators and conspecifics. The decrease in body size sexual dimorphism of *Homo erectus* (Walker and Leakey 1993)

might be due as much to increased dependence on tools/weapons and political skills as to a decrease in polygyny. Once language became an effective means of manipulating others, some could promote the ideology of respecting your elders, which today is a widespread cross-cultural trait. These developments created a more stable male hierarchy so that once a male achieved high status he tended to keep it or lose it only gradually. Whereas previously males past their prime had little chance of mating, once reproductive access depended more on brain than brawn (though brawn didn't hurt) some old males were still able to compete.

For simplicity, assume a "longevity allele" appeared that increased life span by delaying the age of maturity and generally slowing down the life history. If growth rate remained constant, delayed maturity would mean a larger adult body size. It also meant a longer period of dependence and delayed reproduction. Previously, such longevity would not have been selected for since neither males nor females had a chance of reproducing beyond age 40-45, and maturing later only meant less time to reproduce. However, once male status became more long-lasting, any longevity allele in a male who attained high status at age 40+ was selected for because he was able to maintain his status and keep reproducing for several more years. The males who inherited the longevity allele took longer to reach maximum size and strength, but when they did, they were larger and stronger than other males and attained higher status so longevity and dominance became linked. Because male status could be maintained, longer-living males gained more in reproductive success late in life than they lost early in life. Old males who died soon after reproducing also stood little chance of losing their offspring since maternal care continued. Males passed on the longevity allele not only to their sons but also to their daughters, who began to outlive their supply of eggs.

Stage 2: Opposing Selection, Female Choice, and Additional Life Span

Since longevity meant delayed reproduction and, therefore, a greater demand for offspring care, selection in females should have opposed it. For example, if ovarian follicles are exhausted by age 45-50 and females delay reproduction from age 12 until age 18, their reproductive careers would be 6 years shorter and their completed fertility 1.5 children less. Human and chimpanzee females both reproduce for about 20-25 years, yet women have slightly higher completed fertility (Hawkes et al. 1998). They achieve this by having slightly shorter birth intervals. One way for females to shorten birth intervals is to obtain help from others so as to wean offspring sooner. If a female could do that, she could avoid the cost of lower fertility and gain by passing on longevity to her sons. In so doing, she might match or exceed the reproductive success of a rival female who did not inherit longevity. Unlike female chimpanzees (Goodall 1986),

women get help not only from their kin but also from husbands (Marlowe 1999a), and concealed ovulation with continuous receptivity may have been how this was achieved.

If males were forced to provide some care in exchange for sexual access, simultaneous polygyny would become more difficult to achieve, especially if females were continually receptive. In addition, the appearance of menopause meant there were more males competing for fewer females because there were additional reproductive males over age 50 but no additional reproductive females. It would have become more difficult to guard two or more females also because other males had lethal weapons. Consequently, though males strove for polygyny, often the best a male might achieve was serial monogamy (and perhaps a few extra-pair copulations). Serial monogamy, however, gains a male little or nothing in fitness unless it is appropriately timed in relation to his mate's fecundity. Therefore, as his mate reached menopause, a male tried to acquire a younger female, and the higher-status males succeeded in doing so. Selection then favored even greater longevity in males who could double their fitness by starting a second family with a new wife. Selection for male longevity, therefore, may have been the impetus for male care and pair-bonds, which in turn may have resulted in selection for even greater longevity.

EVIDENCE FROM HUMAN LIFE HISTORY AND THE MALE CAREER

The most obvious evidence in support of the patriarch hypothesis is that men's age-specific fertility (here illustrated by the Ache) is more tightly correlated with senescence than is women's (Figure 1). The difference is even more dramatic using reproductive capacity (Figure 2). Some men beyond their peak vigor, which is probably usually no later than age 40, are successful reproducers in many societies. In agricultural societies, however, wealth exaggerates the disparity in male status. Therefore, I will focus only on hunter-gatherers (in the ethnographic present). Among several Australian societies, such as the Tiwi (Hart and Piling 1979), Murngin (Keen 1982), and Aranda (Spencer and Gillen 1927), successful men continue to add to their harems as they age and may have 10 wives when they die at the age of 70+. A man might only acquire his first wife when he is 25–30 years old, and she might be postmenopausal. He might get this wife from an elderly man who inherited the widows of another elderly man. If successful, a man continues to add younger and younger females to his harem as he ages. Granted, the Australians are the best case scenario in support of the patriarch hypothesis, but even among foragers without a gerontocracy, men are often able to acquire wives and have children at age 60, when they are clearly less physically fit than 30- to 40-year-old men.

