

Reproductive Termination in Female Japanese Monkeys: A Comparative Life History Perspective

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ABSTRACT This study explores the question of reproductive termination (loss of reproductive ability) in female Japanese macaques (*Macaca fuscata*) from the Arashiyama West (Texas) troop. We used a large sample of completed lives to identify reproductively terminated female Japanese macaques and to consider reproductive termination in Japanese macaques from a comparative life history perspective, which permits meaningful comparisons to be made with human female menopause. We classified a female as reproductively terminated if the time lag between last parturition and death exceeded two standard deviations of the female's own mean lifetime interbirth interval (Caro et al. [1995] *Int. J. Primatol.* 16:205-220). Seventy of the 95 females in the sample had at least 3 infants over their lifetime (the minimum required for the calculation of a mean and standard deviation), and thus were included in the analysis. Of these 70 females, 20 showed reproductive termination. Reproductively terminated females ranged in age from 14.5-32.7 years, although in females under age 25, reproductive termination was unlikely. The majority of females up to age 25 showed continued parturition. However, after age 25, reproductive termination was population-wide. Length of postreproductive life for reproductively terminated females varied from 0.07-4.4 years, with a mean of 2.08 years. Variation in length of postreproductive life was not related to the age at death of the female.

While the occurrence of population-wide reproductive termination after 25 years does suggest similarities with human female menopause, the age at which this termination occurs is very late in the life span, and it was experienced by only 2.9% of the population. Female Japanese monkeys over age 25 are visibly aged and show outward signs of weakness and deterioration, quite unlike the healthy middle age of menopausal human females. Accordingly, as a life history characteristic, reproductive termination in Japanese macaques does not appear to coincide with menopause as experienced by human females. *Am J Phys Anthropol* 109:455-464, 1999. © 1999 Wiley-Liss, Inc.

The widespread interest in documenting menopause in nonhuman primates has resulted in a proliferation of studies aimed at clarifying the existence and extent of reproductive termination (loss of reproductive ability) in various primate species. Claims for the uniqueness of human female menopause (Jones, 1975; Finn, 1976; Washburn,

1981; Dolhinow, 1984; Lancaster and King, 1985; Prothero and Jurgens, 1987; Russell,

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1987; Kaplan, 1997) vs. those claims for the existence of menopause in nonhuman primate species (e.g., Hodgen et al., 1977; Waser, 1978; Graham et al., 1979; Hrdy, 1981; Nishida et al., 1990) have led to further studies that seek to clarify the existence and the extent of a postreproductive life in various primates. Many of these more recent studies contribute further competing claims for (e.g., Paul et al., 1993) and against (e.g., Johnson and Kapsalis, 1998) the existence of an adaptive termination of reproduction in nonhuman primates. The investigation of an evolved postreproductive life span in primates other than humans has been complicated by at least three methodological and conceptual issues.

The first is the small samples of animals of known age and reproductive history that are available for analysis. Given the difficulty in obtaining accurate lifetime records on large samples of free-ranging nonhuman primates, it is not surprising that much of the available information is anecdotal, or based on very small numbers of animals whose exact ages and reproductive histories are not known.

The second issue relates to the problem of identifying reproductive termination in individual females. Often, the time lag between last parturition and death of the mother (LP-D) is treated as postreproductive, when indeed these females may be dying within a normal interbirth interval. Paul et al. (1993), for example, appear to regard the time lag between last parturition and death (LP-D) as postreproductive, so that mothers of newborn infants are effectively treated as reproductively terminated, simply because they died before having another infant. Nishida et al. (1990) reported median postreproductive periods for the Mahale chimpanzees of 4.2 and 3.6 years as evidence for menopause, but also reported a mean interbirth interval for all females at Mahale as 6 years. Death within a normal interbirth interval, however, is not evidence of the cessation of reproductive capabilities, and the time lag between last parturition and the death of the mother (LP-D) is not automatically "postreproductive."

