2

Reproductive conflict and the evolution of menopause

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Summary

Human females (*Homo sapiens*) exhibit a dramatic form of reproductive skew in which half the age classes of adults contain only nonbreeders. Among other mammals, only pilot (*Globicephala spp.*) and killer whales (*Orcinus orca*) exhibit a similar pattern. The "grandmother" hypothesis suggests that selection can favor post-reproductive survival because older females help their offspring to reproduce. But the indirect fitness gains of helping appear insufficient to outweigh the potential benefits of continued direct reproduction, so this hypothesis cannot explain why women cease reproducing in the first place. Here we present some background on menopause and describe new research which helps to understand both the strange taxonomic distribution of menopause and the timing of reproductive cessation in humans. Specifically, recent models have explored the potential reproductive conflicts that may have arisen in ancestral human families, and the influence of demography on the resolution of such conflicts. These studies suggest that an integrated model which takes into account the potential costs of reproductive competition, as well as the benefits of helping, offers a fuller understanding of the evolution of menopause.

> *Tabar ne maiet hate kana jane bakariyon, lardiyon jyoon!* (How unbecoming of parents to procreate alongside their children like goats and sheep!)
> Saying of the Mogra, Rajasthan, India (quoted in Patel 1994)

Reproductive Skew in Vertebrates: Proximate and Ultimate Causes, ed. Reinmar Hager and Clara B. Jones. Published by Cambridge University Press.

Reproductive skew in human societies

Human societies are characterized by a dramatic and puzzling pattern of reproductive skew. In populations exposed to natural schedules of mortality and fertility (i.e. without access to modern medicine and technology), almost half the age classes of adult human females contain only non-breeders (Figure 2.1). The mean ages at which women give birth to their last child in natural-fertility populations cluster around 39 years (Wood 1994, p. 442), but even in hunter–gatherer societies that lack modern medicine women who reach this age can expect to live well into their sixties (Pennington 2001, Blurton Jones *et al.* 2002). The restriction of reproduction to certain age classes is not in itself unusual for a cooperative vertebrate, but in other species it is almost always older females who breed and younger females who do not (Emlen 1991, 1995). The reverse pattern exhibited by humans is extremely rare – among vertebrates only killer whales and pilot whales are reported to exhibit a similar reversal of breeding roles with respect to age class (Marsh & Kasuya 1986, Olesiuk *et al.* 1990, Whitehead & Mann 2000). Early reproductive cessation represents an evolutionary puzzle because standard life-history theory suggests that there should be no selection for somatic

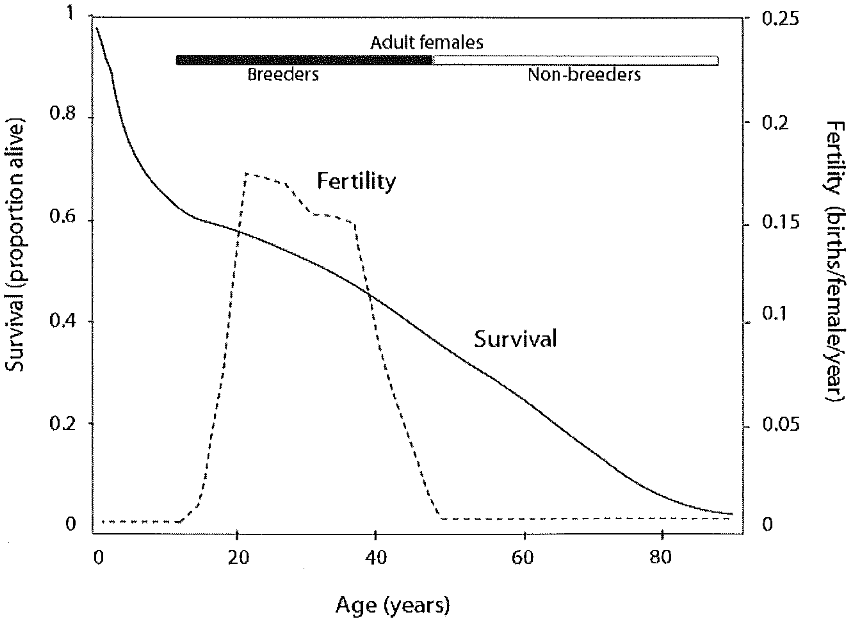

Figure 2.1 Survival and fecundity in a natural-fertility human population. Data from a Taiwanese population in 1906 (redrawn from Hamilton 1966).

maintenance after the end of reproduction. Why then do women cease reproducing so long before they die?

Despite almost 50 years of research on the evolution of menopause, this important question remains open. Current models invoke the kin-selected benefits of helping as a grandmother to explain post-reproductive survival in women, but, as we describe below, quantitative analyses suggest that these models cannot explain why women stop breeding at the time they do. Part of the problem is that current models focus solely on the direct fitness consequences of reproduction, and compare this with the indirect fitness consequences of helping. Helping is assumed to affect the fitness of other group members, while breeding is not. This approach is one-sided because it ignores the potential impact of reproduction on the fitness of other group members. Where there are limited resources within a group for reproduction, the decision to reproduce will depend on whether other females in the group will also reproduce, how many young they will produce, and how one's own young will fare in competition if they do. Reproduction in a social context, therefore, is a game-theoretic rather than an optimization problem. Reproductive skew theory was developed to study exactly this type of problem, and so is an apt framework within which to study the evolution of patterns of reproduction in humans.

In this chapter we take a fresh look at the puzzle of menopause by examining the potential reproductive conflicts in ancestral human societies, and the way in which these conflicts are likely to be resolved. We first review the main adaptive explanations for menopause, the "mother" and "grandmother" hypotheses, and highlight the empirical and theoretical difficulties that these hypotheses have encountered. We then describe results from our own recent research, which focuses on the impact of demography on kin selection across individual lifespans, and how this will affect the resolution of conflicts over reproduction within human social groups. Our aim is to show that these new models offer a fuller explanation for the pattern and timing of reproductive cessation in humans, and help to explain why, of all long-lived, social mammals, it is specifically among the lineages of great apes and toothed whales that menopause has evolved.

How old is menopause?