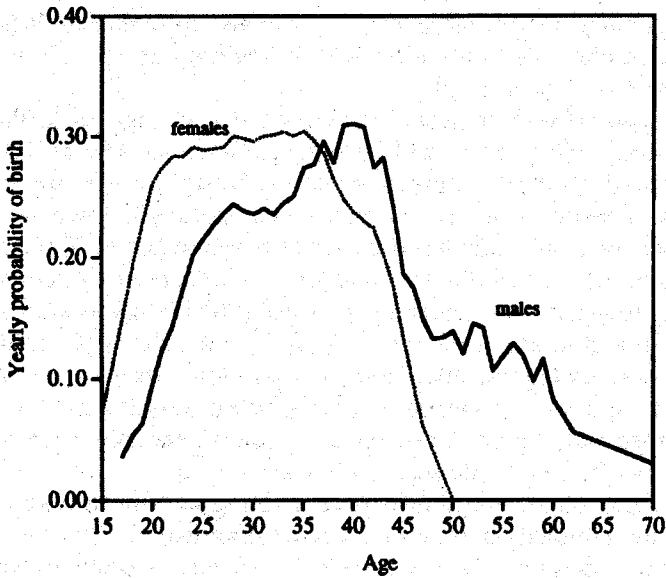


Figure 1. Age-specific fertility for Ache men and women (Hill and Hurtado 1996).

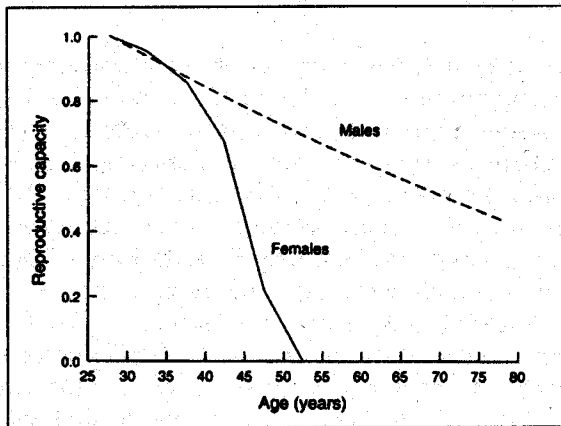


Figure 2. Reproductive senescence for men and women relative to ages 25–29 years (Wood et al. 1994).

Like other African foragers (e.g., !Kung and Efe), the Hadza of Tanzania sit at the other extreme from the Australians. Only about 2–3% of men have two wives simultaneously (serial monogamy is the rule), yet some men appear to add to their reproductive success beyond age 50 (Figure 3), while women cannot (Figure 4). There is nothing like official rank, but subtle variation in male status seems to mirror hunting reputation (measured by the number of times a man is named as a good hunter by others). It appears that the higher a man's hunting reputation, the more likely he is to leave his wife at menopause and get a younger wife. This is reflected in the fact that the magnitude of age difference between a man and his current wife (husband's age – wife's age) is positively correlated with hunting reputation ($r = .376, p = .010, n = 46$) (Figure 5). These men may be 55–60 years old when they leave one wife for a new younger one, and may well produce additional children. This occurs in a foraging society as egalitarian as any, where respect for the elderly is less pronounced than in many societies. Nonetheless, men do reproduce well beyond their prime (though they are usually in remarkably good shape).

