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# Sex and Longevity: Sexuality, Gender, Reproduction, Parenthood

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# The Ecology of Menopause

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## Abstract

Reproductive senescence is a universal characteristic of mammalian females. In some species, however, reproductive senescence occurs close to midlife, and several theories have been proposed to explain how menopause might be adaptive, especially through fitness benefits to a female's grandchildren. Recent research has clarified how menopause can evolve in the absence of such indirect benefits and instead focuses attention on an aging female's abilities as a mother rather than as a grandmother.

Two alternative paradigms have been developed to explain the evolution of menopause. First, menopause occurs at an age where most females have already died due to disease or predation, and thus selection has become too weak to prevent the expression of deleterious genetic traits that were either neutral or beneficial at younger ages (Williams 1957; Hamilton 1966; Charlesworth 1980). Second, menopause is an adaptation that releases elderly females from the costs of further childbirth (Williams 1957; Rogers 1993) or otherwise enables them to redirect their nurturance to grandchildren (Hawkes et al. 1997).

Menopause is often considered unique to humans, but reproductive cessation is virtually ubiquitous in female mammals (Finch 1990; vom Saal et al. 1994). But even though senescence is inevitable (and therefore provides a reasonable explanation for the origins of menopause), it has been difficult to explain why women's reproduction deteriorates so much earlier than somatic function (Hill and Hurtado 1991). However, any analysis of the human menopause is hampered by the difficulties in establishing relevant life tables in the face of modern agriculture, medicine and sanitation. Madame Calment lived 70–80 years beyond menopause, but would she even have reached the age of 50 in a pre-technological society? Nevertheless, many researchers remain impressed by the apparently young age of the human menopause, and thus the grandmother hypothesis retains considerable popular appeal (e.g., Sherman 1998; Angier 1999; Sapolsky and Finch 1999) despite serious theoretical difficulties (Rogers 1993) and little empirical support (e.g., Hill and Hurtado 1991).

Our recent research on wild populations of African lions and olive baboons (Packer et al. 1998) reinforces the suggestion that reproductive senescence can evolve purely from the force of extrinsic mortality: female lions start breeding by

