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Is There Adaptive Value to Reproductive Termination in Japanese Macaques? A Test of Maternal Investment Hypotheses

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Evolutionary biologists often argue that menopause evolved in the human female as the result of selection for a postreproductive phase of life, during which increased maternal investment in existing progeny could lead to enhanced survivorship of descendents. Adaptive theories relating menopause to enhanced maternal investment are known as the mother (first-generation) and grandmother (second-generation-offspring) hypotheses. Although menopause—universal midlife termination of reproduction—has not been documented in primates other than humans, some researchers have argued that postreproductive alloprimates also have a positive impact on the survivorship of first and second generation progeny. We tested the maternal investment hypotheses in Japanese macaques by comparing the survivorship of offspring, final infants, and great-offspring of females that terminated reproduction before death with females that continued to reproduce until death. SURVIVAL analyses revealed no significant difference in the survivorship of descendents of postreproductive and reproductive females, though final infants of postreproductive females were 13% more likely to survive than final infants of females that reproduced until death were. We also explored possible differences between these two groups of females, other than survivorship of progeny. We found no difference in dominance rank, matrilineal affiliation, body weight, infant sex ratio, age at first birth, fecundity rate or lifetime reproductive success. However, postreproductive females are significantly longer-lived than reproductive females and as a result experienced more years of reproduction and

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produced more infants in total. Apart from final infants, offspring survival is marginally lower in postreproductive females. Since offspring survival is not significantly enhanced in postreproductive females, the greater number of infants produced did not translate into greater lifetime reproductive success. Our findings fail to support the maternal investment hypotheses and instead suggest that reproductive termination in this population of Japanese macaques is most closely associated with enhanced longevity and its repercussions.

KEY WORDS: menopause; *Macaca fuscata*; reproductive senescence; grandmother hypothesis; maternal investment.

INTRODUCTION

There are two competing evolutionary approaches to explain the pattern of reproductive senescence (menopause) in the human female. Many evolutionary biologists have viewed the termination of reproduction that occurs in human females around age 50, i.e., midway through the life span, as directly adaptive. Most of these theorists argue that selection has favored cessation of reproduction midway through the life span because, as human females age, there are greater fitness benefits to be had from investing care in existing offspring and great-offspring than from continuing to produce additional offspring (Alexander, 1974; Gaulin, 1980; Hamilton, 1966; Williams, 1957). A second line of explanation is that menopause is an artifact of selection for a long life span, in other words an epiphenomenon of some other adaptive trait, and thus only indirectly selected (Washburn, 1981; Weiss, 1981; Wood, 1994). Within the directly adaptive school of thought on menopause, there are several hypotheses related through the underlying argument that a postreproductive life exists in order to facilitate enhanced parental investment. Peccei (1995a,b) distinguished between the mother hypothesis that is focused on improving survivorship of one's first generation of offspring versus the grandmother hypothesis, focused on increasing survival rates of grandchildren. However, in terms of inclusive fitness, the benefits to females, their children and their 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 sometimes used as the general rubric for postreproductive investment in any existing progeny (Lancaster and King, 1985). Further, the grandmother hypothesis is bifurcating and being refined as research on human populations progresses (Hawkes *et al.*, 1989, 1997, 1998; Hill and Hurtado, 1991, 1996; Kaplan, 1997). For example, in a recent analysis of human grandmothering, Hawkes *et al.* (1998) distinguished between the older question of why the human female would stop reproducing early versus the newly-recognized

enigma of why only human females are capable of living long postreproductive lives. Hawkes *et al.* focused their adaptive explanation on the latter issue. We will refer here to the various direct-adaptation hypotheses as the maternal investment model.

There is further divergence of opinion between those who see the enhanced maternal investment model as applicable only to the case of human females (Hawkes *et al.*, 1989; Lancaster and King, 1985) and those who would extend this adaptive explanation to other species of primates (Hrdy, 1981; Paul *et al.*, 1993; Sommer *et al.*, 1992). While 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 some part of their lives in a postreproductive state. This has generated interest in the possibility that some form of reproductive termination may have been selected for in nonhuman primates.

