In: Primates in Perspective,
Campbell, C., Fuentes, A., MacKinnon, K.C., Panger, M., Bearder, S.(eds).
Oxford University Press (2006)

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Reproductive Cessation in Female Primates

Comparisons of Japanese Macaques and Humans

Linda Marie Fedigan and Mary S. M. Pavelka

THE EVOLUTION OF MENOPAUSE

In the past 25 years or so, menopause has emerged from the private domain of aging women and into public view. As the postwar bulge in the populations of developed nations (the "baby boomers") reached middle age, science and the media alike began to take an increasing interest in understanding why human females universally cease to experience menstrual cycles and fertility around the age of 50. A recent check of a popular search engine with the key word *menopause* garnered close to 9 million results on the worldwide web, and databases for journal articles indicate that more than 5,000 papers have been published on this subject in the biological literature alone. Clearly, this is no longer a topic that is discussed only rarely and guardedly among older women.

The vast majority of the scientific and popular literature on menopause concerns the treatment of its side effects. However, evolutionary biologists and physical anthropologists have also begun to address the issues of why menopause originated, what maintains it, and whether it is unique to humans or common in mammalian species. It was to be expected that the search for an evolutionary context and an animal model of menopause would turn to the accumulating data on life histories and reproductive senescence in the nonhuman primates, our closest relatives.

In this chapter, we first describe the competing explanations for the origin and maintenance (selection) of menopause in humans and then turn to the search for a larger understanding of reproductive senescence in female primates. As a life history characteristic of human females, menopause is universal, it happens halfway through the maximum life span of our species, and it consistently occurs at the average age of 50–52 years in different populations around the globe and throughout history. There is some debate about whether menopause is a discrete event or merely the end point of a long process of follicular depletion (Wood et al. 2001),

whether the term might also apply to reproductive decline in men (Peccei 2001), whether individual variation in age at menopause is affected by genetic and/or environmental factors (Brambilla and McKinlay 1989), and whether increasing life expectancies in developed countries indicate that menopause is a recent artifact of modernization (Sherman 1998, Leidy 1999). We have described/addressed these debates in prior publications (e.g., Pavelka and Fedigan 1991). In this chapter, we focus on competing explanations for the distinctive pattern called menopause in the human female, that is, the pattern of permanent and universal cessation of menstrual cycles in females who live to the age of 60, an aging effect that occurs in middle age, long before the senescence of other somatic systems.

There are three primary evolutionary explanations for menopause, which, as noted by Peccei (2001), are not mutually exclusive. These can be referred to as the adaptation explanation (the grandmother or maternal investment hypothesis) and the two epiphenomenon explanations, antagonistic pleiotropy (the trade-off hypothesis) and the physiological constraint model (the prolonged life hypothesis).

Taking these in reverse order, the *physiological constraint model* argues that during the course of human evolution there was strong selection for a longer life span but that the reproductive system of the human female could not keep pace (Weiss 1981). Judging by brain-to-body ratios in fossil hominids, the maximum human life span increased from about 50 years in early hominids to approximately 120 years in *Homo sapiens* (Bogin and Smith 1996, Hammer and Foley 1996). However, the age at which human females cease to experience ovarian cycles appears to have remained stationary at approximately 50 years, which is not much different from the age at which great ape females cease to cycle (Graham 1979, Nishida et al. 2003). Why would this be the case? One answer is that human females are born with all the oocytes and primordial follicles they will ever possess (approximately 1 million), a mammalian pattern that is referred to as *semelgametogenesis*. It is widely held that oocytes and follicles are depleted throughout a woman's life until they reach a minimum threshold below which hormonal signals fail, at which point cycling ceases (Armstrong 2001). However, there is some recent evidence from mice that it is actually the germline stem cells that deplete and that female mice may be able to produce new oocytes during their lifetimes (Johnson et al. 2004). Nonetheless, this explanation holds that, due to the physiological constraints of what we might refer to as the "shelf life" of eggs, it may simply not be possible to select for longer and longer reproductive life spans in mammalian females. Thus, menopause is viewed as an epiphenomenon or side effect of selection for a prolonged life span.

However, the epiphenomenon explanation that is more commonly endorsed by evolutionary biologists is known as *antagonistic pleiotropy*, or the *trade-off hypothesis* (e.g., Williams 1957, Rose 1991, Gosden and Faddy 1998). According to this model, patterns that have high adaptive value early in the life course (intense reproductive output) will be selected for even if they result in reduced fitness (follicular depletion) later in the life course. Certain genes, such as those governing semelgametogenesis, may be selected if they have pleiotropic fitness effects, that is, beneficial effects at early ages and deleterious effects at later ages. In the wider research on somatic aging, it is commonly accepted that antagonistic pleiotropy is a good explanation for the evolution of senescence (Wood et al. 2001).

In a sense, pleiotropy is an adaptive explanation for menopause since it argues that there is an adaptive benefit to follicular depletion early in life that outweighs its later deleterious effects. However, the *grandmother hypothesis*, developed by several theorists (e.g., Lancaster and King 1985; Hawkes et al. 1989, 1997; Alvarez 2000; Hawkes 2003) is the only one of the three explanations that argues for a direct benefit of midlife cessation of fertility in the human female and is widely regarded as the *adaptive explanation*. This hypothesis proposes that selection has favored cessation of reproduction midway through the life span because as human females age there are greater benefits from investing care in existing children and grandchildren than from continuing to produce additional offspring. In other words, older women will be more reproductively successful if they put their energies toward ensuring the survival of their offspring than they would be by producing yet more children. Within this directly adaptive school of thought, there are several hypotheses related through the underlying argument that a postreproductive life exists in order to facilitate enhanced parental investment. Peccei (2001) distinguished between a "mother hypothesis," focused on improving survivorship and fertility of the first generation of offspring, and a "grandmother hypothesis," directed toward increased survival rates in grandchildren. However, in terms of inclusive fitness, the benefits to females and their children and grandchildren are clearly interrelated. If a female protects or provisions her grandchildren, she may enhance their survival as well as the reproductive success of their parents (her children) and, thus, her own inclusive fitness. Hence, the *grandmother hypothesis* is often used as the general and more memorable term for postreproductive investment in any existing progeny, even though *enhanced maternal investment hypothesis* might be a more global and accurate name.