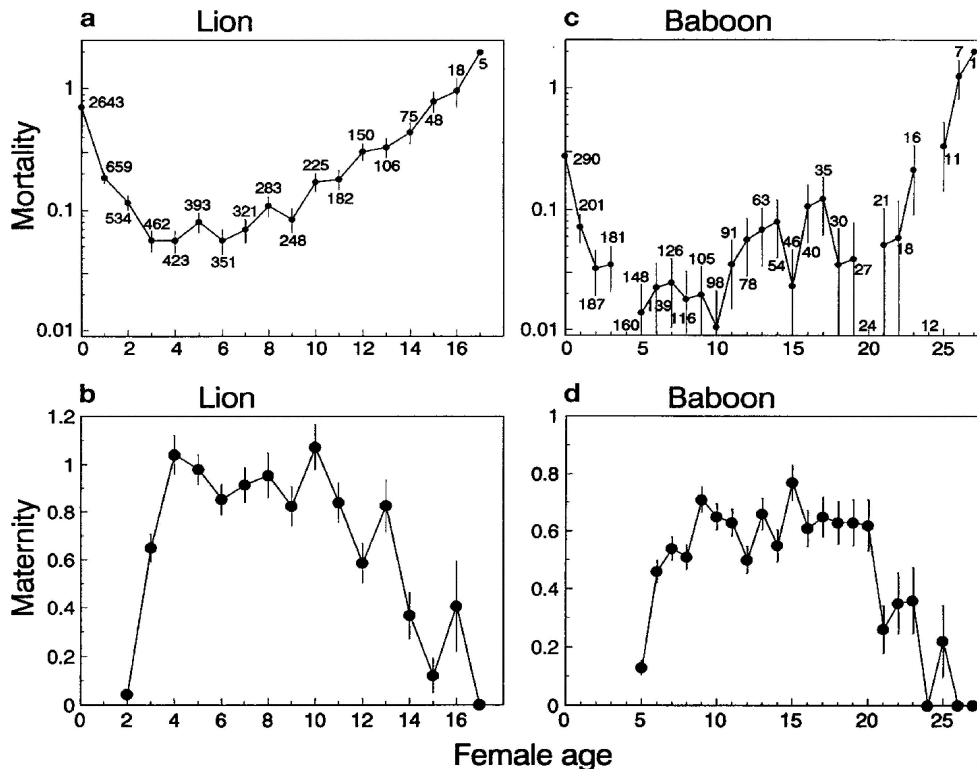


Fig. 1. Age-specific mortality and maternity in female lions and baboons. Bars represent standard errors; numbers are sample size. Annual mortality is estimated from monthly intervals for a, lions (652 yearlings, 18.4% censored) and from weekly intervals for c, baboons (201 yearlings, 60.7% censored). Gross maternity for b, lions and d, baboons is the number of live offspring produced at each age

the age of three to four years, suffer an annual mortality of at least 8%, and undergo an abrupt decline in reproductive rate at the age of 14 (Fig. 1 a,b). Female baboons start breeding by the age of seven to eight years, when annual mortality is only about 2%, and they show an abrupt drop in reproduction at the age of 21 (Fig. 1 c,d).

Although it is difficult to specify the factors that contribute to declining reproduction in female lions, cycling and fertility are easily measured in baboons. During the menstrual cycle, the perineal sex skin undergoes a distinct tumescence during the follicular phase and a sudden detumescence at the onset of the luteal phase, and the perineum turns scarlet shortly after conception (Altmann 1970). In the Gombe baboons, pregnancies were more likely to end in miscarriage at the age of 21, cycles became more irregular at the age of 23, and fertility essentially stopped by the age of 24 (Fig. 2).

Captive baboons at the Southwest Foundation for Biomedical Research (SFBR) experience a slightly earlier onset of reproductive decline than the Gombe baboons. AT SFBR, females show a striking decrease in cycling regularity by the age of 20–23 and a drop in fertility by the age of 20 (with a complete cessa-

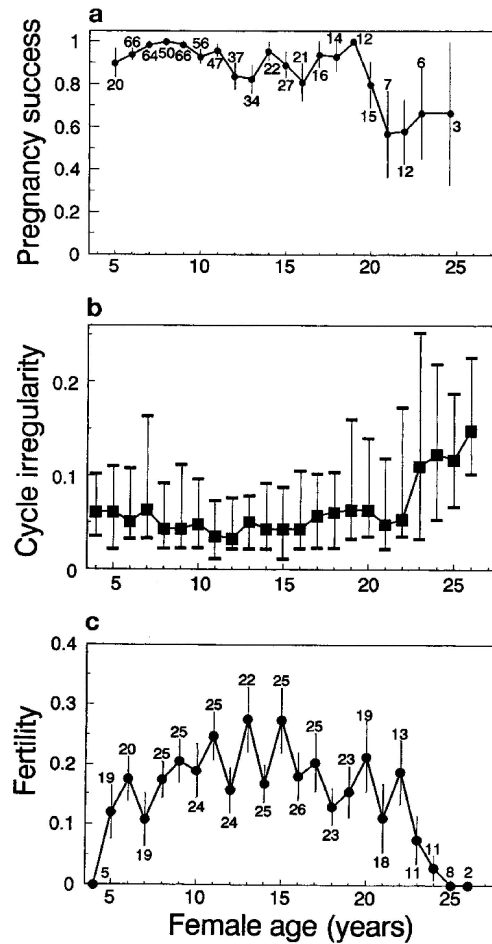


Fig. 2. Age-specific aspects of female reproduction. a, Proportion of baboon pregnancies that ended in live birth. b, Median (■) and quartile (–) “irregularity” of menstrual cycles (irregularity = standardized deviation from the average cycle length, see Packer et al. 1998 for details). c, Mean proportion of cycles resulting in pregnancy (plotted with standard errors and the number of cycling females at each age). Cycles become significantly more irregular while pregnancy success and fertility decline at advanced ages

tion in fertility by the age of 24), and 23 to 29-year-old females secrete far higher levels of follicular stimulating hormone (FSH; Ledford 1998). Such high levels of FSH provide a clear indication of deteriorating ovarian function and eventual menopause, and these same animals also show signs of osteoporosis once they reach their twenties (Lauerman et al. 1992).