For example, Hrdy (1981) hypothesized that a lengthy postreproductive phase of life evolved in female primates in order to maximize the maternal investment they make in their progeny and their lineage, including extant offspring, second-generation descendents and matrilineal relatives. Borries (1988) and Sommer *et al.* (1992) offered some evidence for Hrdy's idea that old female langurs invest considerable time and energy in their grandchildren and supported her view that a postreproductive period in langurs is the result of natural selection. Similarly, Paul *et al.* (1989) argued that macaque mothers that cease to reproduce before death and instead direct energy toward their extant offspring can be expected to have greater lifetime reproductive success than mothers that breed until their deaths and leave orphaned infants behind when they die. They suggest that infants whose mothers die have low survival rates, and they argue that there has been selection for females to increase maternal care as they age, culminating in prolonged and extensive investment in descendents by postreproductive grandmother monkeys and apes. On the other hand, Packer *et al.* (1998) concluded that postreproductive female baboons do not significantly enhance the fitness of their offspring and grandchildren. Nishida *et al.* (1990) also criticized the grandmother hypothesis as an explanation for reproduction cessation in female chimpanzees and Johnson and Kapsalis (1995, 1998) argued that the invocation of the grandmother hypothesis is not necessary to explain the evolution of reproductive senescence in other primates.

At least two problems characterize existing research on the postreproductive lives of nonhuman primate females. The first is small sample size: most publications have relied on a mere handful of aged females of known ages or a single anecdote. Although our sample of Japanese macaque females followed from birth to death ($n = 95$) may seem small by human standards,

it is a very large sample in the literature on reproductive senescence of alloprimates.

The second problem is accurately determining when old females have terminated reproduction. Paul *et al.* (1993) assume that the entire time lag between last birth and death for an aged female is the postreproductive period; however, it is possible that some older females, like some younger females, simply die during an interbirth interval. Takahata *et al.* (1995) calculated the length of postreproductive life in Japanese macaques by subtracting 1.5 years from the time lag between last birth and death.

Pavelka and Fedigan (1999) used a sample of 95 individuals of known reproductive history and age at death and employed a criterion that distinguishes reproductive termination from death in an interbirth interval. We found that reproductive termination occurs by this criterion in Japanese macaque females: 20 of our subjects were reproductively terminated. From a comparative life-history perspective, the reproductive termination of our macaque subjects differed from human female menopause in that it characterized only the oldest surviving members of the population. Most of the postreproductive females were $\geq$25 years old at death and experienced an average postreproductive life of 2 years (range = 0.7–7.6 years). During this phase of life they could have expended extra energy and care to ensure the survival of their existing offspring and grandoffspring.

Female macaques living in matrilineal societies are good candidates for an investigation of the mother and the grandmother hypotheses since the 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 care-giving behaviors could be sufficient to influence survivorship of descendents.

We provide a test of the maternal-investment hypotheses by examining whether females in the Arashiyama West group of Japanese macaques that ceased to reproduce before death experienced greater survivorship of their descendents than ones that continued reproducing until death did. Further, we investigate whether there are differences other than offspring survival rates that might distinguish between female Japanese macaques that become postreproductive and ones that continue to reproduce until death. For example, do these two categories of females differ in dominance ranks, matrilineal affiliations, causes of death, body weights, sex ratio of offspring, age at first

birth or fecundity rates? Thus, in addition to testing the maternal investment hypothesis for a fitness benefit in the form of offspring survivorship, we attempt to determine if there are other traits with possible adaptive value that distinguish females that cease to reproduce before death from ones that do not.

METHODS

The life-history data for this study are from the Arashiyama West population of Japanese macaques, which has been studied over the past 46 years. These monkeys were first found ranging on the outskirts of Kyoto, Japan, in 1954 and have been followed since. In 1966, the Arashiyama population fissioned into two daughter groups, and in 1972, one of them was moved in its entirety to a ranch in south Texas and renamed the Arashiyama West (AW) group. Genealogical records have been maintained on each individual born since 1954, including date of birth, reproductive history, and date of death or disappearance (Fedigan, 1991; Pavelka, 1993).