A few Hadza men remain skilled hunters into their sixties, as reflected in their hunting reputations (Figure 6), daily returns of all food (Figure 7), daily meat returns (Figure 8), and archery skills (Figure 9). Men's scores in an archery competition I arranged showed a steady rise with age and

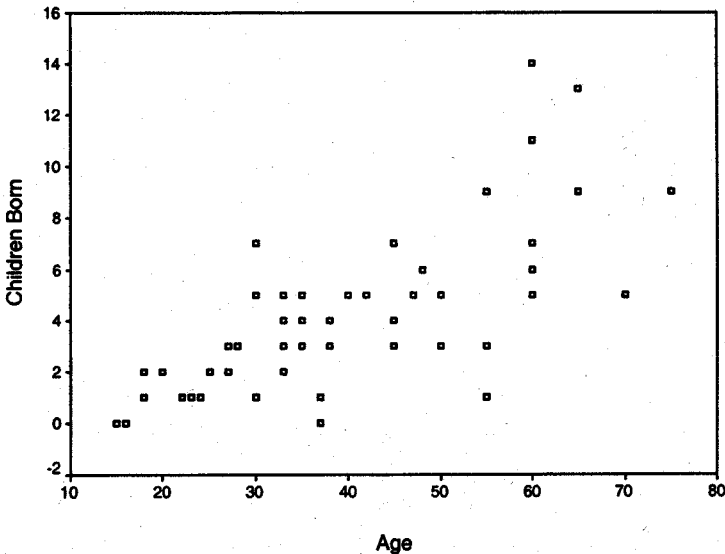


Figure 3. Hadza male fertility as a function of age.

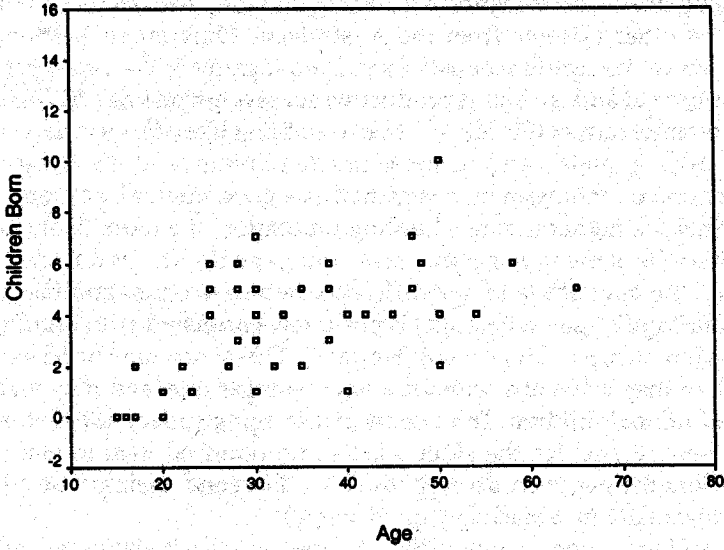


Figure 4. Hadza female fertility as a function of age.

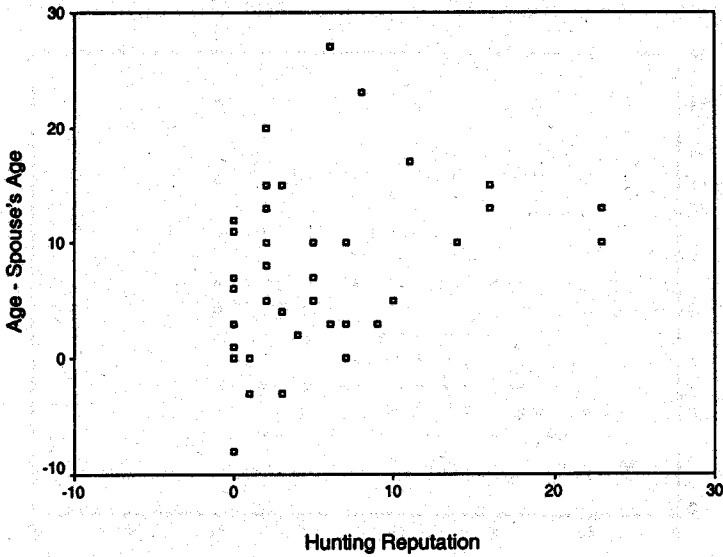


Figure 5. Age difference between Hadza men and their wives (husband's age - wife's age) as a function of a man's hunting reputation (number of times named as a good hunter). ($r = .376, p = .010, n = 46$)

