ANNALS OF THE NEW YORK ACADEMY OF SCIENCES

Issue: *The Biodemography of Reproductive Aging*

Learning, menopause, and the human adaptive complex

Hillard Kaplan,[1] Michael Gurven,[2] Jeffrey Winking,[3] Paul L. Hooper,[1] and Jonathan Stieglitz[1]

[1]Department of Anthropology, University of New Mexico, Albuquerque, New Mexico. [2]Department of Anthropology, UC Santa Barbara, Santa Barbara, California. [3]Department of Anthropology, Texas A&M, College Station, Texas

Address for correspondence: Hillard Kaplan, MSC01-1040 Department of Anthropology, University of New Mexico, Albuquerque, NM 87131. hkaplan@nmu.edu

This paper presents a new two-sex learning- and skills-based theory for the evolution of human menopause. The theory proposes that the role of knowledge, skill acquisition, and transfers in determining economic productivity and resource distribution is the distinctive feature of the traditional human ecology that is responsible for the evolution of menopause. The theory also proposes that *male* reproductive cessation and postreproductive investment in descendants is a fundamental characteristic of humans living in traditional foraging and simple horticultural economies. We present evidence relevant to the theory. The data show that whereas reproductive decline is linked to increasing risks of mortality in chimpanzees, human reproductive senescence precedes somatic senescence. Moreover under traditional conditions, most human males undergo reproductive cessation at the same time as their wives. We then present evidence that after ceasing to reproduce, both men and women provide net economic transfers to children and grandchildren. Given this pattern of economic productivity, delays in menopause would produce net economic deficits within families.

Keywords: menopause; fertility; senescence; intergenerational transfers; human life history

Introduction

Available demographic evidence from hunter-gatherers and forager-horticulturalists without access to modern medicine shows that men and women can expect to live an additional two decades upon reaching age 45.[1,2] This adult age-specific mortality profile is rather uniform across extant traditional societies, and there is paleodemographic evidence suggesting the existence of older adults throughout the upper Paleolithic.[3] This implies that survival into old age is a fundamental feature of human biology. Behavioral data also shows that older postreproductive adults of both sexes are quite productive,[1,4–6] and tend to produce more energy than they consume until about age 70. Reproductive senescence, however, occurs at much earlier ages in women and is largely complete by age 45. This pattern is also rather uniform across human populations, and there is surprisingly little variation in age of menopause cross-culturally.[7] The existence of two nonreproductive decades of adult life raises

the fundamental evolutionary question: under what conditions will organisms evolve for whom general somatic senescence proceeds much more slowly than reproductive senescence?

Evolutionary theories of menopause that propose an adaptive function for reproductive cessation must show that the acceleration in reproductive senescence relative to mortality-related senescence results in higher fitness than the standard simultaneous decline in survival-related and reproductive functions (see Refs. 8–10 for reviews). Such theories need to provide a reason why direct reproduction will yield lower fitness than investing in alternatives, such as existing children and grandchildren. Special conditions must come into play for the following reason. In a diploid sexually reproducing organism, a female will be related to her offspring with Wright's coefficient of genetic relationship, r, of 0.5, whereas her grandchildren will only be half as related to her ($r = 0.25$). Therefore, according to inclusive fitness theory,[11] her investments in grandchildren will have to produce twice the fitness effect

as in children for selection to favor investment in grandchildren.

It is clear that the high dependence of human offspring alone is not sufficient to explain menopause. Women undergo menopause about the time that they have reproducing daughters. If offspring need were the sole driver, selection would more likely favor "helping at the nest" by adult daughters and sons (a very common pattern among nonhumans) rather than reproductive cessation by the older female. After all, an individual is related to its sibling by an *r* of 0.5 if the two siblings share the same mother and father. Holding all else constant, an individual should be indifferent between direct reproduction and helping her mother produce a sibling. Thus, if children need additional investment, why is it that young females (and males) do not defer reproduction to help their mothers reproduce rather than vice versa? Another way to frame the question about menopause is to ask, "Why should women cease to reproduce and help descendants, instead of continuing to reproduce with the help of descendants?" An adaptive theory of menopause must specify the conditions that provide an answer to that question.

This paper presents a new learning- and skills-based theory for the joint evolution of human menopause and extended postreproductive life. *The theory proposes that the role of knowledge, skill acquisition and transfers in determining economic productivity, and resource distribution is the distinctive feature of the traditional human ecology that is responsible for the evolution of menopause.* Moreover, we argue that the traditional hunter-gatherer pattern of production, reproduction, and parental investment depends fundamentally on a cooperative division of labor between men and women. The theory therefore proposes that in addition to female menopause, *male* reproductive cessation and postreproductive investment in descendants is a fundamental characteristic of humans living in traditional foraging and simple forager-horticultural economies. The theory builds on existing ideas—specifically the Grandmother and Mother hypotheses[12,13]—in proposing that menopause and the decrease in fertility with age that precedes it are evolved human traits that have been maintained by selection because women will leave more descendants by ceasing to reproduce and investing in existing descendants. However, the specific causal hypotheses that the theory integrates are new.

The paper begins with a brief presentation of the theory, followed by a discussion of the evidence upon which the theory is built. We begin with a comparative analysis of chimpanzee and human female reproductive senescence. We then examine the age-specific fertility of men and the likelihood of reproducing following menopause of wives. This is followed by behavioral evidence concerning food production and resource transfers across generations by women and men. The next section examines the total expected net caloric consumption of families as it varies over the life cycle, then simulates the caloric effects of adjusting the age schedule of women's fertility, delaying the onset of menopause. The paper concludes by linking these observations to the theory, and discussing directions for future theoretical and empirical research.

A "learning" theory of human reproductive decline and cessation

Although human foragers have lived in virtually all the world's terrestrial habitats, they always occupy one extreme feeding niche, eating the highest quality, most nutrient dense, and difficult to acquire plant and animal foods in their environment.[1,14] More than any other organisms, humans rely on brain-based skills and knowledge to acquire food from the environment. Those mental abilities combine with physical abilities—such as strength, coordination, and balance—to determine the rate of energy acquisition per unit time. In a series of papers, we have shown that peak physical condition in humans occurs in the early to mid-twenties, but that peak economic productivity does not occur until after age 40. This is due to the fact that skill acquisition and learning continue to increase after peak physical condition is reached. Thus, peak economic productivity between 40 and 50 years of age can be more than four times as high as at age 20. After age 50, however, declines in physical condition begin to outpace gains from learning and economic productivity, and people cease to be net producers by around age 70 (see Refs. 1 and 5 and section "Evidence," for supporting data for these claims). Our theory proposes that the nature of the high-skill human foraging niche has a series of implications which, taken together, disfavor old-age reproduction and favor old-age production and kin investment for both women and men, and thus drive the evolution of human reproductive decline and menopause.