There is a growing body of literature that addresses the grandmother hypothesis in humans. A few studies have examined what are considered to be costs of old-age reproduction in human females, such as age-related risks of dying in childbirth, risks to fetuses and neonates resulting from old-age pregnancies, risks to siblings of maternal death during childbirth, and fertility costs to offspring from sibling competition. According to Peccei (2001), the only clearly established cost of old-age reproduction is increased risk of fetal loss, stillbirths, and birth defects. However, Mace (2000) modeled sibling competition and concluded that competition between siblings for food, status, territory, breeding opportunities, or kin support can greatly increase the cost of maintaining a mother's fertility beyond the age of 50 years.

Other studies have looked for fitness benefits of ceasing to reproduce, with mixed results. For example, Hill and Hurtado (1996) addressed the question of whether the presence of living, helpful grandmothers among the Ache of South America significantly enhanced the fertility of their children and the survival of grandchildren. These authors concluded that the presence of postreproductive mothers and grandmothers did not enable their children to raise more offspring. Rogers (1993) developed a theoretical model that came to the same conclusion. However, Hawkes and collaborators (1989, 1997, 2003) provided evidence that postmenopausal Hadza grandmothers supply sufficient surplus calories and babysitting services to allow their daughters to successfully raise more offspring. Blurton-Jones et al. (1999) concluded that grandmothering facilitated the evolution of earlier weaning in hominids, and Mace (2000) showed that babies in The Gambia are more likely to survive if their maternal grandmother is alive. Most recently, Lahdenpera et al. (2004) documented that premodern Finnish and Franco-Canadian women with a prolonged postreproductive life span have more grandchildren. There is scattered evidence from a variety of societies that older women are a substantial help to their progeny, but whether or not this has a significant effect on inclusive fitness is still a matter of debate (e.g., compare Kaplan et al. 2000 to Hawkes 2003, 2004).

There is further divergence of opinion between those who see the grandmother hypothesis as applicable only to the case of human females (Lancaster and King 1985, Hawkes et al. 1989) and those who would extend this adaptive explanation to other species of primates (Hrdy 1981, Sommer et al. 1992, Paul et al. 1993). Although universal midlife termination of female reproduction is not known to occur in any primate species other than humans, there are several reports of individual female monkeys and apes living part of their lives in a postreproductive state. This has generated interest in the possibility that some form of early reproductive termination may have been selected for in nonhuman primate females.

PRIMATE COMPARISONS: THE SEARCH FOR PARALLELS IN OLD-AGE REPRODUCTION

Endocrine Studies of Reproductive Senescence in Captive Female Primates

If menopause is not unique to humans but rather shared with the nonhuman primates as part of our phylogenetic heritage, then we do not need a special explanation for its existence in *Homo sapiens*. Furthermore, if we could find a nonhuman primate model suitable for laboratory research on aging and for testing various clinical aspects of ovarian decline, then we could learn more about this phenomenon in our own species. Thus, it is not surprising that biomedical primatologists spent a good part of the 1970s and 1980s examining cases in which captive female primates lost ovarian function.

Macaques (genus *Macaca*) are the most common type of primate kept in biomedical labs, and several examinations of colony records showed that particular aged female macaques cease to experience ovarian cycles around the age of 22 years, if they live to be that old (e.g., Hodgen et al. 1977, Graham et al. 1979, Graham 1986). Maximum life span in captive macaques is about 30–35 years. Chimpanzees (genus *Pan*) are the nonhuman primates most closely related to humans, and examination of reproductive decline in captive chimpanzees also turned up a few cases of very old female chimpanzees that ceased to cycle close to their deaths at 48–50 years of age, although the majority died while still cycling (Graham 1979, Gould et al. 1981).

The few studies available on the hormonal profiles of aging female monkeys indicate that the decline of ovarian function in nonhuman primates parallels the hormonal events associated with menopause in women—prolonged follicular phases, failure to ovulate, breakthrough bleeding, high plasma luteinizing hormone concentrations, low estrogen levels and/or lack of patterned estradiol/pregnonediol-3-glucuronide dynamics, etc. (e.g., Tardif and Ziegler 1992, Nozaki et al. 1995, Gilardi et al. 1997, Bellino and Wise 2003). A study of aged tamarin females indicated there may be some differences in ovarian ageing between neotropical and Old World primates (Tardif and Ziegler 1992), and we clearly have much more to learn on this topic; however, the general pattern of ovarian hormonal senescence (progression to cycle termination) in human and nonhuman female primates appears similar.

Thus, from an endocrinological perspective, reproductive decline may well follow a similar pattern in all primates, and we could use cases of individual postreproductive monkeys and apes as clinical models of the physiological basis for menopause in women. However, from an evolutionary perspective, these studies fail to demonstrate similarity between reproductive senescence in nonhuman primates and menopause in the human female. Instead, they highlight the critical differences: female macaques and chimpanzees that cease to cycle are very close to age at death, whereas human females cease to cycle in middle age; female macaques and chimpanzees cease to cycle on an idiosyncratic basis, whereas human females universally cease to cycle at the average age of approximately 50 years.

Although a recent book on aging in primates (Erwin and Hof 2002) argues that there is a pressing need for endocrine monitoring of the oldest female primates in captivity to document patterns of reproductive senescence, there has been surprisingly little published on this subject in the past decade (for exceptions, see Tardif and Ziegler 1992, Nozaki et al. 1995, Walker 1995, Gilardi et al. 1997, Bellino and Wise 2003, Coleman and Kemnitz 1998).

Demographic and Behavioral Studies of Reproductive Cessation in Socially Living Primates

In Table 26.1, we summarize the available data on reproductive cessation in primates. There are three problems with this data set. The first is the dearth of studies; especially problematic is the relative lack of information from

Table 26.1 Demographic and Behavioral Estimates of Life History Variables Related to Reproductive Cessation in Primates