A possible non-adaptive explanation for menopause is that it is a simple artifact of the reduction in mortality that followed agriculture and improved sanitation (reviewed by Peccei, 2001a, 2001b). The idea is that the reproductive lifespan of women reflects the expected female lifespan prior to these technological developments, but there has been insufficient time for selection to extend the reproductive period to match the newly elongated lifespan. If this hypothesis were correct, menopause should be absent in hunter–gatherer populations without agriculture or modern medicine because women would rarely survive beyond the age of 50. On the contrary, in the three best-studied hunter–gatherers (the !Kung of the Kalahari, Ache of Paraguay, and Hadza of Tanzania) a large fraction of women survive to post-menopausal age. For example, 64% of non-nomadic !Kung, 46% of Hadza, and 42% of Ache women live until age 50 or more (Pennington 2001). Moreover, women who survive to 45 can expect an average of 20 or more years of life thereafter (Pennington 2001, Blurton Jones *et al.* 2002). A pattern of menopause coupled with prolonged post-reproductive life can be inferred from ancient texts: the Bible (Psalms 90: 10) refers to an expected lifespan of 70 (the familiar "threescore years and ten"), rising to 80 years "by reason of strength", while Aristotle (*c.* 360 BC) and Pliny (*c.* AD 77) cite an age at menopause of around 50 years (Amundsen & Diers 1970). Finally, a recent analysis of fossil molar wear (Caspari & Lee 2004) suggests that the fraction of humans surviving to become grandparents increased five-fold between the Middle and Upper Paleolithic (*c.* 300 000–10 000 years ago), i.e. before the emergence of agriculture. The evidence suggests, therefore, that menopause has been a feature of the life history of human females for at least the last 10 000 or 20 000 years, and possibly much longer.

Reproductive senescence

Menopause is best viewed as the endpoint of unusually rapid *senescence* of the reproductive system relative to somatic systems. Senescence, the general decline in efficiency of bodily functions with age, is an inescapable property of both somatic and reproductive systems in iteroparous organisms. This is because random mortality ensures that older individuals always make up a smaller fraction of the breeding population than younger individuals, so genes which have negative effects on reproduction or survival early in life are more strongly opposed by selection than are genes with negative effects later in life (Medawar 1952, Williams 1957, Hamilton 1966). In theory, senescent decline should strike all body functions at a similar rate, since if one system or organ (for example, the cardiovascular system, or the renal system) declined much more rapidly than others, selection to maintain other systems would weaken, accelerating their rate of decline to match that of the most rapidly senescent (Williams 1957). Consequently, the capacity for reproduction is predicted to decline in tandem with, and at a similar rate to, other somatic systems. In most organisms this expectation is borne out: fertility in old age, like other functions, is much reduced but reproduction is nevertheless still possible (Rose 1991). What in humans (and some whales) could cause the rate of reproductive senescence to become decoupled from the rate of somatic senescence?

To answer this question it is not sufficient to invoke the personal costs of breeding at late ages, since these costs are themselves an evolved property of the system. Increases in, say, the rate of birth defects, or stillbirth, that occur after the age of 40 in humans are a result of, rather than a cause of, the rapid senescence of the reproductive system. Menopause marks the end of a process of rapid reproductive senescence that begins a decade earlier, and one must be careful not to invoke the effects of this rapid senescence in order to explain it. Rather, we need to consider the potential benefits of early reproductive cessation in an ancestral, non-menopausal hominid species in which fertility declined at the same rate as other bodily functions.

Adaptive explanations

Two closely related adaptive explanations for the evolution of menopause are known as the "mother" and "grandmother" hypotheses. These hypotheses differ primarily in whether menopause is assumed to boost the survival or the fertility of existing young. Williams (1957) suggested that early reproductive cessation is a consequence of the long period of offspring dependency in humans. According to this hypothesis, older women may at some point gain from ceasing reproduction to invest in raising their existing children to adulthood, rather than engaging in increasingly risky breeding attempts which could leave their dependent offspring motherless (Peccei 2001a, 2001b). By contrast, other authors have emphasized the benefits of menopause for enhancing the fertility of a woman's existing children (Hamilton 1966, Alexander 1974, Hawkes *et al.* 1998). An older woman whose fertility is declining due to senescence may at some point do best to switch resources from her own breeding attempts to helping to rear grandchildren. In both cases, beyond the age at which helping is more profitable than breeding there is no selection to maintain fertility, and the rate of senescence of the reproductive system is expected to increase sharply. The result is a decoupling of the rates of somatic and reproductive senescence, and a pattern of reproductive cessation long before death.

Empirical data offer little support for the mother hypothesis. The chance of dying in childbirth must be very large for females to prefer reproductive cessation over continued reproduction. We can illustrate this with a simple numerical example. Consider a female at age 40 with four dependent offspring, faced with a decision of whether to cease reproduction or produce one more child. Let d be the chance that she dies in childbirth, which we will assume leads to the certain death of all her existing young. In this example, reproductive cessation will be favored over continued breeding if $4 > 5(1 - d)$, or $d > 20\%$. In reality, the chance of dying in childbirth is minuscule even among hunter–gatherers (e.g. around 1/150 in the Ache: Hill & Hurtado 1996). Data from the United States in the late nineteenth and early twentieth centuries suggest that even for mothers who gave birth at age 45–50, the risk of dying in childbirth was around 5% (Loudon 1993). Quantitative analyses using data from natural-fertility populations have concluded that the risk of death in childbirth is far too small to account for the evolution of menopause (Rogers 1993, Hill & Hurtado 1996). It is tempting to invoke other factors which might devalue late-life reproduction, such as elevated rates of fetal wastage and birth defects, but again it is important to remember that these factors are themselves the outcome of selection for rapid reproductive senescence.