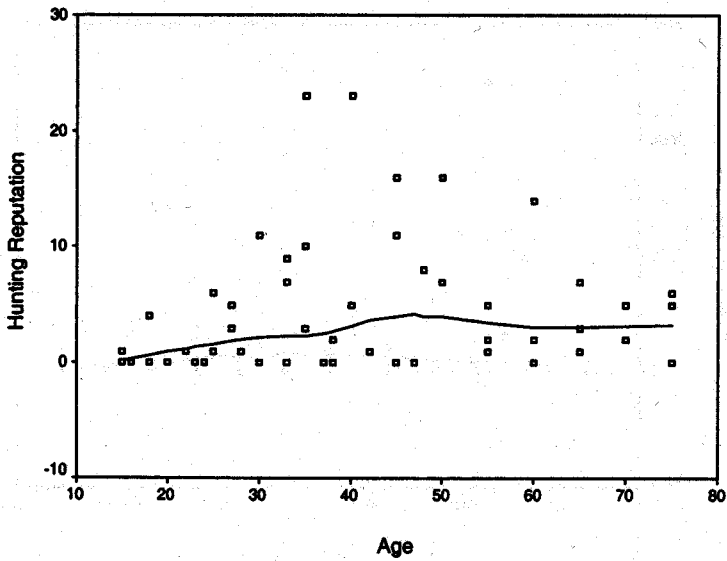


Figure 6. Hadza men's hunting reputation (number of times named as a good hunter) as a function of age.

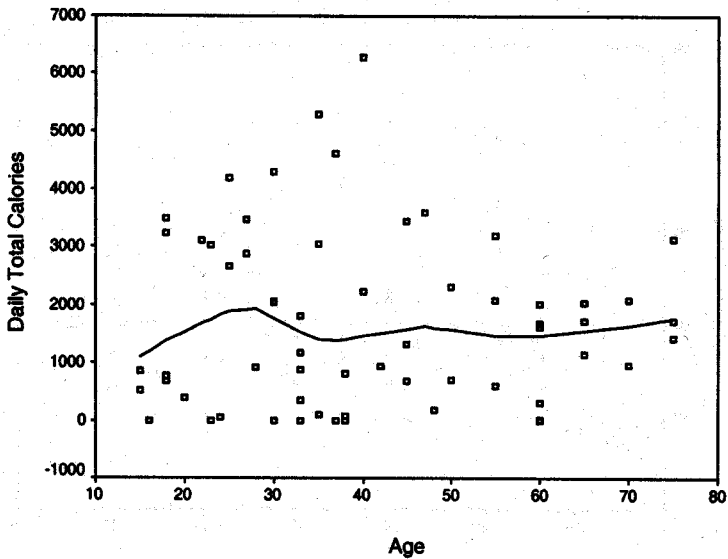


Figure 7. Hadza men's daily foraging returns in kilocalories of all food brought into camp as a function of age. (Men eat much of their food while out foraging, and those calories are not included in these data.)

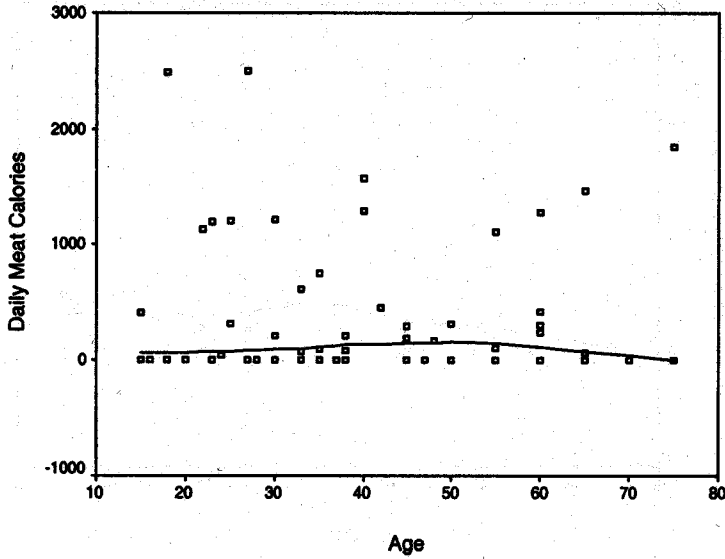


Figure 8. Hadza men's daily foraging returns in kilocalories of meat brought into camp as a function of age.