Do these patterns reflect age-specific selection pressures in nature? Because of high mortality patterns in both lions and baboons, relatively few females survive long enough to suffer from declining reproductive performance. We estimated the strength of selection for lions to be only 0.0026 at the age of 14 years and 0.0015 for 21-year-old baboons, values which might indeed be too weak to eliminate traits that only harm such elderly individuals.

While this interpretation is reasonably consistent with the traditional view of reproductive senescence, female lions live to a maximum age of 18 in the wild and female baboons live to 27+. Thus reproduction starts to deteriorate well before the end of life. Can this “early” onset of reproductive senescence be due to the value of grandmaternal care in these species?

Lions and baboons would seem like ideal candidates for a “grannie effect” since they both live in complex matrilineal societies. Lions are communal breeders that will even nurse each others’ offspring (Packer and Pusey 1997); baboons form kin-based alliances that determine their descendants’ dominance ranks (Gouzoules and Gouzoules 1987). However, we found no evidence that grandmother lions or baboons actually enhanced the survival of their grandchildren, except when lion grandmothers were reproductively active (Fig. 3). Lion mothers rear their cubs in communal crèches, whereas non-mothers are relatively asocial (Pusey and Packer 1994). Thus grandmothers only help their grandchildren when they are reproductively active, and menopause not only costs further direct reproduction but also eliminates the opportunity to nurture their grandchildren.

Alternatively, if the mortality risks of parturition increased sufficiently with advancing age, menopause would extend a female’s life expectancy long enough to “fledge” her older dependent offspring (Nesse and Williams 1994). However, this suggestion does not apply to lions or baboons since they do not resume breeding until their prior offspring have reached independence (see below). Furthermore, parturition is not a significant source of mortality in either species even at advanced ages (Packer et al. 1998).

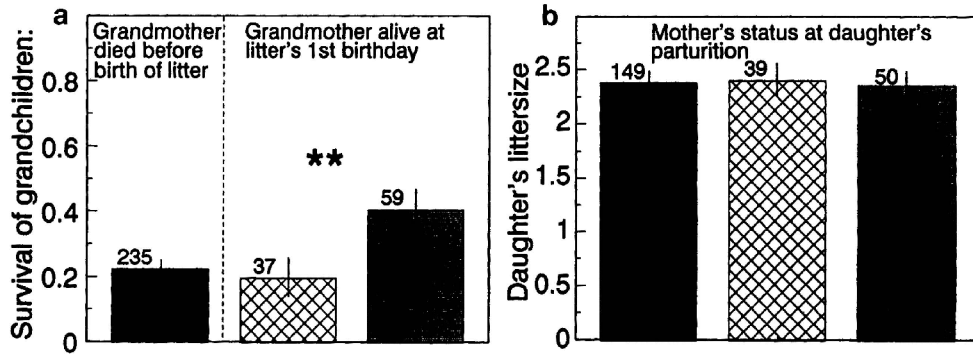
Although maternal survival may not enhance the fitness of their early-born offspring, females will receive no genetic return from their final infant if they die before it is fledged. The interbirth interval is about two years in both species, and lions and baboons suffer high mortality if they are orphaned before the age of two years (Fig. 4). Even if the only individual that suffers from the demise of its mother is the last-born offspring, a long period of infant dependency will nevertheless be expected to influence the timing of reproductive senescence.

Figure 5 shows a hypothetical survival curve with constant mortality. Assume that selection is too weak to prevent the fixation of harmful alleles beyond the age where only 1 % of females are still alive (at the age of 10 years). Assume, too, that a mother rears each brood sequentially, waiting until her prior brood has reached two years of age (and can therefore survive on its own) before giving birth to her next brood. When infant survival depends entirely on maternal care, females will gain no further fitness from any reproduction after the age of eight years.

Thus reproductive senescence will inevitably precede somatic senescence, and the reproductive decline should begin earliest in species with the longest periods of infant dependency. Data on the lions and baboons are roughly consistent with this notion: lion cubs suffer extensive mortality if they are orphaned before the age of one year and the median life expectancy of a 14-year-old female is only 1.8 years. Baboons suffer excess mortality if they are orphaned any time before two years, and the life expectancy of a 21-year-old baboon is 5.0 years.

