

Comments

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While we agree that hardworking “grandmothers” may adjust foraging effort to accommodate selective offspring of kin, we feel uncomfortable about some of Hawkes et al.’s conclusions. We address (a) the theoretical focus on only females in shaping the evolution of a long postreproductive life span, (b) the fitness benefits of postreproductive provisioning of kin, and (c) directions for future study.

Although physiological menopause occurs only in women, this does not necessarily justify the exclusive female focus in explaining its origin and maintenance. If men live to old age but do little reproduction late in the life span, the long life of men also requires explanation. Evidence among !Kung, Ache, and Yanomamo men show declines in age-specific fertility rates similar to those of women but delayed by about five years (Hill and Hurtado 1996:fig. 9.6). These declines are assumed to be driven by mate choice rather than physiology but nevertheless present a life-history dilemma similar to that illustrated with female fertility and survival data. Can male food production be construed as mating investment even when achieved male fertility approaches zero? We do not yet know whether significant male reproduction takes place in old age throughout human history.

Do grandfathers provision kin more intensively than reproductive-aged men? Or did longer life in men evolve only as a by-product of longer-living women’s increasing their relative fitness by provisioning both male and female grandchildren? From the Hadza data, we should at least be able to determine if there exists a relationship between grandfathers’ and fathers’ foraging times and (grand)children’s weight change.

Also, it is unclear why Hawkes et al. focus only on matriline. If grandmothers provisioned their sons’ male and female offspring, a postreproductive life span could still have evolved among hominids even with a history of patrilocality. Indeed, one-fourth of the “grandmothers” in this paper are paternal grandmothers. Although the focus on hunting and male-based cooperation has dominated the thinking within anthropology for years, it does not make sense to proceed in the opposite direction without some empirical or theoretical justification. Hawkes et al. suggest that mother-offspring sharing favors matrilocality, but we see only that it increases benefits for either sex that resides with the mother. Whether the fitness benefits of residing near kin are higher for males or females is still a wide open question (see Wrangham 1996 for a patrilocal view). An important assumption of Hawkes et al.’s explanation for the evolution of a postreproductive life

span is that meat constituted only a small portion of the diet, thereby making the grandmother effect due to foraging highly influential and reducing the role men played in provisioning. We do not believe this is supported by the archaeological record, which suggests significant meat eating by hominids over the past several hundred thousand years.

While we agree that grandmothers’ foraging time affects weight changes among the children they provision, it would be nice to know how these benefits actually increase their inclusive fitness. If benefits are gained by increasing daughter’s fertility rather than (or in addition to) son’s fertility or grandchild survivorship, it must be shown that the effect of grandmother’s foraging time causes a decrease in the length of her daughter’s interbirth intervals and that the length of the postmenopausal life span varies positively with daughter’s completed fertility. Such information is currently lacking.

If grandmothers in other hunter-gatherer populations do not target the kinds of difficult-to-acquire resources that children cannot acquire for themselves, then we must examine alternative ways in which they improve their fitness. They could be protecting children who might otherwise be at risk of death from accidents and predation in dangerous environments. In this scenario (and especially if meat was an important component of early humans’ diet), differences in time spent foraging between nursing and non-nursing mothers might be small and grandmothers’ foraging might not be necessary. If female postmenopausal life span evolved from nonforaging-related benefits to kin, this presents another challenge to the hypothesis that female-based food sharing was the catalyst for the evolution of hominid longevity.

Hawkes et al. set the stage for many interesting questions which need answering before we can understand precisely how postreproductive females increase inclusive fitness enough to select for longevity. Coefficient of relatedness can be a useful predictor of who should receive investment from postreproductive females, but other characteristics such as reproductive value of potential kin recipients might be even more important. Since only two of the eight Hadza “grandmothers” are actually maternal grandmothers, we need to know the alternative opportunities available to all postmenopausal women. In this study, there are no data comparing the relationship between work effort and weight gain for children of various relationships to older women. Do unrelated children show a weight gain correlated to the work effort of randomly chosen “grandmothers”? What exactly is the sharing pattern between older women and other individuals? If we knew how postmenopausal women in the past distributed the foods they acquired (and the degree to which they discriminated against nonkin recipients), we could perhaps estimate the time depth necessary for longevity to have evolved.