Most theories of menopause and the empirical tests they stimulate estimate the age-specific cost of reproduction by the probability of dying in childbirth.[15–18] We propose that the cost of reproducing at advanced ages also includes increased risks of future mortality and reduced expected future productivity due to maternal depletion.[19] For example, maternal immune responses are lowered during pregnancy;[20] as women age and experience immunosenescence, the costs of immunosuppression are likely to increase. The energetic costs of lactation also probably occupy a greater proportion of a woman's physiological reserves as she ages. For these reasons, the cost of reproduction, both in terms of future mortality and future economic production, is likely to be higher for a 45-year-old woman than for her 20-year-old daughter.

Although most species are likely to evidence increasing costs of reproduction with age, late-age reproduction may be particularly costly for humans. Because human productivity is determined by both physical condition and long-developing skills, it is more important to survive long enough and maintain good enough condition to reap the rewards of earlier investments in skill development. This is accomplished by favoring somatic maintenance (and thus future production) over reproduction as the body begins to age.

The payoff to late-age reproduction in humans is also reduced by declining oocyte quality with age. There is significant evidence that oocyte quality declines with age in most mammals.[21,22] Because human offspring require extraordinary levels of investment to reach independence, the cost of continuing to reproduce from a deteriorating stock of oocytes should weigh more heavily in the human case than for most other species. An older mother producing highly dependent offspring may either: (a) risk investment in particularly low-quality offspring; or (b) ensure that she produces only sufficiently high-quality offspring, either by investing more energy in maintaining the quality of her oocytes, or by being more selective in allowing oocytes to implant or come to term. All of these options entail energetic costs, lost investments, or reduced fertility for older females that should be greater in species with heavier parental investment. Evidence presented by Ellison[23] and Haig[24] suggests that much of the burden in maintaining pregnancy prior to implantation depends on chemical signals produced by the embryo to maintain the corpus luteum and spur progesterone production. They suggest that maternal physiology utilizes these signals to detect quality differences in embryos and terminate low-quality pregnancies. We propose that human reproductive physiology may be particularly sensitive to embryo quality, and employ a more stringent selective sieve to prevent inferior embryos from implantation. Particularly long-lived animals may additionally face greater relative declines in oocyte quality over the lifespan (see Refs. 21 and 22 for reviews), which would also lower the returns to direct reproduction at advanced ages in humans.

Although the returns to late-age reproduction are reduced, the returns to old-age kin investment are increased for humans relative to other animals. Because the skills required for efficient food production take time to learn, children in foraging societies do not produce as much food as they consume until they are 18–20 years of age.[1] This means that they must rely on subsidies from other individuals. As the number of overlapping dependents in a young mother's household grows with each birth, total caloric need is expected to outpace a single couple's combined productivity, creating a demand for calories from sources outside the immediate household (see Ref. 25 and section "Evidence"). Older kin enjoying high levels of learning-based productivity and facing increasing costs of direct reproduction are in a prime position to meet this demand. This is true to a greater extent for humans than for most other mammals as a result of the life history characteristics—high productivity late in life, high offspring need, and the simultaneous dependency of multiple offspring—which coevolved with the skills-based human foraging strategy.

Finally, the skills-based foraging niche also provides the conditions that lead most men in foraging societies to undergo reproductive cessation at the same time as their wives. The skills-based economy of humans is associated with unusually high male energetic investment in offspring. In fact, men provide the majority of energetic support for reproduction in most hunting and gathering groups.[26,27] Despite the high need for protein and lipids to support brain growth during development, the mobility, danger, and long-term skill investments involved in human hunting make it largely incompatible with the primate female's evolved commitment to carrying (rather than caching) infants and

lactation-on-demand. This generates a complementarity between male and female inputs into offspring success, a sex-specific specialization in hunting by men, and high returns to male parental investment. Woman, in turn, specialize in a mix of childcare and foraging for plant resources.

The returns to male parental investment and the long overlapping dependence of children interact in producing a dominant pattern of long-term pair-bonding and male reproductive cessation in traditional foraging societies. Given that children remain dependent after their younger siblings are born, men and women in foraging societies face higher costs from switching mates than in many other species. A mother who begins a new union often suffers reduced paternal investment from the father of her previous children. Conversely, for a woman who is about to initiate reproduction, a man who has children from a previous union is less attractive because he already has vessels in which to invest. Consider a 20-year-old woman who is about to begin reproducing. For her, a 50-year-old man is less attractive than a 25-year-old, even though the older man may currently be more economically productive. The 50-year-old has two disadvantages: first, he already has his peak dependency load of existing children; second, his food production will decrease in the future and his mortality risk will increase. If the 20-year-old prefers to have all her children with one man, the younger man is preferable, because of his expected future contributions. This also implies that older men, who also face a trade-off between investing in existing children and grandchildren and seeking a new mate, most often "choose" to remain married and cease reproducing when their wives reach menopause.[28]

Our theory is that these altered age-specific benefits and costs of fertility, production and kin-investment—which derive from the specialized skills-based foraging niche and its attendant shift in economic productivity toward older ages—combine to favor "early" reproductive cessation in both men and women. This pattern has only evolved once. Even in those toothed whales that evidence female menopause, there is no such equivalent in males. In those species, males typically have much shorter lifespans than females and do not invest in offspring.[29] Humans are an outlier species in many senses, from brain size to lifespan to menopause to male parental investment. Special conditions are necessary to produce such an outlier. The combination of a brain-based, knowledge-, and skill-intensive foraging niche with a primate heritage selected for this complex of traits (large brains, long lifespan, long offspring dependence, high selectivity of oocyte quality, high male parental investment, and bisexual reproductive cessation).