Can this pattern account for the timing of menopause in our own species? Reproductive decline in women is pronounced by the age of 40, and data from several non-technological societies shows that 40 year-old women have an average life expectancy of approximately 18–25 years (Hill and Hurtado 1991). This is precisely the timing that would be predicted by extrapolation from the lion and baboon data if the period of human infant dependency is 10 years (Fig. 6).

### LIONS



### BABOONS

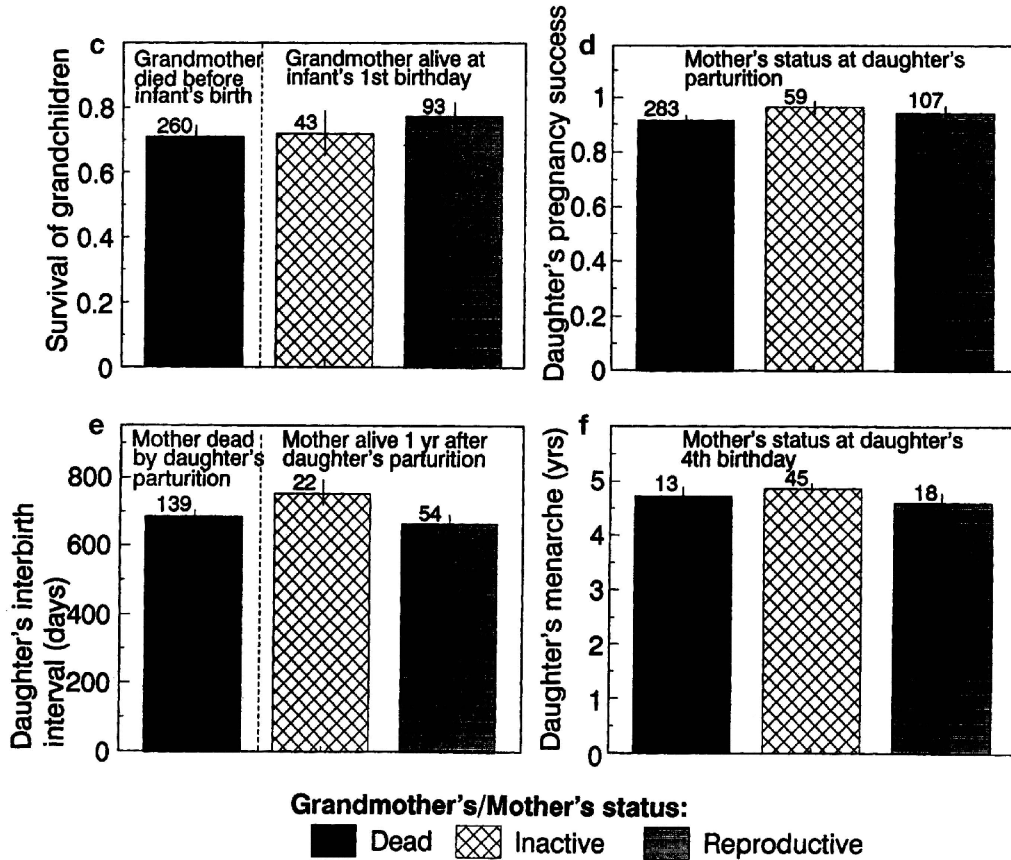


Fig. 3. Effects of female survival and reproduction on descendants' productivity. Females were "inactive" if they had not reproduced during the prior year and for six months thereafter; otherwise they were "reproductive." For lions: a, Proportion of grandchildren in each litter that survived to one year (\*\* =  $p < 0.01$ ). b, Daughters' average litter size. For baboons: c, Proportion of infant grandchildren that survived to one year. d, Proportion of daughters' pregnancies that reached full term. e, Interval from birth of surviving grandchild until the next live birth. f, Age at which daughters reached menarche. The only significant effect was in lions, where grandchildren of reproductively active grandmothers enjoyed higher survival