The original study sample consists of all females (N = 95) that reached reproductive age and were followed from birth to death between 1954 and 1993. Although the genealogical records continue after 1993, we designated this year as the cut-off point for our subjects so that we could examine the survival rates of their offspring beyond 1993. The youngest female to die in this sample did so at age 5 and the oldest at 32 years. Thirty-two years is also the oldest recorded age for any female Japanese macaque. The average age at first birth in Japanese macaques is 5–6 years, with a few outliers first giving birth at 4 or 7 years. Breeding is seasonal, and females can give birth every year, though the average interbirth interval in this population is two years (Fedigan *et al.*, 1986).

We determined reproductive termination according to the interbirth interval criterion of Caro *et al.* (1995), in which LP-D/($\bar{x}$ IBI + 2 s.d.) > 1.0. That is to say, when the time lag between last parturition and death of the mother (LP-D) exceeds two standard deviations of the female's own mean lifetime interbirth interval, we considered her to have ceased to reproduce. Out of the original sample of 95 females, 70 individuals had given birth to $\geq$3 infants, the minimum needed to calculate a mean interbirth interval and standard deviation. Although the criterion of Caro *et al.* (1995) clearly is not direct physiological evidence of ovarian failure, it is a good indicator of reproductive termination in primate populations for which hormonal profiles, ovarian histology and direct measures of menstrual activity are not available.

Having applied a criterion to distinguish between postreproductive (PR) and reproductive (R) females, we tested the prediction of the maternal investment hypotheses that postreproductive life is associated with greater

survivorship of descendents. We compared the two groups of females for three measures of offspring survivorship: (1) mean survival of all offspring; (2) mean survival of daughter's offspring (matrilineal grandchildren); and (3) survival of final offspring. For the analyses of offspring survivorship, we extracted data from the 1996 AW census and used the SPSS-PC program SURVIVAL, which employs both uncensored and censored intervals, and which corrects for censoring. Analyses based only on completed (uncensored) lives can create a bias toward shorter intervals. Therefore, SPSS-SURVIVAL incorporates the analysis of completed intervals, i.e. offspring survival to ages 1 and 5 years, and the intervals that are incomplete or censored because, for example, the offspring/grandoffspring had not reached 1 or 5 years by the end of our study, or in a few cases, because the offspring/grandoffspring had been sold to a zoo. Survival analysis provides median survival times for offspring of PR and R females and performs a Wilcoxon-Gehan test to compare their survival distributions (Norusis, 1993).

To test for differences between our two groups other than offspring survivorship, we used chi-square analyses and t-tests to compare PR and R females for the following variables: mean lifetime dominance rank (high/medium/low), matrilineal affiliation, cause of death, body weight (taken at least once in adulthood when not pregnant), sex ratio of offspring, age at first birth, age at death, reproductive lifespan, fecundity/year, total number of infants born, and lifetime reproductive success (measured as number of offspring $\geq$5 years). Lifetime reproductive success (LRS) of any animal that has reproduced at least once and completed its reproductive life can be measured as the number of its offspring that have themselves lived to reproductive age (Clutton-Brock, 1988). Reproductive age is five years in Japanese macaques (Fedigan *et al.*, 1986). LRS is thus conceptualized as the product of reproductive lifespan (l = age at last birth-age at first birth), fecundity per year (f = total number of infants born divided by reproductive lifespan) and the proportion of infants born that survive 5 years ($= s$). That is to say, LRS = $l \times f \times s$ (Brown, 1988). The relative contributions of f and s to reproductive success vary over the course of a female's lifespan (Williams, 1957).