Investigations of the grandmother hypothesis are more numerous (see Voland *et al.* 2005). Data from modern hunter–gatherers and historical populations provide evidence that grandmothers can indeed boost the reproductive success of their children. Significant positive effects of grandmothers on grandchild survival have been reported in six out of seven studies of grandmothering in pre-medical societies (Lahdenperä *et al.* 2004a, 2004b, Mace & Sear 2005). However, while these studies demonstrate a potential kin-selected benefit of grandmotherhood, quantitative analyses suggest that these benefits are not sufficiently large to explain the evolutionary maintenance of menopause at the age at which it occurs (Rogers 1993, Hill & Hurtado 1996). Hill & Hurtado (1991, 1996), for example, use data from one well-studied hunter–gatherer society (the Ache of Paraguay) to calculate the inclusive fitness payoffs of grandmothering versus continued reproduction for older women. To estimate the latter payoff they assume that in the absence of menopause fertility would decline at the same rate as somatic function. Their calculations suggest that menopause cannot be favored by kin selection in this population because there are few close kin alive for an older woman to help, and because her help has too little impact on the survival or reproduction of these kin. Rogers (1993) uses a different model and dataset (the Taiwan 1906 data used in Hamilton's [1966] classic paper on senescence) but shows a similar result, namely that the impact of an older woman's help on her close kin must be more substantial than has been so far documented for menopause to be favored by kin selection.

Recently, however, Shanley & Kirkwood (2001) presented a model which they claim can account for the evolution of menopause around the age of 50 or 55, again using the Taiwan 1906 dataset. Unfortunately, their model uses the intrinsic rate of increase of the population as the measure of fitness to be maximized by natural selection. This means that offspring and grandoffspring are counted as equally "valuable" to an older female faced with the decision of whether to continue reproduction versus help as a grandmother. As Hamilton (1966) demonstrated, selection for helping versus breeding will depend not only on the number of young produced as a result of helping or breeding, but on the relatedness to these offspring. A mother's relatedness to her own offspring is twice that to her grandoffspring, so the fitness payoff of helping to raise an extra grandchild is, other things being equal, half that of producing another child herself. Shanley & Kirkwood's (2001) model does not take into account relatedness, and so overestimates the fitness benefits of grandmothering by a factor of around two compared to the analyses of Hill & Hurtado (1996) and Rogers (1993). This may explain why Shanley & Kirkwood's analysis can account for the evolution of menopause at around 50 whereas the other analyses cannot.

Physiological constraints and phylogenetic inertia

While women can clearly gain fitness benefits by grandmothering, these fitness benefits are insufficient to account for the timing of reproductive cessation in human women or the evolution of menopause. The problems raised by these quantitative studies can be circumvented, however, if we assume that timing of menopause is a phylogenetic artifact or reflects some form of physiological constraint. Hawkes and co-workers (Hawkes *et al.* 1998, Hawkes 2003) note that the endpoint of reproductive senescence in human females occurs at the same age as in chimpanzees (*Pan troglodytes*), i.e. in the fifth decade of life. Consequently, they argue, it is the extended post-reproductive life of human females, not the timing of menopause, that is the derived trait to be explained (Hawkes *et al.* 1998). Grandmothering effects are invoked to explain the extension of the female lifespan long past the end of the phylogenetically conserved age at reproductive cessation (why males have similarly extended lifespans is not explained by this hypothesis, but see Marlowe [2000] for one perspective).

This argument is unsatisfactory on its own because it assumes that stasis in the face of evolutionary change requires no special explanation. The conservation of patterns of reproductive senescence in the human lineage, despite lengthening lifespan, implies: (1) some physical or physiological constraint prohibiting evolutionary change; (2) an absence of genetic variation upon which selection can act; or (3) some form of stabilizing selection. Comparative evidence lends no support to the first possibility, i.e. that the reproductive lifespan of human females cannot be extended much past the age of 50 due to physiological constraints. Other long-lived mammals continue to breed until the end of life: African elephants (*Loxodonta africana*) reproduce in their sixties (Moss 2001) and blue whales (*Balaenoptera musculus*) into their nineties (Mizroch 1981). Across species, oocyte stocks are evolutionarily labile and are adjusted to lifespan and body weight (Gosden & Telfer 1987). In addition, the initial oocyte stock and rate of follicular attrition in human females is commensurate with a longer reproductive lifespan, but at around the age of 40 there is a marked increase in the follicular hazard rate so that by age 50 follicle stocks have dropped below a minimum required to sustain menstrual activity (Faddy *et al.* 1992, Faddy & Gosden 1996, Figure 2.2). By contrast, in laboratory rodents and rhesus macaques (*Macaca mulatta*) (the only other species for which similar data are available), there is no indication that the rate of follicular attrition increases later in life (Jones & Krohn 1961, Nichols *et al.* 2005).

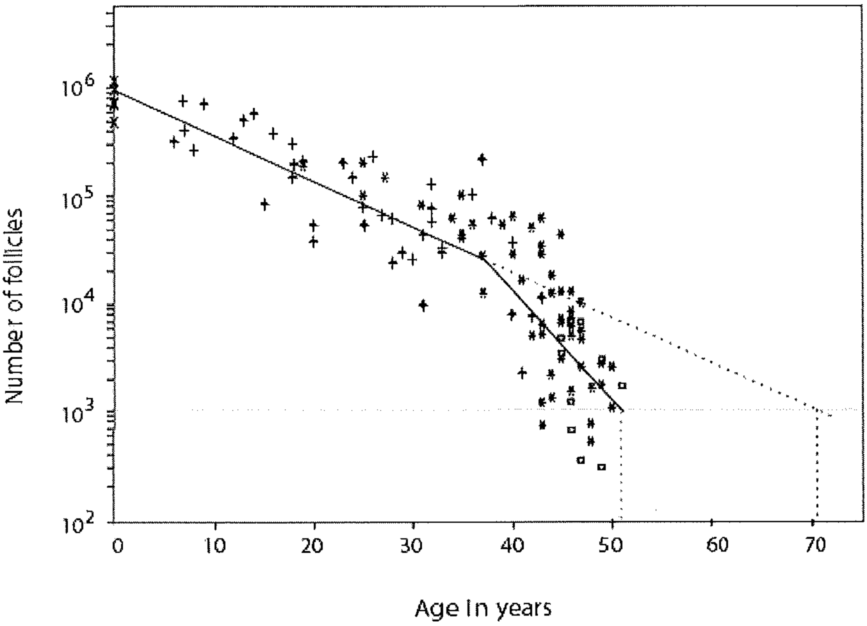

Figure 2.2 The bi-phasic model of declining follicle numbers in pairs of human ovaries from neonatal age to 51 years old (modified from Faddy *et al.* 1992). Data are from four different autopsy studies. Note the logarithmic scale on the *y*-axis. A bi-exponential regression model offers a significantly better fit to the data than a single exponential regression. Follicle numbers decline at a constant exponential rate from birth until reaching a critical figure of around 25 000 at age 37.5 years, after which the exponential rate parameter increases in magnitude. Menopause occurs on average when a threshold of around 1000 follicles remain (Faddy *et al.* 1992).