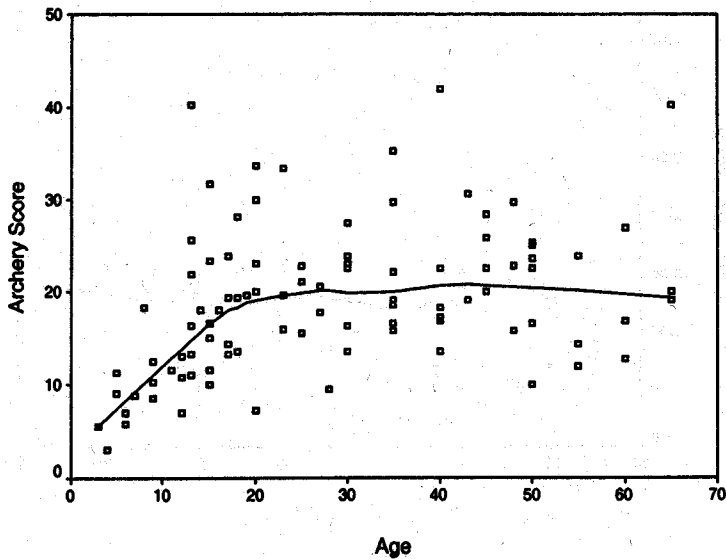


Figure 9. Hadza males' mean archery score as a function of age.

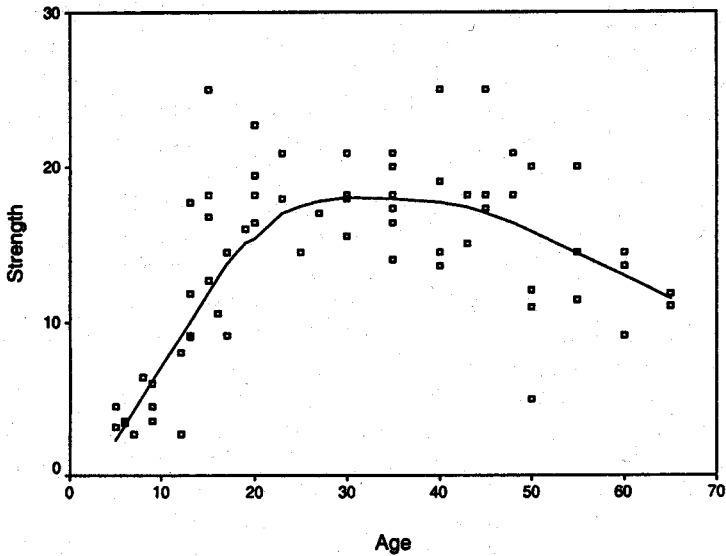


Figure 10. Hadza males' strength in kilograms of force (measured by male pulling on his own bow) as a function of age.

strength until about age 40, then leveled off. A few men were quite accurate at 65; one is among the top three scorers (Blurton Jones and Marlowe n.d.). Men's strength drops more sharply after age 40 (Figure 10), as presumably would their fighting ability. Men's foraging returns do not rise after age 40, but they do not fall much either (Figures 7 and 8). The fact that hunting reputation is correlated with daily total foraging returns ($r = .327$, $p = .010$, $n = 61$), and number of living children ($r = .344$, $p = .010$, $n = 55$), suggests male provisioning may be important. Provisioning is not provided at the expense of direct care either, since the best hunters do not provide less direct care (Marlowe 1999a, 1999b). Thus, while weapons and status may keep old males viable in male-male competition, provisioning may keep them viable in terms of female choice. Of course *Homo erectus* and early *Homo sapiens* males were not using bows and arrows like the Hadza, but senior males may have been effective foragers nevertheless. Even though hunting receives more attention, Hadza men actually bring in more daily calories of honey than meat (Marlowe 1999c).

DISCUSSION

The patriarch hypothesis predicts certain things because it depends on three conditions: (1) oocyte depletion must be a constraint, (2) the relevant

longevity-promoting genes must not be on the Y chromosome, and (3) some old men must reproduce. How plausible are these conditions and what predictions do they entail?