RESULTS

Interbirth Interval and LP-D of Postreproductive versus Reproductive Females

Of the 70 females in our sample that had given birth to $\geq$3 infants, 20 had ceased to reproduce before death, and 50 had died within the range of their normal interbirth interval. Table I shows that both categories of females experienced remarkably similar average lifetime interbirth intervals (19.64

Table I. Application of criterion of Caro *et al.* (1995) to distinguish postreproductive from reproductive females

	Females	N	$\overline{X}$	SD	range	t	df	p
Mean Lifetime IBI (months)	Postreproductive	20	19.64	4.37	12.24–27.30	−0.018	68	0.986
	Reproductive	50	19.62	4.11	13.55–37.63			
Last Parturition to Death (LP-D, months)	Postreproductive	20	60.00	30.15	24–137	−10.49	68	0.000*
	Reproductive	50	12.16	7.72	0–30			
Caro Criterion LP-D/(X IBI + 2SD)	Postreproductive	20	1.80	1.00	1.03–5.06	−0.633	19.9	0.000*
	Reproductive	50	0.38	0.24	0.00–0.83			

and 19.62 months) and standard deviations (4.37 and 4.11 months). However, 20 females classified as postreproductive lived five times longer after last parturition than females classified as reproductive until death (60.0 versus 12.1 months, $p = 0.00$). Further, for the 20 PR females, the time period between last parturition and death was nearly twice (1.8 times) the length of their own normal interbirth interval. Although these differences follow naturally from the criterion of Caro *et al.* (1995) for PR females—ones that died after 2 s.d. of their own mean interbirth interval will by definition have longer postreproductive lives—we present the comparisons here to show the magnitude of the difference between PR and R females in postreproductive lives and to demonstrate that the differences are not driven by their interbirth intervals.

Offspring Survivorship in Postreproductive versus Reproductive Females

Survival analyses did not reveal any significant difference in offspring survivorship between postreproductive and reproductive females. Infant survival rates are remarkably similar for offspring born to PR and R females: 85 versus 83% to age 1 and 71 versus 79% for survival to age 5 (Table II). Note that although not significantly different, survivorship of PR offspring

Table II. Offspring survivorship in postreproductive vs. reproductive females

			% survival				
Generation	Females	N	to age 1	to age 5	W	df	p
Offspring	Postreproductive	191	0.83	0.71	0.806	1	0.396
	Reproductive	379	0.85	0.79			
Daughters' Offspring	Postreproductive	338	0.86	0.80	1.246	1	0.264
	Reproductive	555	0.83	0.77			
Final Offspring	Postreproductive	20	0.85	0.80	1.408	1	0.235
	Reproductive	50	0.72	0.67			

is actually marginally lower than for R females. Further, we found that the survival rates of daughter's offspring did not differ between PR and R grandmothers (86 versus 83% survival of matrilineal grandoffspring to age 1, and 80 versus 77% to age 5).

We found that survivorship of the final infant was greater for PR females than final infants born to R females (85 versus 72% survival to age 1, and 80 versus 67% to age 5); however, these differences are not statistically significant. Since the differences are in the predicted direction (PR > R offspring survivorship) and since PR females experience 13% better survivorship of final offspring, we took a closer look at what might be driving these differences. Could they be attributed to enhanced care of their final infants by PR females or to diminished care of final infants by R females or to both factors? To examine this question, we compared the survivorship of all the infants born to PR females except the final one with the survivorship of final infants. Then we made the same comparison between survival of offspring born to R females. We found no significant difference between the survivorship of all infants versus final infant in PR females ($W = 0.375$, $df = 1$, $p = 0.5404$.) In contrast, there are significant differences between the survivorship of all infants and the final infant in R females ($W = 5.589$, $df = 1$, $p = 0.0181$).

Thus, it seems that the final infants of R females have relatively poor survivorship. We ran a regression on the length of maternal care (defined as the number of months the mother lived after the birth of her final infant) versus the lifespan of the final offspring and found a significant positive relationship between length of maternal care and infant survivorship ($F = 12.485$, $df = 68$, $p = 0.001$, $R = .394$).