SPECIES	FREE-RANGING/ CAPTIVE[1]	ESTIMATED LIFE SPAN (YEARS)	OLDEST AGE AT LAST BIRTH (YEARS)	% LIFE SPAN COMPLETED AT TIME OF LAST BIRTH	SAMPLE SIZE	% SAMPLE REACHING REPRODUCTIVE CESSATION	LENGTH OF PRLS (YEARS)	METHOD FOR CALCULATING PRLS[2]
Pan troglodytes[3]	FP	50.0	40	80.0	39	41.0	4.75	2
Papio anubis[4]	FP	27.0	25	92.6	392	?	?	3
Semnopithecus entellus[5]	FP	34.0	32	94.1	19	21.0	5.1	1
Macaca fuscata[6]	FP	32.7	25	67.3	32	25.0	4.5	4
M. mulatta[7]	SF	34.0	25	73.5	285	10	>2.0	5
M. sylvanus[8]	SF	30.0	28	93.3	12	58.0	5.7	1
Pan troglodytes[9]	C	60.0	36	60.0	15	60.0	9.25	6
Pongo pygmaeus[10]	C	58.7	40	68.1	53	31.9	7.08	6
Gorilla gorilla[11]	C	54.0	28	51.9	12	40.0	4.54	6
Papio anubis/cynocephalus hybrids[12]	C	33.4	17	50.9	13	10.0	3.45	6
M. mulatta[13]	C	30.0	20	66.7	38	13.2	2.58	6
M. nemestrina[14]	C	28.9	20	69.2	209	25.6	4.02	6
M. radiata[15]	C	28.9	19	65.7	13	3.8	6.70	6
Chlorocebus aethiops[16]	C	25.4	17	66.9	12	0	N/A	6
Saimiri sciureus[17]	C	21.0	19	90.5	28	32.1	3.28	6
Saguinus fuscicollis[18]	C	15.8	13	82.3	6	20.0	4.02	6
Leontopithecus rosalia[19]	C	24.7	12	48.6	21	47.4	3.87	6
Callithrix jacchus[20]	C	16.2	10	61.7	14	36.4	2.11	6
Lemur spp.[21]	C	28.7	22	76.7	30	44.8	3.56	6
Homo sapiens[22]	N/A	100–120	50	41.7–50.0	106	99.1	29.26	6

Sources: (source for life span value listed first, source for other life history values in this species listed second):

[1] FP, free-ranging but provisioned; SF, semi-free-ranging and provisioned; C, breeding colonies (usually caged).

[2] PRLS, postreproductive life span, calculated as follows: 1, age at death – age at last birth; 2, D – LP – 5 years; 3, cycling (or cessation thereof) inferred from perineal swellings; 4, D – LP – 1.5 years; 5, >25 years of age + no births for 2 years; 6, LP – D/(xIBI + 2SD). D, age at death; LP, age at last parturition; IBI, interbirth interval; SD, standard deviation.

[3] Nishida et al. (2003), Nishida et al. (2003).

[4] Packer et al. (1998), Packer et al. (1998).

[5] Sommer et al. (1992), Sommer et al. (1992).

[6] Takahata et al. (1995), Takahata et al. (1995).

[7] Walker (1995), Johnson and Kapsalis (1998).

[8] Paul et al. (1993), Paul et al. (1993).

[9] Judge and Carey (2000), Caro et al. (1995).

[10] Judge and Carey (2000), Caro et al. (1995).

[11] Kaplan et al. (2000), Caro et al. (1995).

[12] Judge and Carey (2000), Caro et al. (1995).

[13] Walker (1995), Caro et al. (1995).

[14] Judge and Carey (2000), Caro et al. (1995).

[15] Judge and Carey (2000), Caro et al. (1995).

[16] Judge and Carey (2000), Caro et al. (1995).

[17] Judge and Carey (2000), Caro et al. (1995).

[18] Judge and Carey (2000), Caro et al. (1995).

[19] Judge and Carey (2000), Caro et al. (1995).

[20] Judge and Carey (2000), Caro et al. (1995).

[21] Judge and Carey (2000), Caro et al. (1995).

[22] Kaplan et al. (2000), Caro et al. (1995).

free-ranging and semi-free-ranging primates, from which it is very difficult to obtain data on old age and reproduction. Apart from an anecdotal report of one postreproductive *Cercocebus albigena* female (Waser 1978), there are no studies at all of reproductive senescence in nonprovisioned, free-ranging primates. Second, sample sizes are not large, even from the few studies we have. Again, the reason is that it is difficult to obtain data on the reproductive status and patterns of very old primates of known age. The third problem is that there is very little consistency in how reproductive cessation was determined and how postreproductive life span (PRLS) was calculated in these studies. Some researchers (e.g., Sommer et al. 1992, Paul et al. 1993) treat the time lag between last parturition and maternal death as the postreproductive period, when in fact these mothers may simply have died before they could have another infant. Others (e.g., Takahata et al. 1995, Nishida et al. 2003) subtract a value equal to the weaning age of an infant as part of the calculation so that age at death minus age at last parturition minus weaning age is considered the postreproductive period. Altogether, six different ways of calculating PRLS are presented in this table. In our view, the only method that adequately takes account of the mother's own reproductive history is the formula presented by Caro et al. (1995):

$$LP - D/(\bar{x}IBI + 2\ \mathrm{SD})$$

where *LP* is age at last parturition; *D* is age at death; $\bar{x}IBI$ is mean length of a female's interbirth intervals across her lifetime, and SD is standard deviation.

In order for a female to be classified as postreproductive, this method requires that a mother live (without producing an infant) significantly longer than her own average interbirth interval. Caro's formula reduces the likelihood of categorizing females as reproductively terminated simply because they died before having another baby, and it allows researchers to explore questions about variation within the population at the age at which reproductive termination can occur.

With these shortcomings of the data set in mind, we briefly review here what is presently known about reproductive cessation from demographic and behavioral studies of female primates. Estimated life span in the six free-ranging and semi-free-ranging populations is reported to be 27 years (*Papio anubis*) to 50 years (*Pan troglodytes*). For the 13 examples of captive primates, the estimated life spans range from 16 years (*Saguinus fuscicollis*) to 60 years (*P. troglodytes*). Oldest age at birth in the free-ranging and semi-free-ranging primates is from 25 years (*Macaca fuscata*) to 40 years (*P. troglodytes*), and in the captive populations, oldest age at birth ranges from 10 years (*Callithrix jacchus*) to 40 years (*Pongo pygmaeus*). The length of the postreproductive period ranges 2–9 years, and anywhere from 0% (*Clorocebus aethiops*) to 60% (captive *P. troglodytes*) of the adult females sampled are reported to experience reproductive cessation ($\bar{x} = 28.9\%$, SD = 17.7).

Most nonhuman primate females experience reproductive termination when a large proportion of their life span is already completed (49%–94% of life span completed at time of final birth; $\bar{x} = 72\%$, SD = 14.3). In contrast, human females typically experience reproductive cessation when only 42% of their life span is completed (Table 26.1). Caro et al. (1995) report the example of a human population (eighteenth-century Germans) in which 99.1% of the adult females sampled reached reproductive termination, and they lived an average of more than 29 years in a postreproductive state. As we have previously described, it is universal in human populations for all women who reach the age of 60 to have experienced complete reproductive termination and at a point that is only halfway through the life span. Although life expectancy values are always lower than life spans and are highly variable across time and space, it is nonetheless typical for women to live a substantial proportion of their lives in a postreproductive state.