Turning to the second possibility, age at menopause varies widely among individuals (with ages between 40 and 59 considered normal in both modern and natural-fertility populations), and estimates of the heritability of age at menopause range from 40% to 63% (Snieder *et al.* 1998, Peccei 1999). There would thus seem to be sufficient genetic variation on which natural selection could act, if prolonged fertility were advantageous. Moreover, recent evidence from a pre-industrial Finnish population (Figures 2.3, 2.4) suggests that prolonged reproduction can have a substantial positive influence on a woman's fitness (Helle *et al.* 2005), and that age at last reproduction is also highly heritable (Pettay *et al.* 2005). Taken together, this evidence suggests that any selection to extend the female's reproductive span has been held in check by some form of opposing selection. Indeed, Hawkes (2003, p. 389) reaches a similar conclusion:

> Overall then, the available data on ages at last birth and menopause in chimpanzees show age-specific fertility declines in that species not substantially different from our own. Mammalian fertility, however, can extend to much older ages than it does in humans. This evidence is consistent with the argument that ancestral age-specific fertility declines have been maintained in our lineage, perhaps conserved by stabilizing selection.

Figure 2.3 Extended Lummaa family from nineteenth-century Finland showing several generations. Courtesy of Virpi Lummaa.

Figure 2.4 Photo of nineteenth-century nuclear Lummaa family from Finland with mother, father and all their children. Courtesy of Virpi Lummaa.

This stabilizing selection means that mutations for a later age at menopause must have been selected against, despite selection for a longer lifespan. We are thus back to our initial question: what is the nature of this selection? Why has the reproductive lifespan of human females not increased in line with their longevity, as it has in other long-lived mammals?

Reproductive competition: a new perspective on menopause

We believe that previous models offer an incomplete account of the evolution of menopause because they focus solely on the kin-selected benefits of parenting and helping, and ignore the potential kin-selected costs of co-breeding. Conflict over reproduction in animal societies is expected wherever communal resources are used for the production of offspring, particularly where helpers increase the success if group members and breeders compete for monopolization of those helpers. If two females produce young in the same group at the same time, each offspring will necessarily receive less food (unless twice as much food, or help, is available). Per capita success of young in a communal brood will therefore decrease with the number of young produced, as assumed in standard clutch-size theory (Lack 1947, Cant 1998, Cant & Johnstone 1999). Reproductive conflict is ubiquitous in other cooperative breeders in which there is more than one potential breeder per social group (Keller & Reeve 1994, Clutton-Brock 1998, Beekman *et al.* 2003, Ratnieks *et al.* 2006). Unlike other cooperative breeders, however, the possibility of reproductive competition in ancestral human families has been ignored.

Recently, we have argued that the pattern and timing of reproductive cessation in humans is best understood as an adaptation to minimize the degree of reproductive competition between generations (Cant & Johnstone 2008). Certainly one of the consequences of the mean age at reproductive cessation in humans is that it leads to very low reproductive overlap between generations. Many primate species exhibit a post-reproductive lifespan, but there is nevertheless considerable overlap in the period for which females of older and younger generations are reproductively active. Figure 2.5A shows, for those primate species classified as exhibiting a post-reproductive lifespan (Cohen 2004), the relationship between generational overlap (calculated as the proportional overlap between the maximum lifespans of mother and daughter) and reproductive overlap (calculated as the proportional overlap between the mean reproductive spans of mother and daughter). Humans are not unusual in respect of their degree of generational overlap (77%, compared to 71% for chimpanzees, *Pan troglodytes*, and 73% for gorillas, *Gorilla gorilla*). However, they show an extraordinarily low degree of maximum reproductive overlap compared to other primates (30%, compared to 50% or more for all other species in the sample), far lower than would be expected on the basis of their generational overlap. On average, females from one generation stop breeding at just the time that the females in the next generation start to reproduce (Cant & Johnstone 2008; Figure 2.5B). If we used the regression line shown in Figure 2.5A to "reverse-engineer" the reproductive lifespan of human females, we would predict a mean age at last birth of 62, followed by menopause around 10 years later – an intriguing match to the predicted age at menopause obtained by extrapolating the constant rate of follicular attrition before the age of 40 (Figure 2.2).

If the pattern of rapid reproductive senescence leading to low reproductive overlap in humans is a response to reproductive competition, why do none of the other primate species in Figure 2.5 show similar adaptations to the costs of co-breeding? Reproductive competition is expected where breeding resources are communal or the need for helpers is important and helpers are limiting.