Differences Between PR and R Females in Social, Life History and Reproductive Characteristics

A. *Dominance ranks.* PR and R females did not differ in dominance ranks (Table III; $\chi^2 = 2.450$; $df = 2$; $p = 0.294$). Both categories of females were distributed fairly evenly across the three dominance categories of high, medium and low rank.
B. *Matrilines.* PR and R females did not differ in matrilineal affiliation (Table III; $\chi^2 = .497$; $df = 4$; $p = 0.974$). Both categories of females were fairly evenly represented across the five major matrilines of the Arashiyama West population, comprising 12–25% of each matriline.
C. *Causes of death.* There are significant differences in the causes of death of PR and R females (Table III; $\chi^2 = 10.654$; $df = 3$; $p = 0.014$). PR females were more likely to disappear and R females were more likely to succumb to infectious diseases.

Table III. Social, physical and reproductive characteristics of postreproductive vs. reproductive females

		Postreproductive Females		Reproductive Females	
		N	(%)	N	(%)
Rank	high	8	(40.0)	19	(38.0)
	medium	5	(25.0)	21	(42.0)
	low	7	(35.0)	10	(20.0)
Matriline	BE	3	(18.8)	9	(20.0)
	NO	4	(25.0)	10	(22.2)
	MA	2	(12.4)	8	(17.8)
	PK	3	(18.8)	6	(13.3)
	RH	4	(25.0)	12	(26.7)
Cause of Death[a]	unknown	7	(38.9)	23	(47.9)
	infectious diseases	0	(0.0)	9	(18.8)
	non-infectious diseases	5	(27.8)	13	(27.1)
	disappeared	6	(33.3)	3	(6.2)
		N	Kgs ± SD	N	Kgs ± SD
Body Weight		19	7.80 ± 1.81	32	8.15 ± 3.7
		N	M:F	N	M:F
Infant sex ratiob[b]		191[a]	0.99	377[a]	0.95

[a] Detailed explanation of causes of death, are in Fedigan and Zohar (1997).
[b] Sample size (N) refers to the number of infants born to Postreproductive and Reproductive females.

D. *Body weight.* There is no significant difference in the body weights of PR and R females, females in both groups weighing approximately 8 kilos. PR females that were weighed at least once in adulthood weighed on average 7.96 k, and R females weighed on average 8.15 k (Table III; $t = -0.392$; $df = 49$; $p = 0.697$).

E. *Infant sex ratio.* Both PR and R females produced infants with a sex ratio close to 1:1. The 20 PR females produced 191 infants with a sex ratio of 0.99 and the 50 R females produced 377 infants with a sex ratio of 0.95 (Table III; $\chi^2 = 0.044$; $df = 1$; $p = 0.834$). Also, there is no difference in survivorship of male infants born to PR versus R mothers (survival to age 1 = 84 vs. 88%; survival to age 5 = 71 vs. 78%, $W = 0.85$, $df = 1$, $p = 0.356$). And there is no difference in the survivorship of female infants born to PR versus R mothers (survival to age 1 = 84 vs. 88%; survival to age 5 = 72 vs. 83%; $W = 0.330$, $df = 1$, $p = 0.565$).

F. *Age at first birth.* PR females produced the first infant at 66.3 months, a somewhat earlier age than the average of 72.6 months for R females, but this difference is not significant (Table IV; $t = -1.589$; $df = 68$; $p = 0.177$).