First, is oocyte depletion a constraint? Couldn't selection favor increasing the number of oocytes? In the human female, there are 7 million eggs in the ovaries of a 5-month-old fetus. Of these, only 1–2 million are left at birth and only 250,000 (one-thirtieth the original number) at puberty (Austad 1997). Normally, in each cycle one egg develops at ovulation but a host of others die. The number of follicles in the ovaries declines steadily with age, and then in the last few years of fertility the rate of decline accelerates, until at menopause they have been depleted (Wood et al. 1994). If this rate of decline is fixed, to extend reproduction merely a few years longer would require starting out with many more eggs and, thus, ovaries many times larger, which is why oocyte depletion may be a constraint (unless you are very large, like some whales). Perhaps there is some reason that the size of the ovaries is especially constrained in the short-finned pilot whale. The patriarch hypothesis does not necessarily predict the same cause will explain menopause in other species, but it does predict we should find the size of ovaries to be a widespread constraint on reproductive span for mammals and birds.

Second, the hypothesis requires that the relevant longevity-promoting genes not be on the Y chromosome. Some genes that influence longevity have been found on autosomal chromosomes in flies and mice (reviewed in Turner and Weiss 1994), and it seems reasonable to think the same might exist in humans. Because testosterone has a negative impact on longevity, if the target of selection is getting males to age 65–70 with an optimal level of testosterone to motivate mating effort, we should not be surprised that women, with lower levels of testosterone, reach age 75–80. The hypothesis does not predict selection would have favored female-like levels of testosterone in men, but since male-male competition became less tied to fighting, we might expect lower levels of testosterone in men than in our early hominid ancestors. The fact that castrated males have about the same life span as women (Hamilton 1948; Hamilton and Mestler 1969) might be taken as evidence that the relevant longevity-promoting genes affect both sexes equally, as this hypothesis predicts they should.

Third, the hypothesis requires that some old men reproduce. Gurven and Hill (1997) point out that Ache men's fertility declines only about 5 years after women's. This would seem to imply selection for longevity would be weak. However, only a few old men need to continue reproducing because reproductive access for males is related to status, and status is relative. Remove the dominant male and a lower-ranking male will move up to take his place and reap newfound mating opportunities. We should

not expect to find high average fertility at age 60 because lower-ranking 60-year-old men bring down the average. In each generation only a few get to be high-status old males, and it is those few who have spread longevity. Today, since all men are their descendants and can expect to live long and continue producing sperm, there is little relative advantage to measure, but not having the ability to live long and continue producing sperm would be a disadvantage. Therefore, all we should expect to find is that the few old men who are able to acquire young wives continue to reproduce. The hypothesis predicts that among most natural fertility societies the highest-status males will continue reproducing into old age, and that correlation between status and current reproduction will become greater with age.

If women were selected to live beyond their reproductive spans because of inclusive benefits from grandmothering, as the grandmother hypothesis suggests, why do men live so long? Either (1) they gain from grandfathering (which they must to some extent), (2) they were "dragged along" with female longevity, or (3) longevity evolved for two separate reasons: (3a) grandmothering for females, and (3b) continuous reproduction for males. If males live long because of continuous reproduction, why didn't they do so before grandmothering evolved? If males were only "dragged along" with female longevity, it's odd that the gender "dragged along" stands to benefit more. It is not difficult to see how males might gain from living past 45, but attempts to model how females gain have yielded mixed results (Hill and Hurtado 1991; Pechci 1995; Rogers 1993).

CONCLUSION

The patriarch hypothesis proposes that menopause is the by-product of selection for greater longevity in males. If oocyte depletion is a constraint, females simply experience menopause as a result. I envision first a shift towards less strength-based male-male competition, which selected for greater longevity in males. This meant delayed reproduction and opposing selection on females. This selection pressure favored females who traded sexual access for male care. Pair-bonds then selected for even greater longevity in males. Ultimately, females benefited by (1) obtaining male care, (2) helping kin, and (3) passing on longevity to successful sons. Because menopause occurs in women, no one has thought to look for the answer to the riddle in men—but there is every reason for men to keep living if they can maintain reproductive access. If genes promoting longevity are not limited to the Y chromosome, the consequence is that women will not only outlive their eggs but will outlive men.

Thanks to Martin Muller for noting it makes more sense for females to be "dragged along." Thanks to Peter Gray, Melissa Emery, Amanda Lobell, Amanda Thompson, David Haig, and the anonymous reviewers for comments.

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