In a recent paper, Kaplan and Robson[30] present a formal bioeconomic model for the evolution of aging. They show that reproductive cessation can be optimal prior to the optimal time to cease investing in mortality reduction and future longevity. The Kaplan–Robson model does not include all the considerations elaborated earlier, but provides an analytical result demonstrating the conditions under which menopause can evolve by natural selection. It shows that if (a) the energetic costs of reproduction increase with declining physical condition due to senescence, (b) economic transfers can allow surplus productivity at one point in the life course to be utilized at another point in the life course, and (c) individuals remain economically productive after reproductive cessation, then there is an age at which fitness—measured in terms of the instantaneous growth rate, r, of the lineage—can be maximized by reproductive cessation and the allocation of remaining resources to mortality reduction, physical maintenance, and intergenerational transfers. The present theory is based partially on the insights derived from that formal model.

The remaining sections of the paper will focus on the empirical evidence related to the theory.

Evidence

Chimpanzee and human reproductive decline and its link to somatic senescence

This section provides a comparative analysis of chimpanzee and Tsimane fertility. A recent analysis by Emery Thompson *et al.*[31] showed that while mean chimpanzee fertility rates decline toward the end of life, females in good physical condition show no significant fertility decline with age (Fig. 1, panel A, adapted from Ref. 31). Among females aged 25 and older, healthy individuals have significantly higher fertility than females who died within 5 years of the birth or risk year considered. Their findings suggest that chimpanzee reproductive senescence is tightly linked to somatic senescence and vulnerability to mortality. Using a similar approach for
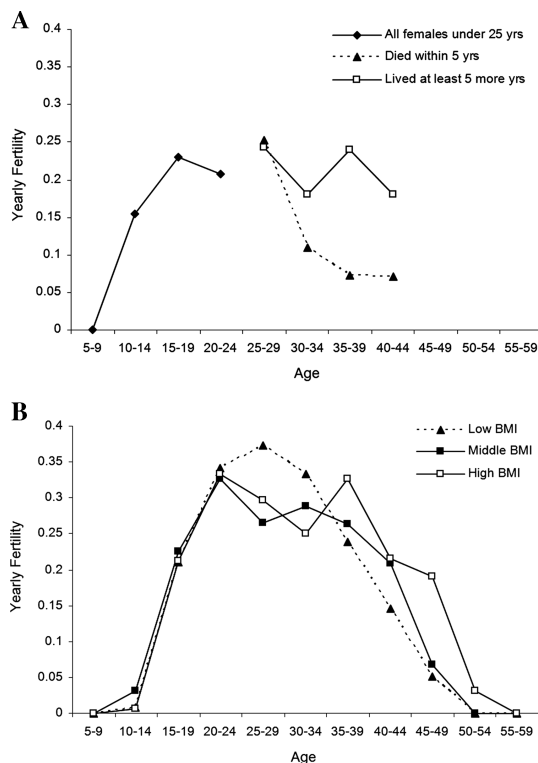
A

B

Figure 1. Impact of physical condition on chimpanzee and human fertility rates. (A) Probability of giving birth among female chimpanzees, stratified by those who died within 5 years of giving birth, and those robust enough to live at least five additional years following a birth. Adapted from Ref. 31. (B) Probability that a Tsimane woman gives birth using prospective data collected from 2002 to 2008, stratifying women into three groups based on their baseline body mass index (BMI). (Sample includes 1267 females between the ages of 5 and 59 and represents a total of 3121 observation years. Because of the rapid change in BMI across adolescence, females under age 20 were separated into BMI terciles within 1-year age intervals, whereas older women were separated into BMI terciles within 5-year age intervals.)

traditional humans, we expect to see a decoupling of somatic and reproductive senescence.

To compare a traditional human case with Emery Thompson *et al.*'s results, we performed a prospective analysis of the effect of physical condition, represented by body mass index (BMI), on age-specific fertility among Tsimane women. We examined the probability of a live birth occurring in each full calendar year following a woman's first nonpregnant BMI measure based on census data collected between 2002 and 2008. Panel B shows the mean fertility of Tsimane women by age divided into low,

Table 1. GEE logistic model of older women's likelihood of giving birth by BMI tercile ($N = 537$ person-years across 224 women aged 35–54 years)

Variable	B	SE	Wald χ^2	P
Intercept	4.723	0.9990	22.348	<0.001
Age	−0.159	0.0243	43.026	<0.001
High BMI	0.642	0.2622	5.990	0.014
Middle BMI	0.236	0.2692	0.766	0.381
Low BMI (baseline)	0	–	–	–

middle, and high BMI terciles. Although women with high BMI have slightly higher fertility at the end of their reproductive careers, all three condition levels show a characteristic decline in fertility that reaches zero for all women by the late 40s or early 50s, regardless of condition, unlike the chimpanzee case.

To further examine decline in fertility, the generalized estimating equations (GEE) method in SPSS 16 was used to test for the effects of age and BMI on the likelihood of giving birth in each year from ages 35 to 54. The woman's identity was included as a random repeated subject variable. Women in the highest BMI tercile have almost twice the likelihood of giving birth than women in the lowest BMI tercile (Table 1). Inclusion of a BMI-by-age interaction term does not yield a significant parameter estimate nor improve the model's goodness of fit, indicating that the slope of the decline in fertility by age is not significantly affected by BMI. This finding again contrasts with the chimpanzee case, in which the fertility of low-condition females declines with age significantly faster than that of high-condition females, who show no significant decline in fertility with age.

Male reproductive cessation

Consistent with the high levels of male parental investment, the majority of marriages among foragers and forager-horticulturalists are monogamous.[32] Although in some societies, such as the Ache and Hadza, there are frequently a series of short-term unions in early adulthood, this is generally followed by a single long-term reproductive union. Cross-culturally, most forager marriages are monogamous. In a sample of 145 hunter-gather societies, the modal percentage of polygynous marriages in a

society is 0–4%, and in most societies fewer than 10% of marriages are polygynous.[33] One of the consequences of monogamy is reproductive cessation among men after their wives reach menopause. For example, Ache foragers have high initial divorce rates when they are young; nevertheless, 90% of men who had more than one child with a woman did not reproduce after their wives reached menopause.[34]

Tsimane demographic data show that 90% of Tsimane men whose wives reached menopause did not reproduce again after their wife's last birth. Of the 10% who did reproduce, half (5.2%) were polygynously married and had a child with a younger co-wife, still within the bonds of marriage. The remainder had affairs outside of marriage (3.1%) or reproduced after the wife's death (1.5%). Given that some men at risk of reproducing after their partner reached menopause are still alive and may reproduce in the future, we conducted a survival analysis of male reproduction following menopause. From the survival curve (Fig. 2, panel A) it is evident that the greatest chance of reproduction is in the first 5 years after the wife's last child, consistent with the pattern of polygynous men reproducing with the younger co-wife. Because the younger co-wives were often reaching middle age as well, most of these men only reproduced once after their first wife reached menopause.