Table IV. Life history values for postreproductive vs. reproductive females

	Females	N	X	SD	Range	t	df	p
Age at First Birth	Postreproductive	20	66.3	11.1	48–99	−1.589	68	0.177
	Reproductive	50	72.6	16.3	60–135			
Age at Death	Postreproductive	20	24.6	4.9	14.5–32.7	−5.475	68	0.000*
	Reproductive	50	17.4	5.0	8.8–25.7			
Fecundity Rate (births per year)	Postreproductive	20	0.74	0.2	0.53–1.25	−1.088	68	0.280
	Reproductive	50	0.78	0.1	0.48–1.03			
Total Infants Born in Lifetime	Postreproductive	20	9.7	2.5	3–16	−2.157	68	0.035*
	Reproductive	50	7.7	3.7	4–14			
# of Reproductive Years (age at final birth-age at first birth)	Postreproductive	20	13.8	4.3	4.0–18.9	3.146	68	0.002*
	Reproductive	50	10.1	4.7	2.9–19.9			
Lifetime Reproductive Success	Postreproductive	20	6.3	1.7	3–9	−1.487	68	0.142
	Reproductive	50	5.2	2.9	0–11			

G. *Age at Death.* PR females lived significantly (7 years) longer than R females, dying on average at the age of 25 as compared to 17 years (Table IV; $t = -5.475$; $df = 68$; $p = 0.000$).

H. *Fecundity*/Year (f). There is no difference in the rate at which PR and R females produced infants per year (Table IV; $t = -1.088$, $df = 68$, $p = 0.280$).

I. *Total Infants Born.* PR females produced significantly more infants than R females did, averaging 9.7 infants born during their lifetimes versus 7.7 infants (Table IV; $t = -2.157$; $df = 68$; $p = 0.035$).

J. *Number of Reproductive Years* (l). We compared the age at final birth with age at first birth for PR and R females and found that PR females had a mean reproductive span of 13.8 years compared to 10.1 years for R females. Thus PR females experienced a significantly greater number of years during which they were producing infants than R females did (Table IV; $t = 3.146$, $df = 68$, $p = 0.002$). This means that PR females not only lived longer in total lifespans (age at death) but also had longer reproductive spans than those of R females.

K. *Lifetime Reproductive Success.* PR females produced an average of 6.3 offspring that survived to ≥5 years, a value that is not significantly greater ($p = 0.142$) than the average of 5.2 offspring ≥5 years old produced by R females (Table IV).

DISCUSSION

We asked whether the 20 females that lived well beyond their own interbirth interval after giving birth to their final infant had greater survivorship

of their descendents than the 50 females that died within the range of their own interbirth interval. Survival analyses showed that in this sample of Japanese macaque females, the cessation of reproduction before death does not result in significantly greater survivorship of immediate offspring or of daughters' offspring. These findings do not support the maternal investment hypotheses.

Paul *et al.* (1989) argued that the final infant may especially benefit from reproductive termination of the mother. Accordingly, we looked in particular at the survival rates of final infants. Although it is here that we found the greatest offspring survivorship difference (13%) between PR and R females, it did not reach statistical significance. It is possible that the lack of statistical significance is due to sample size, though we are unlikely to ever obtain a larger sample size of complete female life histories than the genealogical records of the AW population, and it is also possible the lack of statistical significance is due to insufficient enhancement of survival in final infants of PR females. We found that the survivorship of final offspring is strongly related to the length of time the mothers survive after their birth and that final infants of R mothers do significantly less well than the other infants of R females. In spite of these tantalizing hints that maternal investment plays a role in the survival of final infants, we were unable to document significant effects of a postreproductive life on the survival of progeny.

If not offspring survival rates, what does distinguish these postreproductive females? If we assume that we have identified a biologically meaningful group of females that cease to reproduce before death, then we should be able to discover some other variable that helps us to understand the membership of this group. For example, high ranking females may be more likely to live a long time after producing their final infant, which suggests some type of social factor in becoming postreproductive (cf. human social status in Jaszmann *et al.*, 1969)? Or perhaps, heavier female macaques continue to cycle and reproduce, since percent of body fat has been linked to later menopause in human females (Brambilla and McKinley, 1989). Or, if there were a genetic proclivity to become postreproductive (Caro *et al.* 1995), perhaps it would occur more often in one matriline than another. Because the AW data set is so rich, we were able to test our two groups of females for differences in a wide variety of social and life-history variables. However, we found almost no significant difference in any of these variables.