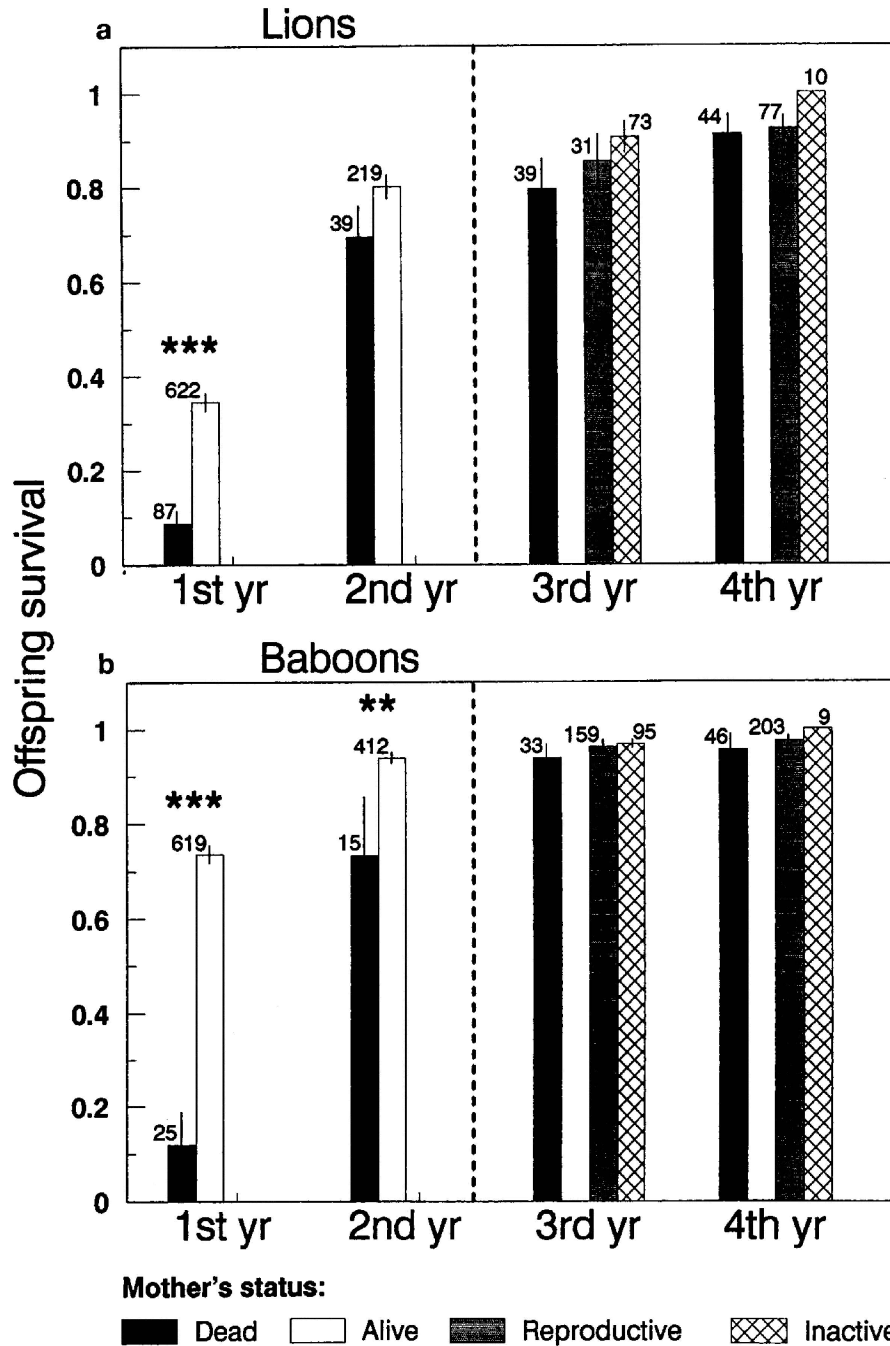


Fig. 4. Effects of female survival and subsequent reproduction on offspring survival in a, lions and b, baboons. Survival was significantly lower for animals orphaned during their first year in both species and during the second year in baboons. The typical interbirth interval for both species is two years (represented by the vertical lines), so effects of subsequent reproduction could only be measured in older juveniles. Mothers who gave birth before their prior offspring's second birthday were "reproductive" for the juvenile's third year, otherwise they were "inactive." Juvenile survival was not influenced by the mothers' reproduction. (\*\* =  $p < 0.001$ ; \*\*\* =  $p < 0.000$ )