Our conclusion is that reproductive cessation in human females (menopause) is quite distinct from the patterns of reproductive senescence and termination found in the nonhuman primates. It was the apparent difference between menopause and other forms of primate reproductive termination and the lack of any substantial data on a large sample of nonhuman primate females that led us to begin a series of analyses on old-age reproduction in the Arashiyama West population of Japanese macaque females. In the rest of this chapter, we will outline our ongoing examination of reproductive cessation in these monkeys and how it compares to the human case.

CASE STUDY: REPRODUCTIVE TERMINATION IN JAPANESE MONKEYS

To address some of the problems of earlier cross-species comparisons, we used a large sample ($n = 95$) of completed lives, for which exact ages and reproductive histories are known, to explore a series of questions regarding reproductive termination and postreproductive life in female Japanese macaques. Data for this study were collected on the Arashiyama West population of Japanese monkeys. These monkeys were studied in Japan from 1954 to 1972, then transplanted as an entire group to a large ranch in south Texas, where they were studied in semi-free-ranging conditions until 1996. (For more information on group history, management, demography, and environment, see Fedigan and Asquith 1991, Pavelka 1993). Genealogical records were maintained between 1954 and 1996 on each individual born into the group, which includes date of birth, reproductive history, and date of death or disappearance. Females first mate around 4.5 years of age and can produce their first infant at 5 years of age. Japanese macaques are seasonal breeders, with a fall mating season and a spring birth season (Fedigan and Griffin 1996). The youngest female in our sample died at the age of 5 years, and the oldest lived to 32.6 years.

Reproductively terminated females were identified by Caro et al.'s (1995) interbirth interval criterion, when $LP - D/(\bar{x}IBI + 2\ \text{SD}) > 1.0$; that is, when the time lag between last parturition and the death of the mother ($LP - D$) exceeds two standard deviations of the female's own mean lifetime interbirth interval. This criterion for identifying reproductive termination does not provide direct evidence for the cessation of reproductive capabilities because it relies on externally observable events to infer internal states. However, it is a good estimate of reproductive termination for populations in which hormonal profiles, ovarian histology, and direct measures of menstrual activity are not available. Out of the sample of 95 females, 70 individuals had given birth to at least three infants (the minimum required to calculate a mean interbirth interval and standard deviation).

Reproductive Termination and Age

From the sample of 70 females that had given birth to at least three infants, 20 (28.5%) were identified as having terminated reproduction using the $LP - D/(\bar{x}IBI + 2\ \text{SD}) > 1.0$ criterion. These 20 females ranged from 14.5 to 32.7 years of age at death, with a mean of 24.6 years. Females that continued to reproduce ranged in age at death from 8.8 to 25.7 years, with a mean of 17.3 years. The difference in the mean age at death of the reproductive and reproductively terminated females was statistically significant (Pavelka and Fedigan 1999). No females under the age of 10 were identified as reproductively terminated. While possible, it is unlikely that a female under the age of 10 would meet the criterion for reproductive termination since she would need to produce three infants, then live significantly longer than her own

interbirth interval, and then die all within 5 years. Reproductive termination was found in approximately 12% of the females between the ages of 10 and 20. Of particular interest are the females aged 20–25 years. Twenty years of age is uniformly regarded as aged for Japanese macaques (e.g., Pavelka 1991, Takahata et al. 1995) since it represents the beginning of the third trimester of the life span for this species. Yet, 81% of these females were still reproductive, with only 19% showing termination. Thus, old females between the ages of 20 and 25 that become reproductively terminated are not representative of their age class. Continued reproduction in these old females is the norm.

After age 25, however, reproductive termination appears to become universal, with 86% of subjects over the age of 25 (12 out of 14 females) becoming reproductively terminated. Neither of the two subjects over age 25 that were classified as reproductive gave birth after age 25. In fact, they are false-negatives in that they gave birth at 23 and 25 years of age and then quickly thereafter died within the normal range of their interbirth interval. Given that there are no records of any female in this (or any Japanese macaque) population ever giving birth after the age of 25, we appear to be dealing with a biologically meaningful cut-off point in the reproductive lives of female Japanese monkeys. This parallels the findings of Walker (1995) and Johnson and Kapsalis (1998), who report reproductive termination after age 25 for the closely related rhesus macaque.

How Old Is a 25-Year-Old Japanese Monkey in Human Years?

Our finding that reproductive termination occurs at a low frequency in female Japanese monkeys between the ages of 10 and 25, becoming a certainty after age 25, suggests some similarities between Japanese macaque and human females. Women too may stop producing infants and even occasionally experience full-blown menopause in the decades before age 50, with termination becoming universal and certain for women who live into their fifties. However, before we can conclude that Japanese monkeys at age 25 experience something equivalent to the human female menopause, other factors must be considered. Menopause, the complete cessation of ovulation, menstruation, and reproductive capabilities at 50 years of age is universal—not idiosyncratic—among women. Further, it occurs only half way through the species life span of 100 years. This termination of reproductive capabilities in women does not occur in association with extreme old age or with advanced deterioration of the organism as it approaches the maximum life span of the species. Thus, we are led to the following question: How old is a 25-year-old Japanese monkey in human years, and how does she compare to a 50-year-old woman?

One way to draw such a comparison would be to use survivorship values to compare our monkey data with a human population whose survivorship values are unlikely to have been affected by the forces of modernization. For example, Howell (1979) reports a 2% survivorship to age 85 for the Dobe !Kung, a value which is comparable to the 2.3% survivorship to age 26 for Japanese macaque females (Pavelka and Fedigan 1999). Based on this comparison, one might argue that in Japanese monkeys reproductive termination is unlikely to occur before the equivalent human age of 85 years. However, the use of survivorship values to make comparisons between species is problematic, due to the fact that survivorship values are environmentally dependent and vary widely among populations of the same species.

The question of how old a 25-year-old monkey is compared to a 50-year-old woman might be better approached using the following equation:

$$\frac{\text{Species A Age at Reproductive Termination}}{\text{Species A Maximum Life Span}} = \frac{\text{Species B Age at Reproductive Termination}}{\text{Species B Maximum Life Span}}$$

There are no reports of Japanese monkeys living longer than the oldest female in our own sample; thus, age 32 is considered the maximum life span of Japanese monkeys. The oldest woman of documented age at death lived to be 122 years (*Detroit News*, 4 August 1997). Using these maximum life span values in the above equation, we could argue that a 25-year-old monkey is the equivalent human age of 95 years. Undoubtedly, the 122-year value represents an exceptionally rare outlier for human maximum life span. Nonetheless, this is the value for the oldest known individual, and there is no other agreed-upon value for maximum life span of humans. Estimates range from 90 (Weiss 1981) to 122 years. Using more modest values of 100 years for the maximum human life span and 30 years for the maximum Japanese macaque life span, we would argue that a 25-year-old monkey is the equivalent human age of 83 years.