In fact, our most salient finding is that PR females are older at death than R females, living on average 7 years longer. Pavelka and Fedigan (1999) demonstrated that reproductive termination in Arashiyama West Japanese macaques is a rare characteristic of extremely long-lived females, seldom occurring in individuals <20 years old and becoming almost universal in females >25 years old. This is very old age in macaques, equivalent to 83 years in human females. Life-table values show that only 2.9% of females born

into the AW population can expect to reach 25 years of age, and only 17% of females that reach reproductive maturity at 5 years can expect to live >25 years.

Fedigan *et al.* (1986) explored the finding that longer-lived females produce more infants over their lifetimes. Now, we show that PR females gave birth to an average of 9.7 infants, which is significantly greater than the average of 7.7 infants produced by R females. Because of this strong relationship, we tried to identify the critical reproductive phase of life in our two groups of females. We found that PR females had significantly longer reproductive lifespans than those of R females. Since age at first birth varied little, PR females must have acquired these extra reproductive years at the end of the reproductive phase of their lives. We conclude that PR females gave birth to more infants because, in spite of experiencing nonreproductive years at the end of their lives, they still lived through more years in which to give birth than R females did.

Why did PR females have a greater total number of infants born in their lifetimes but not significantly greater lifetime reproductive success than R females? Because LRS is the product of fecundity, reproductive lifespan and survivorship. In this study, a postreproductive phase of life is not associated with greater survivorship of one's offspring, in fact PR females experienced marginally lower survivorship of first generation offspring. Thus, we suggest the greater number of infants born to PR females did not translate into significantly higher lifetime reproductive success once survival was factored into the equation. However, on average, PR females had one more offspring that made it to breeding age. Even if not statistically significant at these sample sizes, one additional offspring could be of cumulative importance if it produced many second generation progeny for the females in question.

Our two categories of females also differed in causes of death, though this is confounded by 30 of our 70 subjects being recorded to have unknown cause of death, i.e. their bodies were found but cause of death was not determined. We do not know why PR females should be more likely to simply disappear,—no body found—than R females. The finding that R females were more likely than PR females to die of infectious diseases is very likely related to age at death. A previous study with a much larger sample of mortality causes indicated that death from infectious disease is more common in younger Japanese macaques (Fedigan and Zohar, 1997).

PR females did not differ from R females in dominance ranks, matrilineal affiliation, body weight, or infant sex ratios. The fact that we did not find any way to distinguish between these two categories of females other than variables that follow logically from differential longevity suggests that reproductive termination in this species is associated with very old age and not with any adaptive or genetic package that distinguishes postreproductive females.

The maternal investment model, commonly known as the grandmother hypothesis, might well be the explanation for the universal midlife termination of reproductive capability that occurs in women. However, our data suggest that in Japanese macaques, reproductive termination is characteristic only of a small number of very old females and is likely an epiphenomenon of selection for longevity.

Via analysis of reproductive data from captive populations representing 13 nonhuman primate species, Caro *et al.* (1995) found a range from 0% (vervets) to 60% (chimpanzees) of females terminating reproduction before death according to their criterion. They compared these percentages to those of a human population from Krummhorn, Germany in the 18th and 19th centuries and reported that 99.1% of human females terminate reproduction before death. Caro *et al.* (1995) also reported that the length of postreproductive life in human females is longer than that in nonhuman primates. These comparisons led them to support one of our earlier assertions (Pavelka and Fedigan 1991) that the pattern of reproductive senescence is individually variable in nonhuman primates but universally constant in humans.

Taken together, these findings bring us to the conclusion that menopause in human females is fundamentally different from reproductive senescence in other female primates. And, if menopause is unique, then it requires a separate explanation based on special human characteristics of life history, reproduction and/or offspring care, characteristics that do not occur in other primate species. Why would patterns of reproductive senescence have followed different evolutionary pathways in human and nonhuman primate females?