Hawkes et al. are to be commended for their theoretical discussion of the relationships between female re-

source choice, food sharing, and menopause. We hope that this will lead to more hypothesis testing on how decreased fertility in both sexes is balanced by kin investment in the postreproductive life span among samples of diverse peoples living under different ecological conditions.

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Hawkes, O'Connell, and Blurton Jones have demonstrated that (1) mothers gain considerable assistance from their mothers or mothers-in-law in enhancing the fitness of their offspring and/or to enabling them to produce more offspring and (2), reciprocally, postmenopausal women enhance their fitness through investment in daughters' or sons' offspring. At a more general level, they deal with the phenomenon of menopause in a productive way by forcing us to view it in the context of the evolution of long life spans. Their employment of life-history theory with a simultaneous focus on longevity as a derived trait and menopause as ancestral represents an important breakthrough.

Key to the development of their model is an emphasis on long-term economic dependence of offspring on their mothers, in part a consequence of exploitation of food patches which yield high rates of return for adults but not children—who lack the physical strength, endurance, and skills to harvest such resources efficiently. They fail to note, however, that hunting also fits this model.

The main problem I have with the paper is a lack of focus on the role of men as investors in their own or kin's offspring. For example, Hurtado and Hill (1992) show that paternal loss increases offspring mortality among the Aché (although it has no significant effect among the Hiwi). They claim that compared with a father a "grandmother is a consistently better candidate for the role of mother's helper." Presumably this is so because men spend more energy "showing off" to gain additional mating opportunities (Hawkes 1993). This position challenges the standard hypothesis that biparental care, especially in the area of food provisioning, is a fundamental human adaptation that helps explain marriage. It is not a bad idea to question this hypothesis, which probably originated in observations on the nature of marriage in complex societies with socially imposed monogamy. One way to demonstrate that grandmother is a better candidate would be to document the food-getting activities of fathers and their impact on food allocation to mother and children. This Hawkes et al. have not done.

Whether their model fits male and female investment in common offspring in early hominid society is problematic. It is based on the contention that savanna hunting is "unable to provide a dependable daily flow of nutrients." For documentation, they footnote that children lose weight during the most profitable hunting

season. But we need to know whether rates of return were greater for hunting than for gathering during this time period or whether pooled variance (I assume that game is widely shared among the Hadza) in hunting success subjects children to an unreliable intake. We also need to know how much men contribute through gathering activities.

Hawkes et al.'s evolutionary scenario in relation to Hadza conditions appears inconsistent. In places they seem to assume that (1) longevity evolved in a savanna environment, (2) men allocated a large amount of time to inefficient hunting when they lacked projectile weapons, and (3) men have little or no positive impact on the economic survival of their offspring either through hunting or through gathering. Later they potentially change the locale of this scenario by noting that longevity "may have evolved later in time, perhaps with the appearance of the genus *Homo*," or "might be restricted to anatomically modern *sapiens*." In reference to Aché, where men contribute 85% of the group's calories, they note that grandmothers are likely to have a much less significant effect on grandchildren's fitness. Presumably there would have been little selective value in being a hardworking grandmother if Aché-like conditions had prevailed. Since we don't know at what point in time or where the hominid evolution of long life span originated, the relevance of local Hadza conditions for highlighting the origins of increased longevity remains problematic.

It seems odd to me that the authors fail to grapple with the fact that longevity increased for males as well as females, which leads one to conclude that it evolved for the same reason. (The only other choices we have is that it evolved as a side effect of female longevity or because it solved an adaptive problem peculiar to males.)

Finally, I have two minor problems with their generally high-quality data and analytic techniques. Unless I misunderstand the analysis, there may be a problem of statistical independence with correlations between various components of time allocation data. Time allocated to nonforaging activities must be, to some extent, negatively correlated with that allocated to foraging activities. Since one cannot forage and do something else (e.g., prepare food), any increase or decrease in foraging time will be negatively or positively correlated with nonforaging activities.

Hawkes et al. assume that foraging acquisition rates of nonnursing and postmenopausal women who travel together to the same resource patch will be identical. We have known for some time that this assumption is not true for hunting because of differential expertise in encountering and pursuing game, for example. I would bet on their assumption's being correct, but I believe it is time to turn this assumption into a hypothesis and test it. Testing this assumption is especially important here because the key component of their theoretical model is that there are fundamental differences in gathering efficiency between children, adolescents, and adults based on differences in strength and endurance.