Although it is difficult to obtain exact figures, it is clear that population-wide reproductive termination in Japanese macaques occurs very late in the life course. Reproductive termination at age 25 is much later in the life course of Japanese monkeys than is menopause in women at age 50. Japanese monkeys are widely regarded as old when they reach age 20 (only 7.9% of our population lived to this age), yet those aged 20–25 years are unlikely to experience reproductive termination: 81% of this age group is still reproductive.

Is Reproductive Termination Adaptive in Japanese Macaques?

Female macaques living in matrilineal societies are good candidates for an investigation of the grandmother hypothesis since they frequently engage in kin-directed affiliative behaviors. Pavelka (1991) found that old females in the Arashiyama West population continue to have active social lives and to interact affiliatively with their offspring, relatives, and friends. Grandmother macaques that have ceased to produce infants of their own would be in a position to offer a variety of supportive behaviors to their children

and grandchildren, including carrying, retrieving when lost, predator protection, interventions in agonistic interactions, and alloparental supervision when the mother is absent. They may also lactate longer than usual for their final infant. In theory, these caregiving behaviors could be sufficient to advantageously influence survivorship of descendents. We investigated the possible adaptive value of reproductive termination in Japanese macaques by comparing the survivorship of the descendents of our postreproductive females to those that continued reproducing until death. We compared the reproductive ($n = 50$) and postreproductive ($n = 20$) females for three measures of offspring survivorship: (*1*) mean survival of all offspring, (*2*) survival of final offspring, and (*3*) survival of daughters' offspring (matrilineal grandchildren). Survival analyses did not reveal any significant differences between these two groups (Fedigan and Pavelka 2001). Infant survival rates to age 1 were remarkably similar for those offspring born to postreproductive and reproductive females (85% versus 83%) and were not significantly different for survival to age 5 (71% versus 79%). Survivorship of the final infant was greater for those born to postreproductive females than to reproductive females (85% versus 72% survival to age 1 and 80% versus 67% to age 5); however, this difference was not statistically significant. Finally, we found that the survival rates of daughters' offspring did not differ between postreproductive and reproductive grandmothers (86% versus 83% survival of matrilineal grandoffspring to age 1 and 80% versus 77% to age 5). In this sample of Japanese macaque females, the cessation of reproduction before death does not result in greater survivorship of immediate offspring or of daughters' offspring, and these tests failed to support the grandmother hypothesis. In spite of the fact that female Japanese macaques do direct differential caregiving behaviors to their descendents and other matrilineal relatives, these behaviors do not confer fitness benefits in the form of greater survivorship of descendents.

Other Differences Between Reproductive and Postreproductive Females

Next, we attempted to determine if there are other traits with possible adaptive value that distinguish females that cease to reproduce before death from those that do not and found that reproductive and postreproductive females were not significantly different in dominance, matriline affiliation, body weight, infant sex ratios, age at first birth, or lifetime reproductive success (number of infants surviving to reproductive age). They were, however, significantly different in age at death, the length of time between last parturition and death, cause of death, fecundity (number of infants produced) and reproductive life span (Fedigan and Pavelka 2001). Those 20 females classified as postreproductive lived on average 7 years longer (24.6 compared to 17.4) and specifically lived five times longer after last parturition (60.0 versus 12.1 months). These older postreproductive females were more likely to disappear, whereas reproductive (younger) females were more likely to succumb to infectious diseases, in line with a previous study with a much larger sample of mortality causes which found that death from infectious disease is more common in younger Japanese macaques (Fedigan and Zohar 1997).

Postreproductive females also had more infants (9.7 compared to 7.7) and had a longer reproductive life span (age at final birth – age at first birth). Postreproductive females had a reproductive span of 13.8 years compared to 10.1 years for those that died while still reproducing. Thus, postreproductive females experienced a significantly greater number of years during which they produced infants than did reproductive females. This means that postreproductive females not only were longer-lived in total life spans but also had longer reproductive life spans than did those who died while still reproducing. Since age at first birth varied little, postreproductive females must have acquired these extra reproductive years at the end of the reproductive phase of their lives. A linear regression of fecundity against age at death showed that age at death is highly predictive of fecundity. We concluded that postreproductive females produced more offspring because, in spite of experiencing some postreproductive years at the end of their lives, they still lived through more years in which to give birth than did reproductive females, which died younger.

Why did postreproductive females have higher fecundity but not significantly greater lifetime reproductive success than reproductive females? Lifetime reproductive success was calculated as the number of offspring to reach breeding age at 5 years. We suggest that because living long enough to become postreproductive was not associated with greater survivorship of one's offspring, the greater fecundity of postreproductive females did not translate into significantly higher lifetime reproductive success.

Based on these analyses, we concluded that reproductive cessation in Japanese monkeys is adaptive only in its indication of a set of females that have reached very old age and have lived long enough to produce many infants. However, the grandmother hypothesis predicts that postreproductive females are able to direct additional care to their grandchildren; and in the above analysis, we investigated all postreproductive females, without specifying which were grandmothers. Thus, we undertook an investigation of the availability and adaptive value of reproductive and postreproductive mothers and grandmothers (Pavelka et al. 2002). This allowed us to target not just postreproductive females in general (many of which may not have living adult daughters or grandchildren) but also the theoretically important subcategories of postreproductive mothers and grandmothers in particular. Eight of the 70 females that could be categorized as reproductive or postreproductive did not produce any daughters (and hence grandchildren that were known to us), so this analysis is based on 62 grandmothers and their 175 daughters and 905 grandchildren. For the analyses in which we needed the daughters' death dates, we were able

to use only 88 of the 175 daughters, and only 74 of these produced infants. Of the 905 grandchildren born, we have complete information on 886 individuals that were included in the survival analyses. Of these, 504 survived to age 5. The probability of survival to age 5 is calculated based on the survivorship of all of the 886 individuals in the sample.

Availability of Reproductive and Postreproductive Mothers and Grandmothers

Of the 175 Japanese macaque daughters in our sample, 64 (36.6%) had a deceased mother, 106 (60.5%) had a living reproductive mother, and only 5 (2.8%) had a living postreproductive mother at the time they first gave birth. Therefore, nearly two-thirds of daughters had their mother still alive at the time of their first birth—a mother that could potentially contribute to her daughter's production of infants or to the survivorship of those infants—but the vast majority of these grandmothers were themselves still producing infants. Very few daughters had a postreproductive mother available to them when they began to reproduce.