As we have noted earlier (Pavelka and Fedigan, 1991) and as Hawkes *et al.* (1997, 1998) have argued, it is not reproductive termination at age 50 that is unique to humans, since female chimpanzees and other great apes also produce viable oocytes until the age of 50. In comparison with our closest primate relatives, reproductive termination in human females is not early or premature. Instead, it is the long postreproductive phase of life in human females that requires explanation. In other words, most female Japanese macaques continue to produce infants until they die and the few that terminate spend only 8.7% of their lives in a postreproductive state (Pavelka and Fedigan, 1999). Female chimpanzees can produce infants almost until they die at a maximum life span of approximately 50 years. Human females continue to ovulate until approximately 50 years old, but can live $\geq$50 years beyond reproductive termination.

One reason for a longer postreproductive life in human females might be that 50 years is the maximum shelf life of mammalian oocytes—few female mammals (Austad, 1997) have been observed to reproduce past 50 years of

age. Degeneration of a nonrenewable supply of eggs may be unavoidable in humans since all oocytes are present in mammalian ovaries at birth and no new germ cells are produced during a female's lifetime. If 50 years represents an inherent maximum of the mammalian system, then the human female egg supply may have been unable to keep pace with increased longevity during human evolution. That is, over the course of hominid evolution, there was evidently selection for increasing our life span from the hominoid maximum of 50 years to the present maximum of $\geq$100 years, but no discernable selection for longer viability of oocytes.

However, the most commonly proposed reason for a long postreproductive life in human females is the potential for grandmothers to enhance their reproductive success and that of their children by lavishing extra care on their progeny when they no longer need expend their energy on gestation and lactation. Tests of the maternal investment model in humans are still fragmentary and controversial. Hill and Hurtado (1991, 1996) were not able to find support for the grandmother hypothesis in their extensive study of Ache hunter-gatherers in South America. They modeled the effects of continued versus early termination of reproduction (also see Rogers 1993, 1994), and found that the effects of older women on the survival and fertility of their offspring would have to be quite dramatic and pronounced in order for menopause to be favored. Conversely, Hawkes *et al.* (1989, 1997, 1998) have argued that long postmenopausal life stages in humans evolved along with the practice of mother-child food-sharing. In a study of hardworking Hadza grandmothers, they demonstrated that postmenopausal women can have a significant beneficial effect on the nutritional intake of grandchildren and other relatives still in the juvenile stage, and on the fertility of their daughters. Both Hawkes *et al.* (1997) and Kaplan (1997) have linked the support of younger kin by postreproductive females to a human foraging strategy that emphasizes difficult-to-acquire foods.

We concur that if menopause has been directly selected in human females (as opposed to being simply an epiphenomenon of mammalian constraints on oocyte viability) then the area in which human mothers and grandmothers differ significantly from monkey grandmothers is in their provisioning of juvenile offspring with food. Older Japanese macaque females extend affiliative and potentially beneficial behaviors to their younger matrilineal kin, but they do not provision juvenile kin, which are capable of feeding themselves from weaning age. Macaques do not share food with or provide food for juvenile offspring and grandoffspring, the primary caregiving behavior that is described in the human literature on the mother and the grandmother hypothesis (Hawkes *et al.*, 1989, 1997, 1998; Hill and Hurtado, 1991, 1996; Kaplan, 1997; Lancaster and King, 1985; Lancaster and Lancaster, 1983; O'Connell *et al.*, 1999).

Perhaps the absence of provisioning by mothers and grandmothers of juvenile macaques is the reason why the care-taking behaviors that PR Japanese monkey females direct toward their progeny do not confer sufficient benefits to result in significantly greater offspring survivorship. Or in Hill and Hurtado's (1991) terms, the effects of care-taking behaviors in PR Japanese macaques are not pronounced enough to enhance offspring survival significantly. In any case, our findings fail to support the enhanced maternal investment hypotheses and instead suggest that reproductive termination in this population of Japanese macaques is adaptive only insofar as it indicates a set of females that have achieved significantly greater longevity and therefore a larger total number of infants born than is found in females that reproduce until death.

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