The linkage of men's reproductive schedules with women's can also be seen from the age-specific fertilities of the two sexes. The male curve is shifted to the right of the female curve by about 5 years, consistent with the age differences among spouses (Fig. 2, panel B). The tail of the male curve stretches out a bit from the female curve due to some men being more than 5 years older than their spouse and the few men who reproduce after their wife's menopause. The male and female curves for expected future fertility (i.e., reproductive value) are strikingly similar, after age differences in marriage are taken into account (Fig. 2, panel C).

Physical condition, age profiles of productivity and intergenerational transfers

Age profiles of productivity and intergenerational transfers among human hunter-gatherers and forager-horticulturalists have been documented in a series of publications.[1,5,6,35,36] Those data show that children remain dependent on their parents until 18–20 years of age, with a peak dependency in
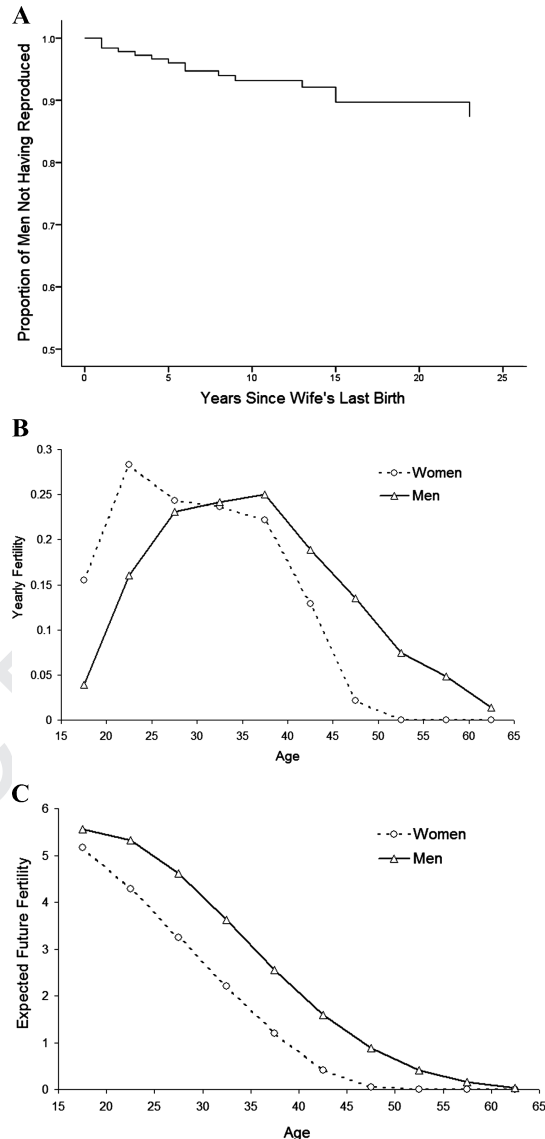

Figure 2. Male and female reproductive cessation among the Tsimane. (A) Probability that a Tsimane man did not reproduce after his wife had her last birth (see text for details). (Sample based on retrospective reproductive histories including 188 final female births, and 182 husbands; 6 were married polygynously to two wives.) (B) Age-specific fertility rates for Tsimane men and women, given in 5-year intervals. (Sample based on retrospective reproductive histories of 431 women and 391 men covering the period 1950–2002; this includes 12,394 risk years and 2238 births for women, and 12,514 risk years and 1943 births for men aged 15–64.) (C) Expected future fertility by age considers the cumulative sum of remaining future reproduction discounted by the probability of surviving to those ages. Survivorship data are from Ref. 46.

early adolescence (from birth, caloric requirements grow faster than productivity until about age 12 or 13 years).

Peak productivity in adulthood for both men and women occurs well after strength and physical condition peak. For example, among Ache foragers of Paraguay, men's strength peaks at around 25 years of age but both meat acquired and hunting return rates (amount acquired per hour spent hunting) peak between 40 and 50 years of age.[37] Data on strength and hunting ability among Tsimane men show the same pattern;[5] moreover, skill in successfully pursuing prey is the most important determinant of hunting success.

Figure 3 shows the age-profiles of food production and consumption among Tsimane men and women. Both male and female production peaks after age 40. Males produce as much as they consume by about age 20 years, and females by age 28 years. The caloric deficit in childhood is compensated for by a caloric surplus in adulthood. The increase in total food production is driven by two effects. First, there is an increase in efficiency (production per unit time) until the mid-40s. Second, there is a corresponding increase in work effort, probably reflecting the increase in dependency load. The decrease in production with age is driven primarily by declines in efficiency.

Figure 4 examines physical decline with age. Panel A shows the decline in strength with age for both men and women, and panel B shows pain-related fatigue among women while they pound rice. Both figures show considerable declines before peak productivity is reached.

Food sharing data allow for a more direct understanding of inter-generational wealth flows. Figure 5 plots the *net* transfers between pairs of related individuals. Net transfers are calculated by taking the total amount of food given from individual *A* to individual *B* and then subtracting the total amount given from *B* to *A*. Those amounts are derived from data on the consumers of food acquired by all family members. In the figure we present those nets from fathers to children, mothers to children, grandfathers to grandchildren, and grandmothers to grandchildren. Even though food is transferred in both directions between these pairs of individuals, the figure shows that *net transfers flow downward across generations*. The downward flow from both mothers and fathers to their children continues into adult-
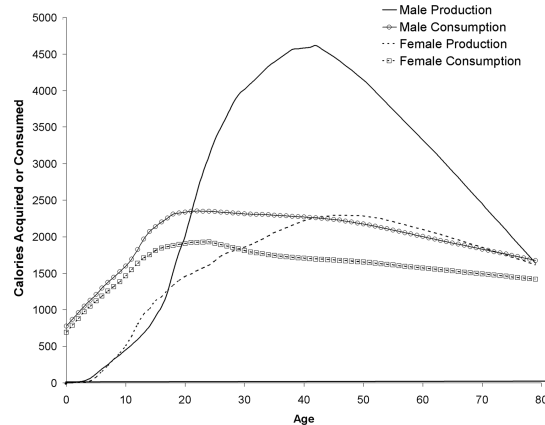