Takahata et al. (1995) calculated the length of postreproductive life by subtract-

ing 1.5 years (the number of years required for the offspring of a Japanese macaque female to become able to survive without the mother's care) from the time lag between last parturition and death. Johnson and Kapsalis (1998) classified a female rhesus monkey as "postmenopausal" if she had not given birth for 2 consecutive years (the standard interbirth interval for both Japanese and rhesus monkeys) and if she was over 25 years of age. However, given that there is inter- and intraindividual variation in interbirth intervals, and in the time required for offspring to reach independence, a method that takes this variation into account would be more precise. Further, there may be variation in the age at which reproductive termination occurs, and ideally one would not preclude this possibility.

Recently, Caro et al. (1995) set out a criterion for identifying reproductive termination based on the mean interbirth interval for each individual female over her lifetime. Individual females are classified as reproductively terminated when the time lag between last parturition and death of the mother exceeds that of the female's own average interbirth interval by more than two standard deviations. This method requires that an individual female live significantly longer than her own lifetime interbirth interval, and thus reduces the likelihood of categorizing females as reproductively terminated simply because they died before having another baby. It also allows researchers to explore questions about variation within the population in the age at which reproductive termination can occur.

The third issue in the investigation of an evolved postreproductive life span in nonhuman primates involves the criterion for defining menopause as a life history characteristic of a species. In a review of the literature (Pavelka and Fedigan, 1991), we argued that the case for menopause in nonhuman primates rests heavily on a small number of individuals who could not be considered typical of their species. The vast majority (of the small sample) of old nonhuman primates described in the literature, mostly based on laboratory studies, had continued to cycle and even produce infants until the end of their lives. We noted that the repro-

ductive declines described in the literature were idiosyncratic rather than constant across individuals and that, when they did occur, it was at the end of the life span and was associated with extreme deterioration of all systems.

The competing claims for the uniqueness or commonality of menopause appear to result from differences in the importance attached to a small number of old individuals that have stopped reproducing (Caro et al., 1995). A handful of individual monkeys or apes who share some of the endocrinological features of menopause may meet the requirements for a clinical model in which it is the physiological changes in the reproductive system that define menopause. But as a life history characteristic of female *Homo sapiens*, which we seek to understand in evolutionary terms, menopause is characterized by the universal termination of reproduction in women at approximately age 50, only halfway through the species life span. Thus a comparative analysis must consider factors such as the proportion of the population who will live to experience reproductive termination, and the proportion of the life span lived postreproductively. Claims for the existence of menopause in nonhuman primates, from a comparative life history perspective, cannot be based on idiosyncratic cases or atypical individuals.

In the present study, we used a large sample ($N = 95$) of completed lives, for which exact ages and reproductive histories were known, to explore the question of reproductive termination and postreproductive life in female Japanese macaques. First, we used the criterion set out by Caro et al. (1995) to identify reproductively terminated females and then we considered postreproductive females from a comparative life history perspective, in order to compare reproductive termination in Japanese monkeys to human menopause. We asked the following questions: what is the age at which reproductive termination occurs? What proportion of the population is experiencing reproductive termination and a postreproductive life? What proportion of the total life span of these females does this stage represent, and

how does the length of postreproductive life relate to the age at death of the female?

METHODS

Data for this study were collected from the Arashiyama West population of Japanese monkeys (for more information on group history, management, demography, and environment, see Fedigan and Asquith, 1991; Pavelka, 1993). Genealogical records have been maintained on each individual born into the group since 1954, which include date of birth, reproductive history, and date of death or disappearance. Females can experience first estrus at age 4.5 years and produce their first infant at age 5 years. Japanese macaques are seasonal breeders, with a fall mating season and a spring birth season (Fedigan and Griffin, 1996).

The original study sample for this paper consisted of the completed lives of 95 individual females who reached reproductive age and were followed from birth to death. The data were extracted from cumulative genealogical records up to the end of 1993. The youngest female in the sample died at age 5 years, and the oldest female in the sample lived to 32.6 years. Reproductively terminated females were identified by the interbirth interval (IBI) criterion of Caro et al. (1995), in which $LP-D/(\bar{x} \text{ IBI} + 2 \text{ SD}) > 1.0$, i.e., 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. Out of the sample of 95 females, 70 individuals had given birth to at least 3 infants (the minimum required to calculate a mean interbirth interval and standard deviation).