The mean length of reproductive life for the sample of 74 daughters was 9.71 years. Over half of the reproductive years of the daughters in our sample (5.26 years, 54.2%) were lived without a mother present at all. During the other half (4.45 years or 46% of the daughter's reproductive life), the grandmother was available, but the vast majority of these years were spent with a grandmother that was herself still reproducing. Only 4.2% of the reproductive life span of the daughter was spent with a postreproductive grandmother available to help the daughter. This represents less than 5 months for the average female in the population.

This pattern is further reflected in the next generation in the time available for a postreproductive grandmother to have an impact on her grandchildren's survival—the essence of the grandmother hypothesis. Most of the grandchildren's first 5 years of life was spent without a living grandmother (3.6 years, or 72%). Grandchildren that survived to age 5 had a living grandmother available to them for only 1.4 years, or 28% of that time; and during most of that time, the grandmother had an infant of her own. Only 0.2 years, or 4%, of the first 5 years of life of the grandchildren in our sample—that is, 2 months on average—was spent with a postreproductive grandmother available to offer the extra caregiving behavior predicted by the grandmother hypothesis.

Thus, grandmother Japanese macaques proved to be less common than we had expected. This study showed that while nearly two-thirds of newly adult females have a living mother when they first give birth, the mother will likely remain alive for less than half of her daughter's reproductive life. Furthermore, postreproductive grandmothers are exceedingly rare. Only 5 out of 175 daughters had a postreproductive mother available to them when they reached reproductive age, and the average adult daughter had a postreproductive mother available to her for less than 6 months of her reproductive years. The average grandchild had a postreproductive grandmother available to it for less than 2 months. This surprisingly restricted availability of postreproductive grandmothers, even in a long-lived, multigenerational, provisioned population such as the Arashiyama West Japanese macaques, must limit opportunity for the classic maternal investment models to operate.

Adaptive Value of Reproductive and Postreproductive Mothers and Grandmothers

In the Arashiyama West population, most Japanese macaque females do not have their mothers around and free to help them with their infants because the living grandmothers are still reproducing themselves. Likewise, the vast majority of grandchildren do not have a postreproductive grandmother around to help take care of them. Still, it is interesting to explore the possible effects that a female (grandmother) can have on the reproduction of her daughter. Does having a living mother improve any aspect of a daughter's reproduction? For example, do females whose mother is alive start to give birth earlier, or do they have shorter interbirth intervals? Do the grandchildren survive better if the grandmother is alive, especially in the rare case of a grandmother that is alive and postreproductive? In these Japanese macaque data, having a mother alive did appear to be associated with improvements in some of the daughter's reproductive parameters. Females whose mother was alive were more likely to give birth at age 5 rather than age 6, although it did not matter if that mother was reproductive or postreproductive. The presence of a mother also appears to be of some benefit to females in terms of shortening their interbirth intervals from 19.2 months for females whose mother was dead to 18.1 months for females whose mother was alive. Moreover, if the mother was alive and postreproductive, the interbirth intervals of the daughters dropped to 16 months, although this trend is not quite statistically significant (Pavelka et al. 2002).

Thus, despite being less common than expected, we found evidence that the presence of a living mother—most of whom were still reproductive—is advantageous to the reproduction of their daughters. Females with a living mother were more likely to begin reproducing at age 5 rather than age 6. This may be because the presence of the mother improves a young female's chance of having a "successful" first fertile cycle (one that results in a conception) at age 4.5. The first proceptive period for female Japanese monkeys requires that these young females venture out of the tight female kinship units for the first time to establish contact with unrelated adult males—animals with which they would have had little need or opportunity to interact previously. The inexperienced behavior of these young Japanese monkey females increases the likelihood that adult males will target them for aggression (McDonald 1985). In vervet monkeys, adult daughters whose mothers were still living in the group received less aggression and were defended more often than were young adult females whose mothers had died (Fairbanks 1988). Thus, the mother of the pubescent female, through

the agonistic support she provides to her daughter, may help to increase confidence on the part of the daughter and/or reduce the frequency and intensity of serious aggression from adult males, thus increasing the likelihood of the daughter forming a successful consortship.

The essence of the grandmother hypothesis is that grandmothers, specifically postreproductive grandmothers, are able to enhance the survivorship of their grandchildren. Do the grandchildren in this Japanese macaque population survive better if the grandmother is alive and especially if she is alive and no longer producing infants of her own? Interestingly, given the initial survival analysis above, we found that they do: there is a significant difference in survivorship to age 1 depending on the status of the grandmother. Specifically, grandchildren with a living postreproductive grandmother were significantly more likely to live to age 1 than were grandchildren with either a dead grandmother or a live one that was herself still reproducing. There are no differences in the survivorship of grandchildren to age 5 based on whether the grandmother was dead, alive and reproductive, or alive and postreproductive.

Our earlier test of all 20 reproductively terminated females compared with all 50 reproductive females (irrespective of whether these females were mothers or grandmothers) found no difference in the survivorship of first- or second-generation descendants. Reproductive termination was characteristic of only a small cohort of very old females, and postreproductive females were significantly older at time of death than were reproductive ones, supporting the conclusion that reproductive termination in this population is a by-product of selection favoring longevity. Yet, in the present study, in which we were able to target the theoretically important postreproductive mothers and grandmothers, we are seeing some tantalizing evidence for the adaptive value of postreproduction. Those few grandchildren that had a postreproductive grandmother present during their first year of life were significantly more likely to survive (95%) than were those who had a dead grandmother (85%) or a living and reproducing grandmother (89%). The first year of life is critical as most mortality of immatures occurs in this period (Fedigan and Zohar 1997) and most infants are weaned at 1 year. However, the presence of a postreproductive grandmother did not enhance the survival of grandchildren to age 5, so the effects appear to be restricted to the infant or preweaning stage of life. Recall, however, that by this stage almost 75% of the grandchildren no longer have a grandmother alive. Grandmothers have a much better opportunity to affect survival to age 1 than to age 5 because they are more available during the earlier years of the grandchildren's lives.