Figure 3. Age-specific caloric production and consumption profiles for Tsimane. Daily production was estimated for non-rice foods from interviews covering the previous 2 days of food production. These data covered 43,656 sample days over 749 individuals. Rice production was estimated from interviews concerning the amount of rice harvested in the previous year. These data covered 589 individuals from the non-rice sample. Credit for rice production was based on the proportional time spent in field labor from the 2-day production interviews. Loess curves were fit over the daily non-rice and rice production rates by age and sex. The loess prediction curves were then summed to produce the final curves. Consumption was estimated by first calculating the total energy expenditure (TEE) based on the age, sex, and weight of individuals.[47] These were plotted by age and the maximal consumption level was estimated to be 2770 calories per day for the Tsimane. The TEE of each individual was divided by this to determine the proportion of consumer (POC). The number of production days sampled was multiplied by each individual's POC and these were then summed to determine the total number of consumer days. The total production during the sampling period was then divided by this sum to determine the true caloric intake of the maximal consumer, which equaled 2661 calories per day. Each individual's POC was multiplied by 2661 to determine their consumption level. We then fit a loess curve to the consumption levels by age and sex.

hood, even when their children become adults and have children of their own. During the postreproductive period of life (after age 45), transfers to existing children dominate during middle age, with an increasing proportion of resources being transferred to grandchildren, especially in the 60s. Net transfers approach zero after age 70.

From Figure 5, it can also be seen that men transfer more calories to descendants than do women. However, women's work in childcare, food processing, and household maintenance exceeds that of men, and both sexes spend similar amounts of total time in work.[38] This division of labor appears to be universal in foraging societies, although the
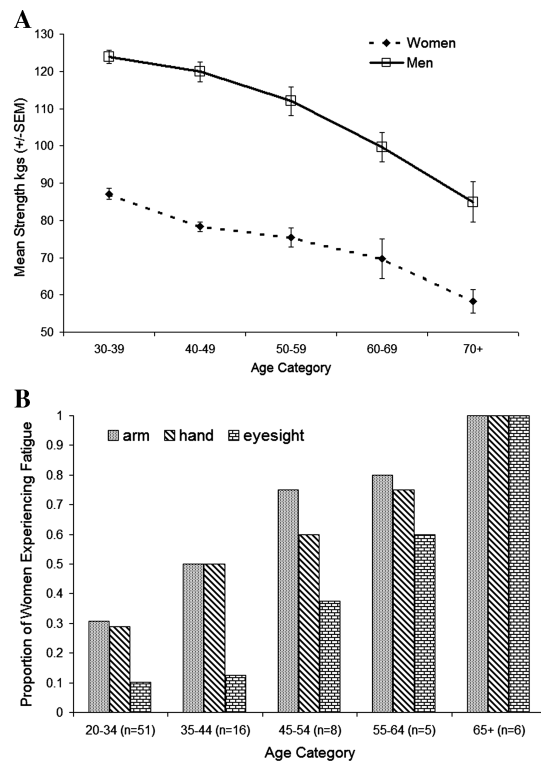
A

B

Figure 4. Physical decline with age among Tsimane adults. (A) Strength is the sum of chest, shoulder, thigh, leg, and hand grip strength, measured using the Lafayette Manual Muscle Tester and Smedley III Analog Grip Strength Tester. (Sample includes 416 women and 428 men.) (B) Proportion of Tsimane women that report experiencing physical problems during rice pounding. Problems include arm and hand pain and poor eyesight. (Sample includes 104 women.)

relative energetic contributions of the two sexes vary according to local ecology. For the sample of 10 forager societies for which quantitative data exist, men, on average, acquired 68% of the calories and almost 88% of the protein; women acquired the remaining 32% of calories and 12% of protein.[26]

Transfers, calories, and menopause

Just as food production increases with age during the reproductive period, so too do the caloric demands of dependents. In fact, the caloric demands on parents increase faster than does their productivity.[25] Figure 6, panel A, shows data from the Tsimane on the net productivity of parents, the net caloric demands of children and the net surplus or deficit of families as a function of a woman's age. This figure shows that as families grow, their net deficit increases, even though parental productiv-
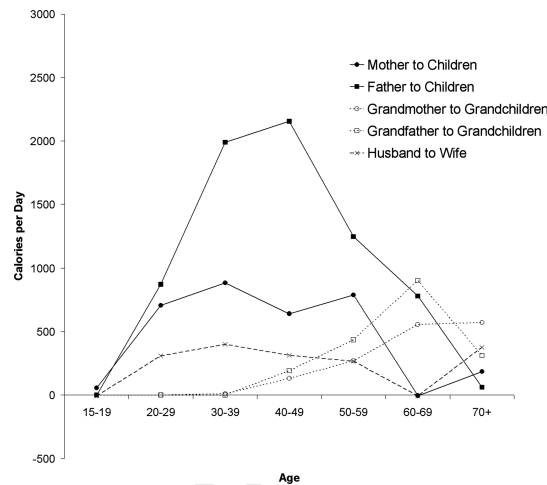

Figure 5. Net caloric transfers between kin groups across three generations. Transfers were calculated using data from 3850 consumption events by 674 individuals during instantaneous scan observations. The number of events in which individual *A* was the acquirer of food consumed by individual *B* divided by the total number of times individual *A* was named an acquirer was interpreted as the proportion of individual *A*'s production that went to individual *B*. (For foods with multiple acquirers, each acquirer was assigned a proportion of credit, and these credits were the values actually tallied.) The proportional distribution to each kin member was then calculated for each aggregated age-sex group, as the number of observations per individual was low. To capture the observed population age structure, each individual alive in a 25-community census was assigned their age- and sex-specific daily production and proportional distribution levels. Daily production (represented in Fig. 3) was multiplied by proportional distribution to determine gross transfers. These were summed in both directions for each kin dyad to determine net transfers. Averages were then calculated for each age-sex group.

ity is increasing as well. Most importantly, it can be seen that the deficit of growing families is compensated for by the net surplus of postreproductive individuals, who provision descendant kin (see also Fig. 5).