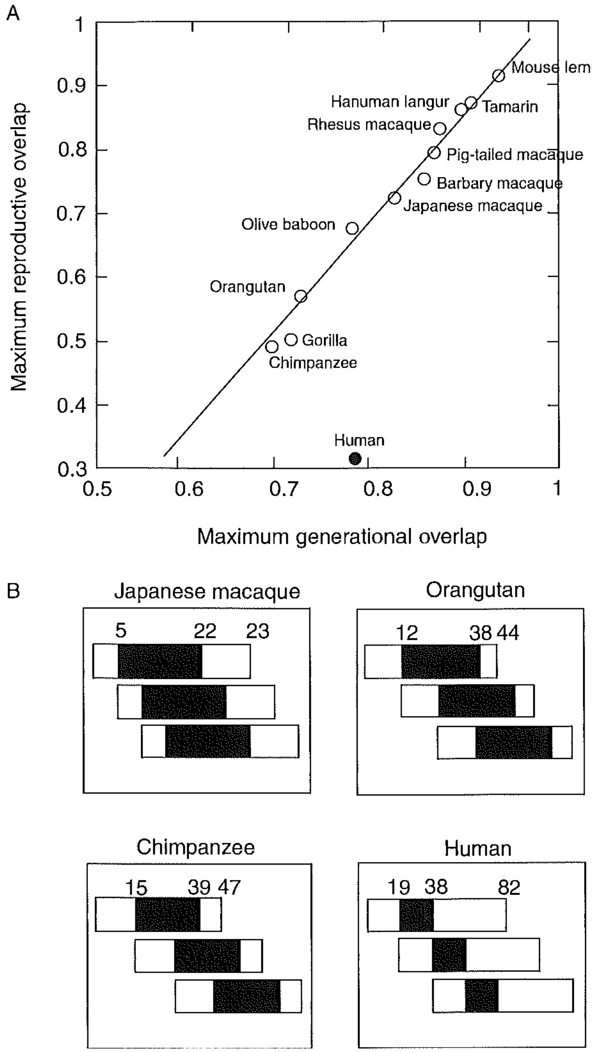

Figure 2.5 Patterns of reproductive overlap in 12 primate species recently classed as exhibiting a post-reproductive lifespan (Cant & Johnstone 2008). Panel A shows maximum reproductive overlap versus maximum generational overlap. Maximum generational overlap is defined as (*MLS* – *AFB*)/*MLS*, where *AFB* is average age at first birth and *MLS* is maximum recorded lifespan. Maximum reproductive overlap is defined as (*MRS* – *AFB*)/*MRS*, where *MRS* is the maximum reproductive span, calculated as maximum age at last birth (*MALB*) minus *AFB*. For four species (chimpanzees, orangutans, Japanese macaques, and humans), published data are sufficiently detailed to calculate average reproductive overlap, defined as (*ARS* – *AFB*)/*ARS*, where *ARS* is the average reproductive span (i.e. mean *ALB* minus *AFB*). Panel B summarizes the pattern of overlap for these four species. For each, horizontal bars represent the maximum lifespans of three successive generations, scaled to a standard length and offset in accordance with the value of *AFB* relative to *MLS*, with average reproductive spans shaded. The average reproductive overlap values for Japanese macaques, orangutans and chimpanzees were 0.71, 0.52, and 0.39 respectively, compared to an average reproductive overlap for humans of 0.00. For reference sources and values used to plot the figure see Cant & Johnstone (2008).

Compared to most other primates, such competition will be particularly intense in humans because they exhibit a unique degree of food sharing, and are cooperative breeders, in the sense that adults other than parents make important contributions to raising offspring (Emlen 1991, Mace & Sear 2005). In most other primates mothers look after their own young in the early years of life, provisioning them with milk during infancy, and helping them to gain experience in finding their own food – usually fruits and other plant matter. Mothers and their offspring are not reliant on shared food resources obtained by adult helpers, so co-breeders are likely to have little direct impact on each other's reproductive success. Humans, by contrast, provision their children into adulthood and parents rely on the other group members to gather food. Food acquisition is divided between family members on the basis of sex and age class, and food collected or hunted by different group members is combined into a shared resource (Kaplan & Hill 1985, Gurven *et al.* 2004, Gurven 2005). Additional offspring within the same family will therefore draw on the same communal resource pool. Unless the presence of an extra female breeder somehow generates twice as much food for the group, co-breeding females will have fewer resources with which to raise their children than a female who is able to monopolize reproduction within the group.

Unfortunately, the reproductive separation of generations in humans is so pronounced that it is difficult to obtain direct data on the costs of co-breeding. For example, in the natural-fertility Gambian dataset (for which data were collected between 1950 and 1974), only 5.6% of children (89/1588) had a reproductively active maternal grandmother when they were born, and there were no children born who had a reproductively active paternal grandmother (Sear *et al.* 2000); similar patterns also occur in pre-modern Western populations (V. Lummaa, personal communication). In many societies the reproductive separation of generations is further reinforced by cultural taboos. Among the Nyakyusa of Tanzania and some West African populations, women are required to stop breeding as soon as their first grandchild is born (Wilson 1957 p. 137, Cavalli-Sforza 1983), and similar proscriptions are found in some Asian societies (Patel 1994 p. 162 [quote at head of this chapter], Islam & Yadava 1997, Skinner, 2004). Though there are almost no data on the costs of co-breeding between generations, we can get some insight into the potential costs of co-breeding within a single family by examining offspring success under polygyny. Women in polygynous marriages (i.e. marriages in which two or more women are married to a single man) are on average less fertile than their monogamous counterparts (Isaac & Feinberg 1982, Pebley & Mbuga 1989). A large dataset from six West African countries suggests that, after controlling for socioeconomic and demographic factors, polygyny is associated with a 50%

increase in neonatal mortality, and a doubling of post-neonatal child mortality (Amey 2002). These costs of polygyny to children have been attributed to crowding and disease transmission (Isaac & Feinberg 1982, Roth & Kurup 1988) and to reduced access to resources (Strassmann 1997) - two factors that would also apply to co-breeding between generations.

While co-breeding is likely to involve costs, it remains puzzling why older women should choose to cease reproduction in the face of competition from younger women. In other animals, when two or more generations of females are present in a social group it is almost always older females that "win" the conflict over reproduction and retain breeding status, while younger females remain in the group as reproductively suppressed helpers. Why should humans be different? A critical factor is the unusual demography of humans (Cant & Johnstone 2008, Johnstone & Cant 2008). A "kinship dynamics" model suggests that the unusual dispersal and mating patterns of great apes, and some cetaceans, predispose these species to the evolution of early reproductive cessation and late-life helping behavior, in contrast to the majority of other mammalian species (Johnstone & Cant 2008). Moreover, relatedness asymmetries that arise as a result of demography are predicted to give younger females a decisive advantage in reproductive conflict with older females (Cant & Johnstone 2008). Analyses that incorporate demography can therefore help to explain both the unusual taxonomic distribution of menopause and the timing of reproductive cessation in humans, as we describe below.

Demography and kin selection across the lifespan

Demography is important to consider in a model of menopause because the relatedness between a female and other breeders in her group can change as she ages, thereby affecting the strength of kin selection for acts such as helping or early reproductive cessation. Building on the infinite-island modeling framework (Wright 1931, Taylor 1992), Johnstone & Cant (2008) construct a general model of "kinship dynamics" to explore the impact of sex-biased dispersal and intra- versus extra-group mating on the strength of kin selection across the lifespan. They derive general formulae which track the changes in genetic similarity between males, females, and offspring in a local group (or "island") as some individuals disperse, and others die and are replaced. These patterns of relatedness are then used to determine how the strength of kin selection across the lifespan varies for eight representative patterns of demography, which differ as to whether dispersal is male- or female-biased, and whether mating occurs locally or outside the group.