SUMMARY

Human females are unique among the primates in experiencing menopause—the universal permanent cessation of menstrual cycles and reproductive capability at only halfway through the maximum life span for the species. Biological anthropologists and evolutionary biologists interested in the evolution of this peculiar trait (generally speaking, natural selection should favor reproducing phenotypes) have developed two categories of explanation. Either menopause is a by-product of increased life span or of traits with high selective value early in life or menopause is directly adaptive because non-reproducing middle-aged women can better maximize their inclusive fitness by aiding their daughters and grandchildren in reproduction and survival than by continuing to reproduce themselves. A small number of individual monkeys and apes that have ceased to reproduce and that show endocrine changes similar to menopausal women have been identified in captivity; however, in addition to being rare individuals, they are very old and close to the known maximum life span for their species. Reproductive cessation has also been reported for a few free-ranging nonhuman primates, although the problem of distinguishing reproductive termination from death in an interbirth interval plagues these reports.

We investigated reproductive termination in a large sample of free-ranging Japanese macaques by using a female's own reproductive history to determine when she had lived significantly longer than her own average lifetime interbirth interval without reproducing. We found that reproductive termination was uncommon in individuals under 25 years of age but universal after that. A 25-year-old Japanese monkey, however, is a rare creature as only just over 2% of the population will live to this age. A 25-year-old Japanese monkey is estimated to be equivalent to an 85-year-old woman. There was no difference in the survivorship of the grandchildren of these females that lived long enough to become postreproductive; however, this group did produce significantly more infants than those that died while reproducing because fecundity and longevity are positively correlated. For a Japanese monkey female in our sample, the key to having many infants was living a long life, even though this meant living a few years beyond reproductive ability before death in very old age. In the very rare cases when a reproductively terminated female also had a live grandchild to which she could direct caregiving behaviors, those grandchildren did have an improved chance of surviving to age 1. We conclude that the reproductive termination that we have documented in female Japanese macaques of the Arashiyama West population probably occurs too late in life, with too few females reaching and remaining in this stage for any substantial proportion of their descendants' lives, to have sufficient inclusive fitness effects to compensate for the loss of the grandmother's direct reproductive output, as theorized by the grandmother hypothesis. Our findings here suggest that increased survivorship of grandchildren during their first year of life and more rapid production of young by their daughters may be a secondary benefit enjoyed by those few postreproductive females that find themselves without an unweaned infant of their own but with a grandchild available to benefit from their free time and energy.

Thus far, our investigation of Japanese monkeys has focused on the benefits that might be associated with reproductive termination. However, the grandmother hypothesis is based on the assertion that the benefits of ceasing to reproduce will outweigh the costs of continuing to reproduce. Thus, we are continuing this investigation by turning to the other side of the equation and considering the possible costs for older females of continuing to reproduce.

REFERENCES

Alvarez, H. P. (2000). Grandmother hypothesis and primate life histories. *Am. J. Phys. Anthropol.* 113:435–450.

Armstrong, D. T. (2001). Effects of maternal age on oocyte developmental competence. *Theriogeneology* 55:1303–1322.

Bellino, F. L., and Wise, P. M. (2003). Nonhuman primate models of menopause workshop. *Biol. Reprod.* 68:10–18.

Blurton-Jones, N., Hawkes, K., and O'Connell, J. F. (1999). Some current ideas about evolution of the human life history. In: Lee, P. C. (ed.), *Comparative Primate Socioecology*. Cambridge University Press, Cambridge. pp. 140–166.

Bogin, B., and Smith, B. H. (1996). Evolution of the human life cycle. *Am. J. Hum. Biol.* 8:703–716.

Brambilla, D. J., and McKinlay, S. M. (1989). A prospective study of factors affecting age at menopause. *J. Clin. Epidemiol.* 42:1031–1039.

Caro, T. M., Sellen, D. W., Parish, A., Frank, R., Brown, D. M., Voland, E., and Borgerhoff Mulder, M. (1995). Termination of reproduction in nonhuman and human female primates. *Int. J. Primatol.* 16:205–220.

Coleman, R. J., and Kemnitz, J. W. (1998). Aging experiments using nonhuman primates. In: Yu, B. P. (ed.), *Methods in Aging Research*. CRC Press, Boca Raton. pp. 249–267.

Erwin, J. M., and Hof, P. R. (eds.) (2002). *Aging in Nonhuman Primates. Interdisciplinary Topics in Gerontology*, vol. 31. S. Karger, Basel.

Fairbanks, L. A. (1988). Vervet monkey grandmothers: effects on mother–infant relationships. *Behaviour* 104:176–188.

Fedigan, L. M., and Asquith, P. J. (eds.) (1991). *The Monkeys of Arashiyama: Thirty-Five Years of Research in Japan and the West*. State University of New York, Albany. pp. 54–73.

Fedigan, L. M., and Griffin, L. (1996). Determinants of reproductive seasonality in the Arashiyama West Japanese macaques. In: Fa, J. E., and Lindburg, D. G. (eds.), *Evolution and Ecology in Macaque Societies*. Cambridge University Press, Cambridge. pp. 369–388.

Fedigan, L. M., and Pavelka, M. S. M. (2001). Is there adaptive value to reproductive termination in Japanese macaques? A test of maternal investment hypotheses. *Int. J. Primatol.* 22:109–125.

Fedigan, L. M., and Zohar, S. (1997). Sex differences in mortality of Japanese macaques: twenty-one years of data from the Arashiyama West population. *Am. J. Phys. Anthropol.* 102:161–175.

Gilardi, K. G., Shideler, S. E., Valverde, C., Roberts, J. A., and Lasley, B. L. (1997). Characterization of the onset of menopause in the rhesus macaque. *Biol. Reprod.* 57:335–340.

Gosden, R. G., and Faddy, M. J. (1998). Biological bases of premature ovarian failure. *Reprod. Fertil. Dev.* 10:644–661.

Gould, K. G., Flint, M., and Graham, C. E. (1981). Chimpanzee reproductive senescence: a possible model for evolution of the menopause. *Maturitas* 3:157–166.

Graham, C. E. (1979). Reproduction function in aged female chimpanzees. *Am. J. Phys. Anthropol.* 50:291–300.

Graham, C. E. (1986). Endocrinology of reproductive senescence. In: Dukelow, W. R., and Erwin, J. (eds.), *Comparative Primate Biology. Reproduction and Development*, vol. 3. Alan R. Liss, New York. pp. 93–99.

Graham, C. E., Kling, O. R., and Steiner, R. A. (1979). Reproductive senescence in female nonhuman primates. In: Bowden, D. J. (ed.), *Aging in Nonhuman Primates*. Van Nostrand Reinhold, New York. pp. 183–209.

Hammer, M. L. A., and Foley, R. A. (1996). Longevity and life history in hominid evolution. *Hum. Evol.* 11:61–66.