**TIMING OF SENESENCE**

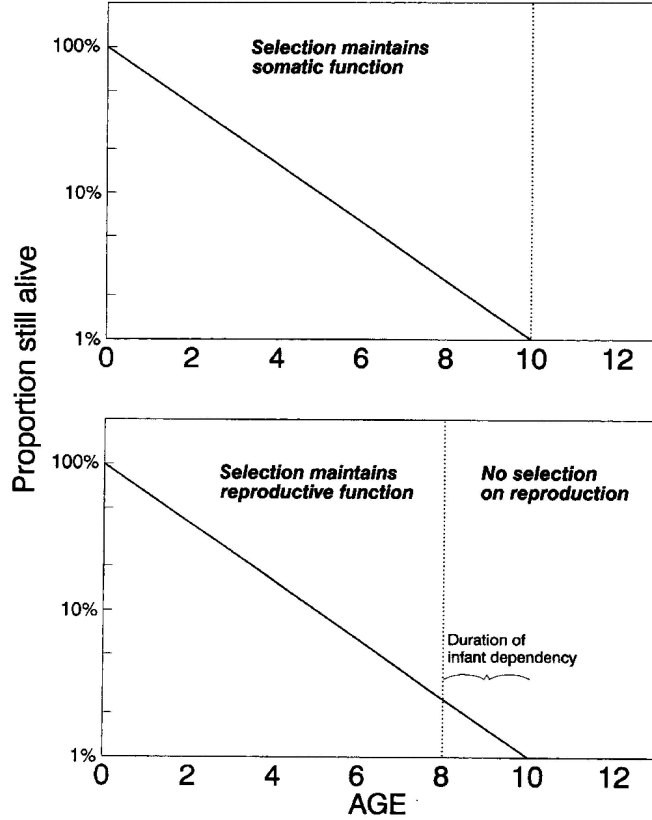


Fig. 5. Idealized survival curves for a hypothetical species with constant mortality such that only 1% of individuals survive to the age of 10 years. The duration of infant dependency is two years

Discussions of the human menopause often confound the *existence* of menopause with the *timing* of menopause. Reproductive cessation is a fundamental feature of mammalian females; any hominid ancestor who lived long enough would have experienced reproductive senescence. Thus, models of adaptive menopause should not center on *whether* women undergo reproductive cessation but *when*. Humans show prolonged periods of infant dependency, but is the effect of being orphaned at 10 years of age really strong enough to account for a midlife menopause as we have plotted in Figure 6? Are we even correct in assuming that human menopause occurs in the middle of the life span? The survival curves of contemporary non-industrial societies may bear little resemblance to life in a pre-technological world. We have no idea what percentage of stone-age 40-year-olds ever experienced menopause – let alone reached 58–65 years of age.

Regardless of the precise demography of our ancestors, women certainly differ from most other mammalian females in their relatively rapid reproductive rates. A woman's interbirth interval is far shorter than the duration of infant dependency, thus she may often have to divide her care among an age-graded brood of offspring. If parturition becomes sufficiently hazardous with increasing maternal age, menopause could theoretically improve a woman's lifetime fitness