The results indicate that where dispersal is male-biased and mating occurs locally, the average relatedness of a female to the offspring produced in her local group decreases as she ages (Figure 2.6A). In these circumstances acts which benefit relatives, such as helping or reproductive restraint, are favored more strongly earlier rather than later in life. By contrast, female-biased dispersal and local mating leads to an increase with age in the average relatedness of a female to the offspring produced in her local group (Figure 2.6B). This effect arises under female-biased dispersal because a female's relatedness to local male breeders, initially low, increases as her sons mature and remain in the group (relatedness among local female breeders, by contrast, starts low and remains low because daughters disperse). In these circumstances acts which benefit other group members are favored later, rather than earlier in life. Female-biased dispersal, therefore, predisposes females to early reproductive cessation and late-life helping.

Most social mammals exhibit male-biased dispersal and female philopatry (Greenwood 1980, Pusey & Packer 1987, Clutton-Brock 1998, Lawson Handley & Perrin 2007). By contrast, three lines of evidence suggest that the evolutionary history of *Homo* has been characterized by female-biased dispersal and male philopatry. First, our closest primate relatives, chimpanzees, bonobos (*Pan paniscus*), and gorillas, are unusual among primates because they exhibit female-biased dispersal, and male dispersal is rare (Pusey *et al.* 1997, Boesch & Boesch-Ackermann 2000, Nishida *et al.* 2003, Stokes *et al.* 2003, Yamigawa & Kahekwa 2004, Eriksson *et al.* 2006). Second, patterns of variation in mitochondrial DNA and the Y-chromosome are consistent with greater rates of female than male dispersal (Seilstad *et al.* 1998, Oota *et al.* 2001), at least on the relevant, local scale (Wilder *et al.* 2004). Finally, female-biased transfer is common in modern human hunter-gathers (Ember 1978). For example, an influential analysis by Ember (1978) concluded that only 16.2% of 179 hunter-gatherer societies show a matrilocal pattern of residence. More recent analyses (Alvarez 2004, Marlowe 2004) have contested Ember's classification, mainly because in the majority of human societies dispersal is merely biased towards, rather than restricted to, one sex or the other (and so, it is argued, should be classed as "bilocal"). Leaving this controversy over "strict" patrilocality aside, it remains the case that female-biased dispersal is considerably more common than the reverse pattern (Marlow 2004).

Taken together, these three independent lines of evidence suggest that mutations affecting female reproductive lifespan are likely to have arisen in an ancestral social environment in which dispersal was female-biased. Johnstone and Cant's (2008) model suggests, therefore, that humans were predisposed to evolve early reproductive cessation and late-life helping because the

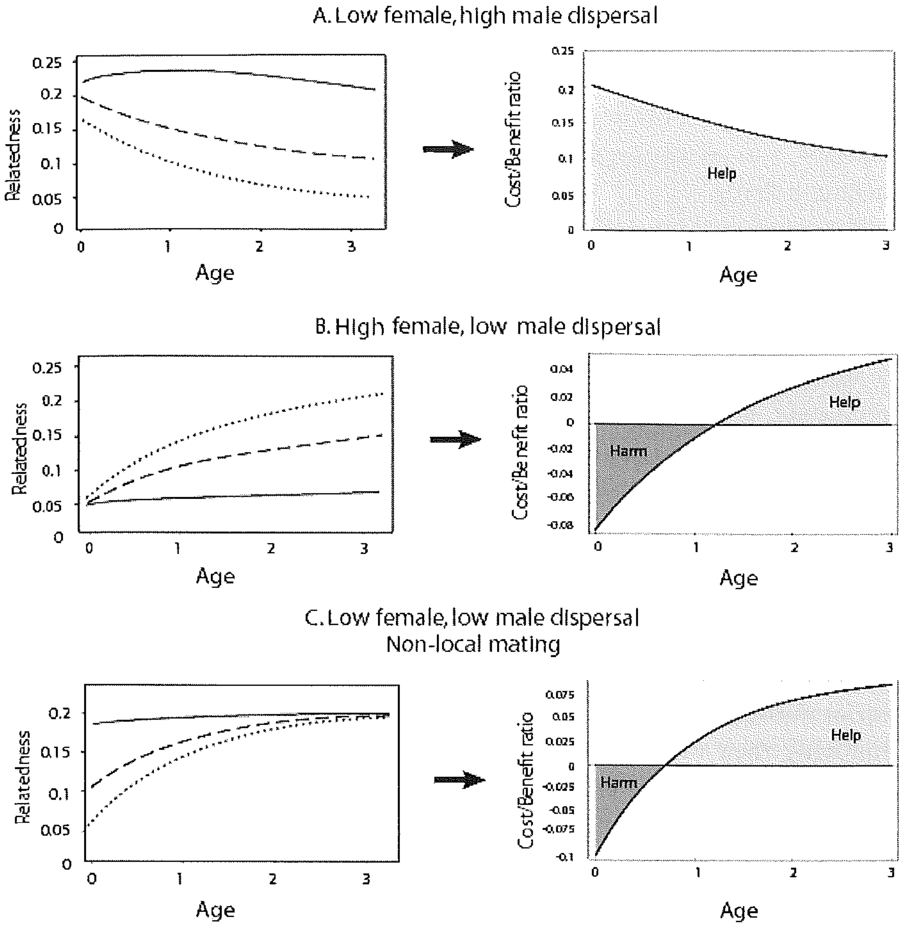

Figure 2.6 Effect of demography on patterns of age-specific relatedness and selection for social acts across the lifespan (modified from Johnstone & Cant 2008). Graphs on the left show age-specific relatedness to a breeding female of other females (solid lines) and of males (dotted lines) in her group, as a function of her age. The dashed curves show mean relatedness to a female of other breeders, averaging across both sexes. Age is scaled relative to mean generation time. Results are plotted for three different demographic systems. (A) A high rate of male dispersal and a low rate of female dispersal, with mating occurring within the local group. (B) High female dispersal and low male dispersal, with mating occurring within the local group. (C) Low male and low female dispersal, with mating occurring outside the local group. Graphs on the right show the patterns of kin selection across the lifespan associated with these three systems. A female can perform social acts which result in an immediate gain of b offspring for other breeders in the group, at an immediate cost of c offspring to herself. The graphs plot the absolute magnitude of the c/b ratio below which a social action may be favored in females of different ages. Positive values indicate that selection will favor helping behavior (i.e. acts for which $b > 0$) when c/b falls above zero but below the value shown (in the lightly shaded area), while negative values indicate that selection will favor harming behavior (i.e. $b < 0$) when c/b falls below zero but above the value shown (in the heavily shaded area). For more details see Johnstone & Cant (2008).

relatedness of a female to the offspring produced in her local group increased as she aged. By contrast, most other social mammals exhibit male-biased dispersal, and so are predisposed to the evolution of early-life, rather than late-life, helping.