Figure 6, panel B, simulates the caloric effects of a delay in reproductive decline and menopause. The average net caloric demand of children in families headed by mothers in their 30s was extended throughout the 40s; the net caloric demand of children beyond the 40s then continued 10 years behind schedule (so that a 60-year-old was experiencing the typical progeny dependency of a 50-year-old). In this case, the surplus provided by older people continues to be consumed by their dependent children. Figure 7 shows the cumulative net caloric
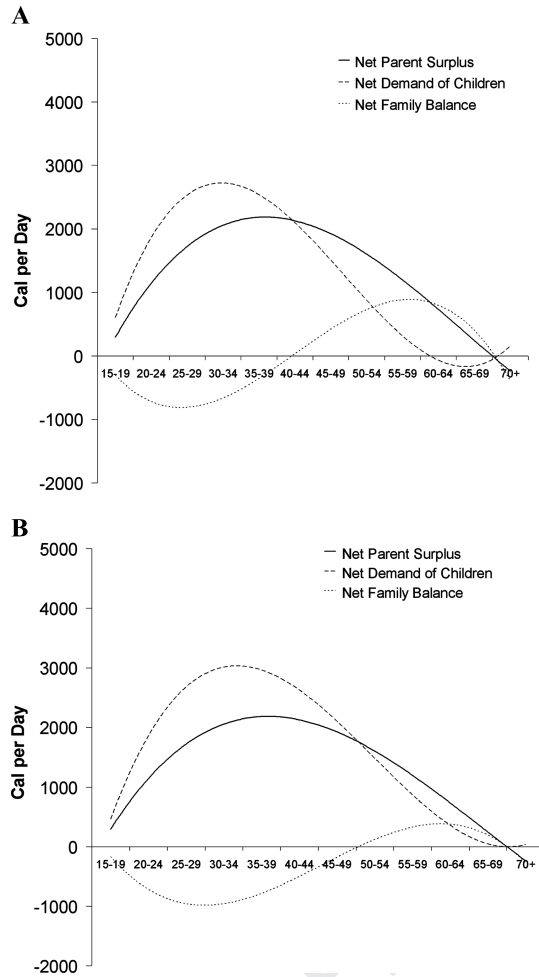
A

B

Figure 6. Parental production, children's demands, and net family production. (A) Observed Tsimane pattern. These calculations are based on rice and non-rice production data from 106 families, including 561 individuals who were sampled for an average of 67 days. (B) Simulation based on delayed menopause (see text). Daily caloric production and estimated consumption levels were summed for parents and children within families. Parental production and child demand levels were then aggregated over 5-year age intervals to calculate overall family balances. Because cumulative mortality risk leads to a larger number of families headed by younger parents than families headed by older parents, those families that do survive must produce surpluses that more than make up for their previous deficits. To take into account the effects of mortality, summed net balances for all age intervals were divided by the number of families in the 15–19 age interval in an attempt to include in the denominator those families that were lost to mortality. Third-order polynomial curves were fit to the mean values of each age interval.
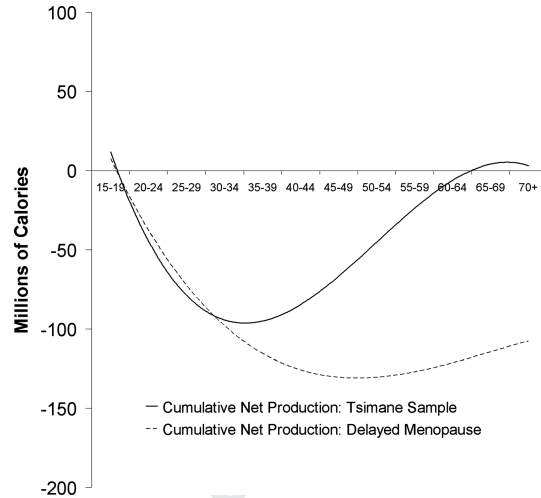

Figure 7. Cumulative net caloric balance of families given the Tsimane sample and the delayed menopause simulation from Figure.

balance, given the Tsimane sample and the delayed menopause simulation. The "contrary to fact" delayed menopause simulation shows genetic lineages with a fertility and economic transfer regime that would be in net economic deficit, and therefore could not support itself.

Discussion and conclusions

The theory presented in this paper builds on existing adaptive hypotheses for the evolution of menopause. Most adaptive explanations have focused on women's roles as mothers and grandmothers.[4,12,13,15,16,39–41] The mother version emphasizes the long period of juvenile dependence in humans, and its possible links to brain development.[13,39] According to this view, women stop reproducing at the expected age at which they will be able to raise their last child to maturity before dying. If children require 20 years of parental investment, then ceasing to reproduce at age 45 would make sense with an expected age of death of 65, given survival to that age. The grandmother version proposes that women cease reproducing in order to invest in grandchildren and help their daughters reproduce.[12,40,41] According to Hawkes *et al*., the strength-intensive nature of human foraging means that grandmothers can acquire more than children and help provision them.

The present theory extends and modifies those ideas in three important ways. First, it specifies the unique ecological conditions responsible for the evolution of the temporal separation of reproductive and somatic senescence in humans. Second, it identifies the important role that men play in the human life history strategy, and highlights that premature reproductive cessation occurs in men as well as women. Third, it addresses the question of why reproductive cessation and downward kin-investment by elders should be favored over the alternative of continued reproduction supported by younger, nonreproductive "helpers at the nest."

The fundamental premise of our theory is that the role of brain-based skills and learning in economic production for both men and women during our evolutionary past is at the far end of the evolutionary continuum. Skills and knowledge are accumulated throughout life, but physical condition, from strength to immune function, declines throughout adulthood. As a result, human economic productivity—which is a function of both cumulatively learned abilities and physical strength and endurance—continues to increase even after physical condition begins to decline. We propose that this disjunction between economic and physiological aging is the ecological key to human menopause. It simultaneously generates two conditions: (1) the physiological cost of later reproduction is rendered high for women, but their economic productivity and that of their husbands remains high; and (2) infants, juveniles, and adolescents produce less food than their growing bodies require.

A key feature of our theory is that it incorporates declining oocyte quality and increasing physiological costs of reproduction. We argue that declining oocyte quality with age has a larger impact on the trade-off between reproducing and investing in descendants for humans than it does for chimpanzees and most other mammals. Here we base our argument on evidence showing that human reproductive physiology is replete with mechanisms designed to ensure that investment is curtailed in low-quality oocytes and embryos from the follicular development phase through implantation and placental development.[23,42] We further propose that it is the length of human parental investment that selected for more stringent mechanisms of quality control, to allocate investment in high-quality offspring rather than "waste" it on low-quality offspring. The logical

extension of this argument is that across species, optimal levels of selectivity with respect to oocyte quality will increase as parental investment increases.