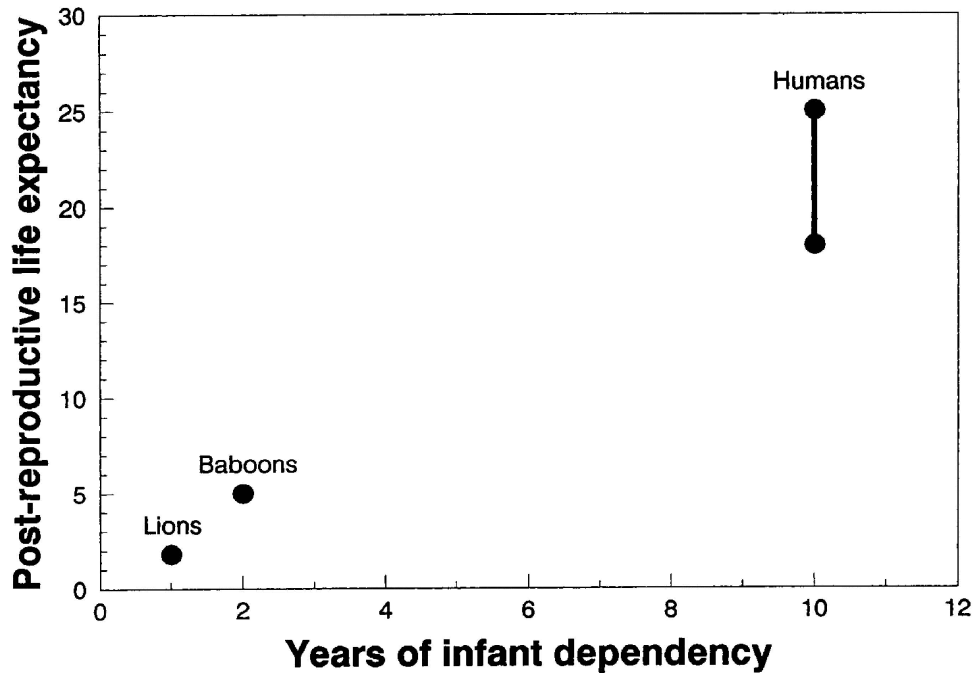


Fig. 6. Observed relationship in lions and baboons between the duration of infant dependency and the median life expectancy at the onset of reproductive decline. Values for humans assume a 10-year period of infant dependency and are extrapolated as follows: for baboons (life expectancy at the onset of reproductive decline) / (duration of infant dependency) = 5.0 years/2 years = 2.5; for lions, 1.8 years/1 year = 1.8

(Williams 1957; Rogers 1993). However, if this idea is correct, women always undergo menopause before reaching the presumed age of high-risk childbirth, and thus the risks of late-aged pregnancy cannot be measured. How can this hypothesis ever be tested?

Menopause results from the loss of ovarian function (Wise et al. 1996); the success of *in vitro* fertilization depends on the age of the donor rather than of the recipient (Stolwijk et al. 1997). Post-menopausal women can be impregnated artificially, and this procedure provides an experimental population in their 50s and 60s. Although these are wealthy women with access to the most advanced forms of obstetrical care, any measure of their health during pregnancy would be very valuable.

It should be noted, however, that the “risk of pregnancy” hypothesis ultimately depends on patterns of senescence: aging women are presumed to be increasingly vulnerable to the rigors of childbirth. Thus any “advantages” of menopause would merely reinforce the pattern of reproductive senescence illustrated by Fig. 5. Indeed, newspaper accounts of post-menopausal pregnancies largely focussed on whether these women would be able to cope with the rigors of raising teenaged children.

The “grannie effect” might also accelerate the human menopause: if women typically reach middle age soon after their firstborn offspring have started pro-

ducing grandchildren, the grandmother might leave more descendants if she helped her adult children rather than tried to continue breeding herself. In its most extreme form, this argument has been proposed as the sole explanation for menopause, but it is difficult to accept on at least two grounds.

First, most helping behavior is facultative in social vertebrates: yearling birds generally remain as “helpers at the nest” only when they lack breeding opportunities themselves (see Stacey and Koenig 1990). Why should women be “hard-wired” to stop reproduction when they may reach middle age without any adult offspring? In fact, menopause occurs at significantly younger ages in women who have never had children (van Noord et al. 1997). A grannie-related menopause should show precisely the opposite pattern.

Second, in many social species, adults coerce their offspring into acting as helpers. In several carnivores and non-human primates, the social unit consists of an adult breeding pair and their mature offspring. If there is reproductive suppression within the group, the dominant pair always suppresses the subordinates. Why would middle-aged matriarchs forego their own breeding opportunities in favor of their sons and daughters? According to kinship theory, a matriarch would have to raise an additional two grandchildren for every child she “lost” through an early menopause.