The same model predicts that another unusual pattern of dispersal and mating can give rise to an age-specific increase in local relatedness: one in which both sexes are philopatric but mating occurs outside the local group (Figure 2.6C). Interestingly, this is precisely the demographic system exhibited by menopausal cetaceans. Both male and female resident killer whales are philopatric, but mate outside of the local group (Baird 2000, Whitehead & Mann 2000); it is not known whether transient killer whales, which do disperse, also exhibit menopause). Short-finned pilot whales (*Globicephala macrorhynchus*) are thought to exhibit a similar pattern – there is clear evidence for their sister species the long-finned pilot whale (*G. melas*) (Amos 1993), and the available genetic data suggest that the short-finned and long-finned species are comparable (Amos 1998). Again, the predicted increase in relatedness with age in this case is driven by relatedness through males. Consequently in these species mothers should direct their help towards sons, with the aim of improving their extra-group mating success. Observations of resident killer whales fit well with this prediction: mothers maintain closer associations with their adult sons than with their adult daughters, and may aid their son's foraging efforts, or form effective alliance partners for them in agonistic encounters with other males (Baird 2000).

Relatedness asymmetries and conflict resolution

What would be the consequences of female-biased dispersal for the resolution of reproductive conflict in ancestral hominids? This question can be explored using a simple model of the human social unit (Figure 2.7A; Cant & Johnstone 2008). We assume that males and females are socially monogamous, but allow for a proportion p of offspring to be fathered by unrelated males. For simplicity we assume in the basic model that only females disperse, but the qualitative results of our analysis hold where dispersal is merely biased toward, rather than restricted to, females. Females leave their natal groups at maturity, pair with a male of similar age, and join his natal social group. Consequently, when a young female first arrives in the group, she has no other genetic relatives present. This female can choose to breed herself and produce offspring to whom she is related by 1/2, or to refrain from breeding and assist the breeding attempts of the older female (i.e. the mother of her mate). This older female produces offspring to whom the younger female is

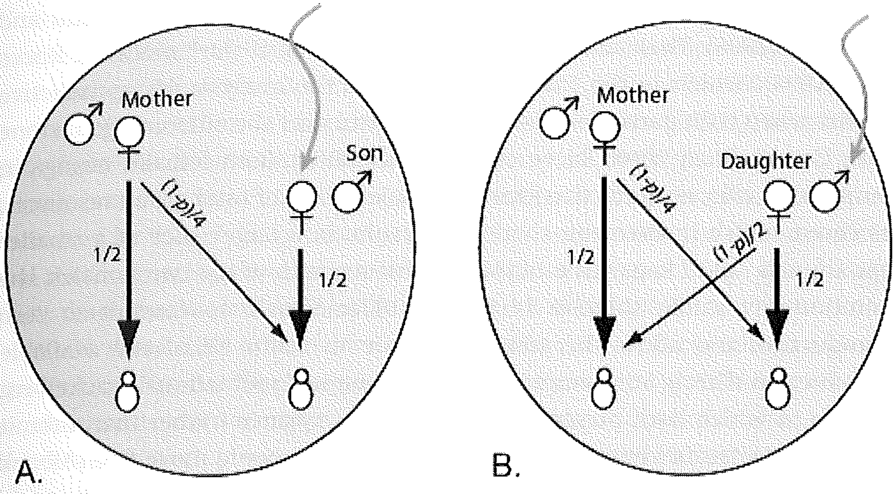

Figure 2.7 Schematic representation of relatedness asymmetries between generations under sex-biased dispersal (from Cant & Johnstone 2008). Male and female symbols represent parents. (A) Where females disperse and immigrate into a patrilocal group, a mother is related to the offspring of a daughter-in-law by $(1-p)/4$, where p is the probability of extra-pair paternity. The daughter-in-law, by contrast, is completely unrelated to the mother's offspring. Thus the difference in relatedness to own versus other offspring is greater for younger than for older females. (B) Where males disperse and immigrate into matrilocal groups, by contrast, the difference in relatedness of a female to her own versus the other breeder's offspring is greater for the mother than for the daughter.

unrelated. The difference in relatedness to offspring produced directly versus offspring produced by helping is therefore 1/2.

The older female, by contrast, can choose to breed and produce offspring of relatedness 1/2, or refrain from breeding and help to rear grandoffspring, to whom she is related by $(1-p)/4$. The relatedness differential between breeding and helping for the older female is therefore $1/2-(1-p)/4$, or $(1+p)/4$. This means that so long as there is any chance that her son fathered her putative grandchildren (i.e. $p<1$), the difference in relatedness to offspring produced by breeding rather than helping is lower for the older female than for the younger female. As a result, a younger female will have an advantage in reproductive competition with older females because she is insensitive to the costs she inflicts on an older female by breeding. This contrasts with the situation where dispersal is male-biased (as in most social mammals). Here relatedness asymmetry favors older females over younger females, so older females are expected to have an advantage in reproductive conflict with the younger generation (Figure 2.7B).