To this logic, we add the observation that the physiological cost of reproduction increases with maternal age, not only due to increased risks of death in childbirth, but also due to maternal depletion that should affect survival and productivity at future ages. Given the disjunction between physiological aging and economic aging in humans and given the low productivity of children who have yet to learn, those physiological costs of reproduction should weigh more heavily on women than on females of other species. Human females have more to give by living longer, and thus should be less willing to risk death than other species.

Finally, our theory is two-sex, in that it proposes that reproductive cessation occurs regularly among human males as well as females. We argue that human males also face a similar trade-off between investment in existing descendants and continued reproduction. However, instead of facing increased physiological costs of reproduction with age, males become less attractive as mates as they age. This is due to two reasons. First, the importance of male investment in offspring and the long term dependence of young in humans have resulted in longterm monogamous pair-bonds between men and women. Marriage to an older man is less attractive to a young woman, because he is likely to die before she completes her reproductive career. Second, given that older men are likely to have existing dependent young, their investment in children produced by a new marriage will likely be lower.

We compare chimpanzee decline in fertility with age to that of Tsimane females. The data compiled by Emery Thompson *et al*. show that aging chimpanzees in relatively good condition do not reduce fertility with age (or reduce fertility at later ages).[31] In contrast, the Tsimane data show that while women with higher BMI, one measure of condition, do have higher fertility late in life, the decline in fertility with age in women is more dramatic than among healthy chimpanzees. This is even more striking given that chimpanzee females in relatively good condition in their 30s are still in worse condition than most women at that age, showing much more advanced signs of aging. This suggests that in response to declining oocyte quality, chimpanzee female reproductive physiology is less

selective than that of human females. We used data from the Ache and Tsimane data to show that men have a low probability of reproducing after their wives reach menopause, and that their age-related fertility decline is very similar to that of their wives.

We then presented evidence for both men and women that caloric production in traditional economies does not exceed consumption until adulthood, and that middle- and old-age adults produce a caloric surplus. The data also show that intergenerational wealth flows are downward within families, and that both men and women invest in existing children and then grandchildren after they cease reproducing. We then examined the joint economic and reproductive life histories of families by plotting the expected caloric demands of children, the net productivity of parents, and the resulting household net caloric surplus (or deficit) as functions of a woman's age. Those results showed that energetic burden of reproducing families produces a caloric deficit, which is compensated for by the caloric surpluses of postreproductive individuals.

The impacts of reproductive cessation on calorie balance were then illustrated by simulating the continued reproduction of women at their 30-year-old rate until age 50. That simulation revealed that all of the caloric surplus of older people would be consumed by the extension of the reproductive period, and the whole family lineage would remain in caloric deficit.

The evidence presented in this paper cannot be considered a test of the theory, because the theory was developed in response to the evidence. In addition, most of the evidence is "circumstantial" in that it is consistent with the theory, but does not demonstrate that the relative importance of foraging for high-quality resources using learning-intensive acquisition strategies is the primary ecological driver of menopause. Given that menopause has evolved so infrequently and its particular two-sex form in humans is unique, ecological tests may prove elusive.

Nevertheless, individual components of the theory may be testable with comparative data. For example, there is a growing corpus of data on whales that should allow for comparative tests. Some toothed-whales show clear evidence of menopause and a long postmenopausal lifespan in females.[29,43] It is interesting to note that this branch of the cetacean line shows some broad similarities in its

foraging niche to humans. Killer whales, for example, demonstrate ecologically diverse foraging strategies, strongly based on cultural traditions passed through matrilineal kin from old to young (see Ref. 44 for a detailed review of learned cultural traditions in cetaceans). Their foraging strategies and brains also reflect complex cognitive processes.[45] Similarly, comparative research on complementarity, male parental investment and the linkage between male and female reproductive strategies could test other components of the theory.

Future research should focus on investigating the costs of reproduction, selectivity with respect to oocyte quality, and economic transfers. We still know very little about maternal depletion in traditional natural fertility societies, and how aging affects the costs of reproduction in terms of future longevity, health, and productivity. Another area for investigation is species differences in oocyte quality control. Do humans and chimpanzees differ in the selectivity of oocytes prior to ovulation, during fertilization and the completion of meiosis, or during embryogenesis? Food sharing in traditional societies is also very complex. There are both within and between family transfers, and the mix of kinship, reciprocity and other factors determining those transfers is still poorly understood. A clearer understanding of those phenomena will help evaluate the present theory and provide insight into the evolution of human reproductive cessation.

Acknowledgments

Conflict of Interest

The authors declare no conflicts of interest.

References

1. Kaplan, H., K. Hill, J. Lancaster & A.M. Hurtado. 2000. A theory of human life history evolution: diet, intelligence, and longevity. *Evol. Anthropol.* **9:** 156–185.

2. Gurven, M. & H. Kaplan. 2007. Longevity among hunter-gatherers: a cross-cultural comparison. *Popul. Dev. Rev.* **33:** 321–365.

3. Konigsberg, L.W. & N.P. Herrmann. 2006. The osteological evidence for human longevity in the recent past. In *The Evolution of Human Life History*. K. Hawkes & R. Paine, Eds.: 267–306. School of American Research Press. Santa Fe.

4. Hawkes, K. 2003. Grandmothers and the evolution of human longevity. *Am. J. Hum. Biol.* **15:** 380–400.

5. Gurven, M., H. Kaplan & M. Gutierrez. 2006. How long does it take to become a proficient hunter? Implications on the evolution of delayed growth. *J. Hum. Evol.* **51:** 454–470.

6. Kaplan, H. 1994. Evolutionary and wealth flows theories of fertility: empirical tests and new models. *Popul. Dev. Rev.* **20:** 753–791.

7. Thomas, F. *et al.* 2001. International variability of ages at menarche and menopause: patterns and main determinants. *Hum. Biol.* **73:** 271–290.

8. Austad, S. N. 1997. *Why We Age.* Wiley. New York.

9. Armstrong, E. & D. Falk. 1982. *Primate Brain Evolution: Methods and Concepts.* Plenum Press. New York.

10. Sherman, P.W. 1998. The evolution of menopause. *Nature* **392:** 759–761.

11. Hamilton, W.D. 1964. The genetical evolution of social behavior. *J. Theor. Biol.* **7:** 1–52.

12. Hawkes, K. *et al.* 1998. Grandmothering, menopause, and the evolution of human life histories. *Proc. Natl. Acad. Sci. USA* **95:** 1336–1339.