The “grannie hypothesis” is most plausible if we again assume some underlying level of senescence. As aging women become less able to raise their own offspring, they might eventually reach a point where they are better off directing their remaining energies toward grandchildren. This idea is presented graphically in Figure 7. A woman’s own reproductive rate is assumed to decline after the age of 40, whereas there is a more gradual decline in the number of *additional* surviving grandchildren that would be produced through intensive grandmaternal care. Although a woman might never enhance her children’s reproduction sufficiently to overcome the costs of menopause during her prime years, her personal rate of reproduction might eventually decline below her impact on the production of grandchildren – at which point menopause would finally be favored.

Thus if a “grannie effect” were particularly important in human evolution, we might expect women to show a more precipitous decline in reproductive performance than females in other species (with the onset of reproductive decline still being set by the duration of infant dependency, as in Fig. 5). However, the rate of decline in human reproduction is very similar to patterns in lions and baboons (Fig. 1 b,d), suggesting that the human menopause may not be that different from other species after all.

A more rigorous test of this idea could be performed by tracking women’s competence as mothers and as grandmothers through their 30s and 40s to see if maternal competency decreases more rapidly than their proficiency as grandmothers (as assumed in Fig. 7). But the key test (as we performed in Fig. 3) will be to determine whether women are ineffective grandmothers when they are trying to raise their own infants. Unless there is a trade-off between maternal care and grandmaternal care, there would be no reason for women to stop reproduction.

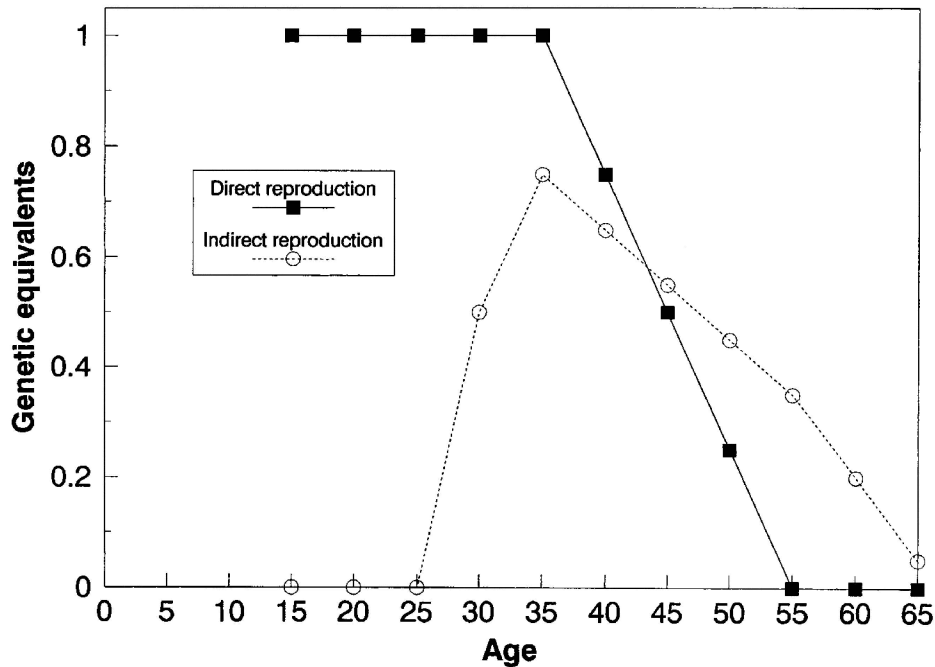


Fig. 7. Hypothetical age changes in a female's ability to produce surviving offspring ("direct reproduction") or surviving grandchildren ("indirect reproduction"). Units of "genetic equivalents" are arbitrary, but a female must help her sons and/or daughters raise an additional two grandchildren to have the same genetic equivalent as one offspring of her own. Maternal productivity is assumed to decline at a constant rate from the age of 40. A female's capacity for indirect reproduction depends on the maturation of her firstborn offspring and then declines with advancing age. As drawn here, indirect reproduction exceeds direct reproduction at 45 years

Does any of this matter? Unlike the most extreme rendering of the reproductive senescence hypothesis, our view suggests that women are adapted to survive menopause – but not for long. To many modern women, menopause is an unremitting biological clock that limits the age at which they can start a family. For women who started their families much earlier, reproductive senescence may enforce a more exclusive interest in grandchildren, but as one of my friends in her 50s once put it to me, "The great thing about grandchildren is that their parents take them home when you get tired!"

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