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

Hawkes, K. (2004). The grandmother effect. *Nature* 428:128–129.

Hawkes, K., O'Connell, J. F., and Blurton Jones, N. G. (1989). Hardworking Hadza grandmothers. In: Standon, V., and Foley, R. (eds.), *Comparative Socioecology of Mammals and Man*. Blackwell, London. pp. 341–366.

Hawkes, K., O'Connell, J. F., and Blurton-Jones, N. G. (1997). Hadza women's time allocation, offspring provisioning, and the evolution of long postmenopausal life Spans. *Curr. Anthropol.* 18:551–577.

Hill, K., and Hurtado, A. M. (1996). *Ache Life History. The Ecology and Demography of a Foraging People*. Aldine de Gruyter, New York.

Hodgen, G. D., Goodman, A. L., O'Conner, A., and Johnson, D. K. (1977). Menopause in rhesus monkeys: model for study of disorders in the human climacteric. *Am. J. Obstet. Gynecol.* 127:581–584.

Howell, N. (1979). *The Demography of the Dobe !Kung*. New York, Academic Press.

Hrdy, S. B. (1981). Nepotists and altruists: the behavior of old females among macaques and langur monkeys. In: Amoss, P. T., and Harrell, S. (eds.), *Other Ways of Growing Old: Anthropological Perspectives*. Stanford University Press, Stanford, CA. pp. 59–96.

Johnson, J., Canning, J., Kaneko, T., Pru, J. K., and Tilly, J. L. (2004). Germline stem cells and follicular renewal in the postnatal mammalian ovary. *Nature* 428:145–150.

Johnson, R. L., and Kapsalis, E. (1998). Menopause in free-ranging rhesus macaques: estimated incidence, relation to body condition, and adaptive significance. *Int. J. Primatol.* 19:751–765.

Judge, D. S., and Carey, J. R. (2000). Postreproductive life predicted by primate patterns. *J. Gerontol.* 55A:B201–B209.

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

Lahdenpera, M., Lummaa, V., Helle, S., Tremblay, M., and Russell, A. F. (2004). Fitness benefits of prolonged post-reproductive lifespan in women. *Nature* 428:178–181.

Lancaster, J. B., and King, B. J. (1985). An evolutionary perspective on menopause. In: Borwn, J. K., and Kerns, V. (eds.), *In Her Prime. A New View of Middle-Aged Women*. Bergin and Garvey Press, S. Hadley, MA. pp. 13–20.

Leidy, L. E. (1999). Menopause in evolutionary perspective. In: Trevathan, W. R., Smith, E. O., and McKenna, J. T. (eds.), *Evolutionary Medicine*. Oxford University Press, New York. pp. 407–427.

Mace, R. (2000). Evolutionary ecology of human life history. *Anim. Behav.* 59:1–10.

McDonald, M. (1985). Courtship behavior of female Japanese monkeys. *Can. Rev. Phys. Anthropol.* 4:67–75.

Nishida, T., Corp, N., Hamai, M., Hasegawa, T., Hiraiwa-Hasegawa, M., Hosaka, K., Hunt, K. D., Itoh, N., Kawanaka, K., Matsumoto-Oda, A., Mitani, J. C., Nakamura, M., Norikoshi, K., Sakamaki, T., Turner, L., Uehara, S., and Zamma, K. (2003). Demography, female life history, and reproductive profiles among the chimpanzees of Mahale. *Am. J. Primatol.* 59:99–121.

Nozaki, M., Mitsunaga, F., and Shimizu, K. (1995). Reproductive senescence in female Japanese monkeys (*Macaca fuscata*): age and season-related changes in hypothalamic–pituitary–ovarian functions and fecundity rates. *Biol. Reprod.* 52:1250–1257.

Packer, C., Tatar, M., and Collins, A. (1998). Reproductive cessation in female mammals. *Nature* 392:807–811.

Paul, A., Kuester, J., and Podzuweit, D. (1993). Reproductive senescence and terminal investment in female Barbary macaques (*Macaca sylvanus*) at Salem. *Int. J. Primatol.* 14:105–124.

Pavelka, M. S. M. (1991). Sociability in old female Japanese monkeys, human versus nonhuman primate aging. *Am. Anthropol.* 93:588–598.

Pavelka, M. S. M. (1993). *Monkeys of the Mesquite: The Social Life of the South Texas Snow Monkey.* Kendall/Hunt Publishing, Dubuque.

Pavelka, M. S. M., and Fedigan, L. M. (1991). Menopause: a comparative life history perspective. *Ybk. Phys. Anthropol.* 34:13–38.

Pavelka, M. S. M., and Fedigan, L. M. (1999). Reproductive termination in female Japanese monkeys: a comparative life history perspective. *Am. J. Phys. Anthropol.* 109:455–464.

Pavelka, M. S. M., Fedigan, L. M., and Zohar, S. (2002). Availability and adaptive value of reproductive and postreproductive Japanese macaque mothers and grandmothers. *Anim. Behav.* 64:407–414.

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

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

Rose, M. R. (1991). *Evolutionary Biology of Aging.* Oxford University Press, Oxford.

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

Sommer, V., Srivastava, A., and Borries, C. (1992). Cycles, sexuality and conception in free-ranging langurs (*Presbytis entellus*). *Am. J. Primatol.* 28:1–27.

Takahata, Y., Koyama, N., and Suzuki, S. (1995). Do the old aged females experience a long post-reproductive life span? The cases of Japanese macaques and chimpanzees. *Primates* 36:169–180.

Tardif, S. D., and Ziegler, T. E. (1992). Features of female reproductive senescence in tamarins (*Saguinus* spp), a New World primate. *J. Reprod. Fertil.* 94:411–421.

Walker, M. L. (1995). Menopause in female rhesus monkeys. *Am. J. Primatol.* 35:59–71.

Waser, P. M. (1978). Postreproductive survival and behavior in a free-ranging female mangabey. *Folia Primatol.* 29:142–160.

Weiss, K. M. (1981). Evolutionary perspectives on human aging. In: Amoss, P. T., and Harrell, S. (eds.), *Other Ways of Growing Old: Anthropological Perspectives.* Stanford University Press, Stanford, CA. pp. 25–58.

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

Wood, J. W., O'Conner, K. A., Holman, D. J., Brindle, E., Barson, S. H., and Grimes, M. A. (2001). The evolution of menopause by antagonistic pleiotropy. Working paper 01-04. Center for Studies in Demography and Ecology, University of Washington, Seattle http://csde.washington.edu/pubs/wps/01-04.pdf.