A formal game-theoretic treatment of this model is provided by Cant and Johnstone (2008). Their analysis is based on the "tug-of-war" model of Reeve *et al.* (1998), which is the standard model for the analysis of reproductive conflict when both parties exhibit partial control over the outcome (Johnstone 2000, Cant & Shen 2006, Reeve & Hölldobler 2007). Both females engage in competition over reproductive shares at the expense of total group resources. Increased selfish investment, therefore, results in a larger slice of a smaller reproductive "pie." Regardless of the relative strength of the two females, the evolutionarily stable solution is for the older female to commit to zero reproduction and allow the younger female to claim all of the available reproduction. This is an example of an "endogenous" or "natural" Stackelberg solution in which both players prefer to act in sequence (rather than submit simultaneous "sealed bids"), and both agree on who should move first (Albaek 1990, van Damme & Hurkens 1999). Endogenous Stackelberg equilibria are interesting from a biological perspective because they can explain the evolution of *commitment* strategies which are profitable precisely because they cannot credibly be changed (Nesse 2001, Cant & Shen 2006). Thus, in the conflict between older and younger females the older female's first move of zero investment is advantageous only if it is perceived to be irreversible by the younger female. Permanent sterility as a consequence of rapid reproductive senescence would be one highly effective way to commit credibly to a first move of zero investment in reproduction.

Conclusion

To summarize the above arguments, a social environment in which dispersal is female-biased generates relatedness asymmetries between older and younger females and the offspring they produce. Conflict over reproduction in these circumstances is predicted to favor older females who commit to zero reproduction when females of a younger generation start to breed. Given a pattern of female-biased dispersal during the period of lengthening human lifespan, there would be little selection to extend or maintain female reproductive capacity beyond the age at which a woman might expect to become a paternal grandmother. This can account for the high and accelerating rate of oocyte loss in humans (Figure 2.2) leading to sterility in mid-life, and the exceptionally low reproductive overlap between generations in humans (Figure 2.5). The intensity of reproductive competition and the magnitude of the benefits that can be conferred by helping must also be important, however, because chimpanzees and bonobos exhibit strongly female-biased dispersal but are not unusual in their degree of reproductive overlap (Figure 2.5A).

A number of studies have reported that the presence of a paternal grandmother has relatively little effect on offspring survival compared to that of a maternal grandmother (Bereczkei & Dunbar 1997, Sear *et al.* 2000, 2002), or even a negative effect on offspring survival (Beise & Voland 2002). For example, data from the Krummhörn region of Germany in the eighteenth and nineteenth centuries show that the chance of stillbirth for a daughter-in-law was increased by 35% if the paternal grandmother was present in the household, and these mortality costs are particularly high at the start of the daughter-in-law's marriage (Beise & Voland 2002, Voland & Beise 2005).

While these data offer evidence of reproductive conflicts between generations in human families, the positive impact of maternal grandmothers seems at odds with our assumption of a female-biased dispersal system. It is important to distinguish, however, between the evolutionary origins of a life-history trait and the behavioral strategies that are employed once that trait has evolved. The universality of menopause in modern humans, despite vast differences in social systems and access to resources, illustrates the flexibility of behavior compared to the physiological processes underlying rapid reproductive senescence. The reproductive conflict model does not imply that older females should not help daughters if the social system subsequently changes to become less female-biased, or mothers are able to maintain kin ties with their daughters. Indeed, given a choice between helping daughters versus sons, mothers should direct their help preferentially towards daughters, since grandchildren through sons may have been fathered by extra-pair males. From a woman's perspective, therefore, a flexible or "bilocal" system that allowed her to direct care toward daughters late in life would be preferable to strict patrilocality throughout her life. Most modern forager societies exhibit a degree of flexibility of this kind (Alvarez 2004, Marlowe 2004).

The model is of course simplistic in many respects, but it remains a useful tool with which to make testable predictions. For example, the assumptions of the model could be tested by examining whether relatedness asymmetries exist within family units of natural-fertility populations using genealogical and/or genetic data. Given a larger sample size, from either current or historical populations, one should be able to detect a cost to females of breeding alongside reproductive grandmothers, similar to the demonstrated costs of co-breeding within generations in polygynous marriages. The fact that the ancestral social system may have changed in more recent times offers an opportunity to test our model. Attempts to test the predictions of the model could utilize the wide variety of patterns of dispersal and marital residence exhibited by modern humans (Ember 1978, Marlowe 2004). If a system of male-biased dispersal and matrilocality were to persist for many generations, our model predicts that selection to minimize reproductive overlap would weaken. Consequently, we would predict mean age at last birth to be higher in historically matrilocal compared to patrilocal societies, and cultural restrictions on reproduction by grandmothers to be less prevalent in the former than the latter. The stability of the dispersal system over time could be inferred from genetic data, since genetic studies show that matrilocal societies show less variation in mitochondrial DNA, and greater variation in Y-chromosome DNA, than patrilocal societies (Oota *et al.* 2001). More speculatively, if the rate of reproductive senescence is adjusted on an individual level we might predict that women who have only daughters (or have daughters first) should cease reproduction (and perhaps undergo menopause) later than women who have only sons (or have sons first).

The models described in this chapter raise their own questions about the evolutionary origins and taxonomic distribution of menopause. Why is this particular life-history pattern so unusual among mammals, and absent from other vertebrates? Male philopatry and female-biased dispersal is characteristic of other primates which do not exhibit menopause, such as the hamadryas baboon (*Papio hamadryas*: Pusey & Packer 1987, Hammond *et al.* 2006) and red colobus (*Piliocolobus rufomitratus*: Marsh 1979). It is also the pattern exhibited by large cooperatively breeding canids (Moehlman & Hofer 1997), and the majority of cooperatively breeding birds (Greenwood 1980, Brown 1987). Clearly, neither male-biased philopatry nor a benefit of cooperative breeding are sufficient to account for the evolution of menopause. The magnitude and nature of the potential fitness benefits that can be conferred by helping will be of key importance. Cetacean biologists have suggested that the main benefit that can be conferred by older female killer whales and pilot whales is information and experience (McAuliffe & Whitehead 2005). The potential benefits of information transfer are probably even greater in humans, and other aspects of human social biology (e.g. communal food-gathering, short inter-birth intervals, tool use) may also contribute to making helping a cost-effective strategy later in life. It is important to remember, however, that the indirect fitness benefits of helping represent just one side of the equation. The reproductive life history of highly social animals such as humans and toothed whales will also be shaped, in substantial part, by conflict over reproduction. An integrated approach which considers all the potential inclusive fitness consequences of social acts within ancestral families promises to yield a much-improved understanding of menopause.

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