13. Peccei, J.S. 2001. Menopause: adaptation or epiphenomenon? *Evol. Anthropol.* **10:** 43–57.

14. Kaplan, H.S. 1997. The evolution of the human life course. In *Between Zeus and the Salmon: The Biodemography of Longevity*. K. Wachter & C. Finch, Eds.: 175–211. National Academy of Sciences. Washington, DC.

15. Hill, K. & A.M. Hurtado. 1991. The evolution of reproductive senescence and menopause in human females. *Hum. Nat.* **2:** 315–350.

16. Rogers, A. 1993. Why menopause? *Evol. Ecol.* **7:** 406–420.

17. Sear, R., F. Steele, I. McGregor & R. Mace. 2002. The effects of kin on child mortality in rural Gambia. *Demography*. **39:** 43–63.

18. Sear, R., R. Mace & I.A. McGregor. 2000. Maternal grandmothers improve the nutritional status and survival of children in rural Gambia. *Proc. Biol. Sci.* **267:** 1641–1647.

19. Tracer, D.P. 1991. Fertility-related changes in maternal body composition among the Au of Papua New Guinea. *Am. J. Phys. Anthropol.* **85:** 393–405.

20. Heyborne, K. & R.M. Silver. 1996. Immunology of postimplantation pregnancy. In *Reproductive Immunology*. R.A. Bronson, N.J. Alexander & D. Anderson, Eds.: 383–417. Blackwell Science. Oxford.

21. Ottolenghi, C. *et al.* 2004. Aging of oocyte, ovary, and human reproduction. *Ann. N.Y. Acad. Sci.* **1034:** 117–131.

22. vom Saal, F.S., C.E. Finch & J.F. Nelson. 1994. Natural history and mechanisms of aging in humans, laboratory rodents and other selected vertebrates. In *Physiology of Reproduction*, Vol. 2. E. Knobil, J. Neill & D. Pfaff, Eds.: 1213–1314. Raven Press. New York.

23. Ellison, P.T. 2001. *On Fertile Ground: A Natural History of Human Reproduction.* Harvard University Press. Cambridge, MA.

24. Haig, D. 1993. Genetic conflicts in human pregnancy. *Q. Rev. Biol.* **68:** 495–532.

25. Gurven, M. & R. Walker. 2006. Energetic demand of multiple dependents and the evolution of slow human growth. *Proc. Biol. Sci.* **273:** 835–841.

26. Kaplan, H.S., K. Hill, A.M. Hurtado & J. Lancaster. 2001. The embodied capital theory of human evolution. In *Reproductive Ecology and Human Evolution*. P.T. Ellison, Ed.: 293–317. Aldine de Gruyter. Hawthorne, NY.

27. Marlowe, F. 2001. Male contribution to diet and female reproductive success among foragers. *Curr. Anthropol.* **42:** 755–760.

28. Winking, J., H. Kaplan, M. Gurven & S. Rucas. 2007. Why do men marry and why do they stray? *Proc. Biol. Sci.* **274:** 1643–1649.

29. Foote, A. 2008. Mortality rate acceleration and post-reproductive lifespan in matrilineal whale species. *Biol. Lett.* **4:** 189–191.

30. Kaplan, H. & A. Robson. 2009. We age because we grow. Proc. Biol. Sci. **276:** 1837–1844.

31. Emery Thompson, M. *et al.* 2007. Aging and fertility patterns in wild chimpanzees provide insights into the evolution of menopause. *Curr. Biol.* **17:** 2150–2156.

32. Marlowe, F.W. 2004. The mating system of foragers in the standard cross-cultural sample. *Cross-Cult. Res.* **37:** 282–306.

33. Binford, L.R. 2001. *Constructing Frames of Reference.* University of California Press. Berkeley, CA.

34. Hill, K. & A.M. Hurtado. 1996. *Ache Life History: The Ecology and Demography of a Foraging People*. Aldine. Hawthorne, NY.

35. Gurven, M.D. & H.S. Kaplan. 2006. Determinants of time allocation to production across the lifespan among the Machiguenga and Piro Indians of Peru. *Hum. Nat.* **17:** 1–49.

36. Kaplan, H. & A. Robson. 2002. The emergence of humans: the coevolution of intelligence and longevity with intergenerational transfers. *Proc. Natl. Acad. Sci. USA* **99:** 10221–10226.

37. Walker, R., K. Hill, H. Kaplan & G. McMillan. 2002. Age-dependency in skill, strength and hunting ability among the Ache of eastern Paraguay. *J. Hum. Evol.* **42:** 639–657.

38. Gurven, M. *et al.* 2009. A bioeconomic approach to marriage and the sexual division of labor. *Hum. Nat.* **20:** 151–183.

39. Lancaster, J.B. & B.J. King. 1985. An evolutionary perspective on menopause. In *In Her Prime: A View of Middle Aged Women*. V. Kerns & J.K. Brown, Eds.: 13–20. Bergen and Garvey. Garden City, NJ.

40. Williams, G.C. 1957. Pleiotropy, natural selection and the evolution of senescence. *Evolution.* **11:** 398–411.

41. Hawkes, K., J.F. O'Connell & N. Blurton Jones. 1989. Hardworking Hadza grandmothers. In *Comparative Socioecology of Humans and Other Mammals.* V. Standen & R.A. Foley, Eds.: 341–366. Basil Blackwell. London.

42. Hunt, P. & T. Hassold. 2008. Human female meiosis: What makes a good egg go bad? *Trends Genet.* **24:** 86–93.

43. Ward, E.J. *et al.* 2009. The role of menopause and reproductive senescence in a long-lived social mammal. *Front. Zool.* **6:** 1–10.

44. Rendell, L. & H. Whitehead. 2001. Culture in whales and dolphins. *Behav. Brain Sci.* **24:** 309–382.

45. Marino, L. *et al.* 2007. Cetaceans have complex brains for complex cognition. *PLoS Biol.* **5:** 0966–0972.

46. Gurven, M., H. Kaplan & A. Zelada Supa. 2007. Mortality experience of Tsimane Amerindians: regional variation and temporal trends. *Am. J. Hum. Biol.* **19:** 376–398.

47. FAO. 2001. Human energy requirements. Food and Nutrition Technical Report Series.