Differences in the age of terminated and nonterminated females were investigated using a t-test. For some analyses, the study subjects were divided into the following age categories: 1, 5.1–10 years ($N = 5$); 2, 10.1–15 years ($N = 13$); 3, 15.1–20 years ($N = 17$); 4, 20.1–25 years ($N = 21$); and 5, ≥ 25.1 years ($N = 14$).

The proportion of the population experiencing reproductive termination was examined using life table analysis (SPSS-PC SURVIVAL analysis, Norusis, 1993). Survival analysis makes use of both censored (dead

TABLE 1. *Reproductively terminated females of the Arashiyama West population (1972–1993)*

Name	Age at death	Last parturition to death (LP-D) in years	Mean IBI + SD (years)	Length of postreproductive life	Proportion of life span
MA 60	14.5	5.50	1.09	4.41	0.30
PK 6576	16.0	2.00	1.89	0.12	0.01
BE 58	16.9	3.92	1.84	2.08	0.12
ME 71	18.7	2.58	2.51	0.07	0.004
RH 58	22.3	11.40	3.81	7.59	0.34
SH 64	22.3	3.33	3.12	0.21	0.01
DE 65	23.4	3.42	2.00	1.42	0.06
BE 586469	24.0	2.25	1.97	0.28	0.01
BE 5864	25.7	2.50	2.20	0.30	0.01
PE 64	25.8	5.50	4.01	1.49	0.06
MI 64	26.1	4.00	2.64	1.34	0.05
RO 63	26.8	3.83	3.31	0.52	0.02
MI 66	26.9	5.92	3.52	2.40	0.09
NO 62	27.0	3.92	3.13	0.79	0.03
WA	27.3	5.25	3.20	2.05	0.08
NO 61	27.7	7.67	3.21	4.46	0.16
MA 58	27.7	4.75	2.61	2.14	0.08
PK 60	29.3	5.42	4.72	0.70	0.02
ME	31.8	6.42	4.36	2.06	0.06
RA	32.7	10.42	3.16	7.26	0.22
Mean	24.59	5.00	2.92	2.08	0.087

females) and uncensored (those sold or alive) intervals. Data for this analysis included all the females ($N = 613$) born into the Arashiyama West population from 1972–1993. For each 1-year age interval, we reported on the proportion of the total female population alive at the start of that interval.

The proportion of the total life span spent in a postreproductive state was calculated by dividing the number of years lived postreproductively by the total number of years lived (age at death). We did not consider the entire LP-D time lag to be postreproductive, since this would have us regarding a female as reproductively terminated the day after giving birth to her last infant. Thus, the number of years lived postreproductively was defined as the time from the end of the female's own average interbirth interval plus two standard deviations to the time of death ($LP-D - \bar{x} IBI + 2 SD$). Where Takahata et al. (1995) subtracted 1.5 years from LP-D to avoid this problem, we subtracted the more precise measure of two standard deviations plus the mean interbirth interval for that particular female.

RESULTS

From the sample of 70 females who had given birth to at least 3 infants, 20 (28.5%)

were identified as having terminated reproduction using the $LP-D/(\bar{x} IBI + 2 SD) > 1.0$ criterion (see Table 1). These 20 females ranged from age 14.5–32.7 years, with a mean age at death of 24.6 years. Females who continued to reproduce ranged in age at death from 8.8–25.7 years, with a mean age at death of 17.3 years. The difference in mean age at death of the reproductive and reproductively terminated females was statistically significant ($t = 5.475$, $df = 68$, $P < 0.0001$).

The distribution of reproductive and reproductively terminated females by age category (see Fig. 1) shows that the proportion of reproductively terminated females increased with age, from 0% in age category 1 (5–10 years) to 86% in age category 5 (25+ years). Note that, while possible, it is unlikely that a female under age 10 would meet the criterion for reproductive termination, since she would need to produce 3 infants and then live significantly longer than her own interbirth interval, and then die, all within 5 years. In age categories 2–4, i.e., among females aged 10–25, reproductive termination can occur, but reproductively terminated females in this age group were a minority, ranging from 8% of 10–15-year-olds to 19% of 20–25-year-olds. Of particular interest were the females aged 20–25

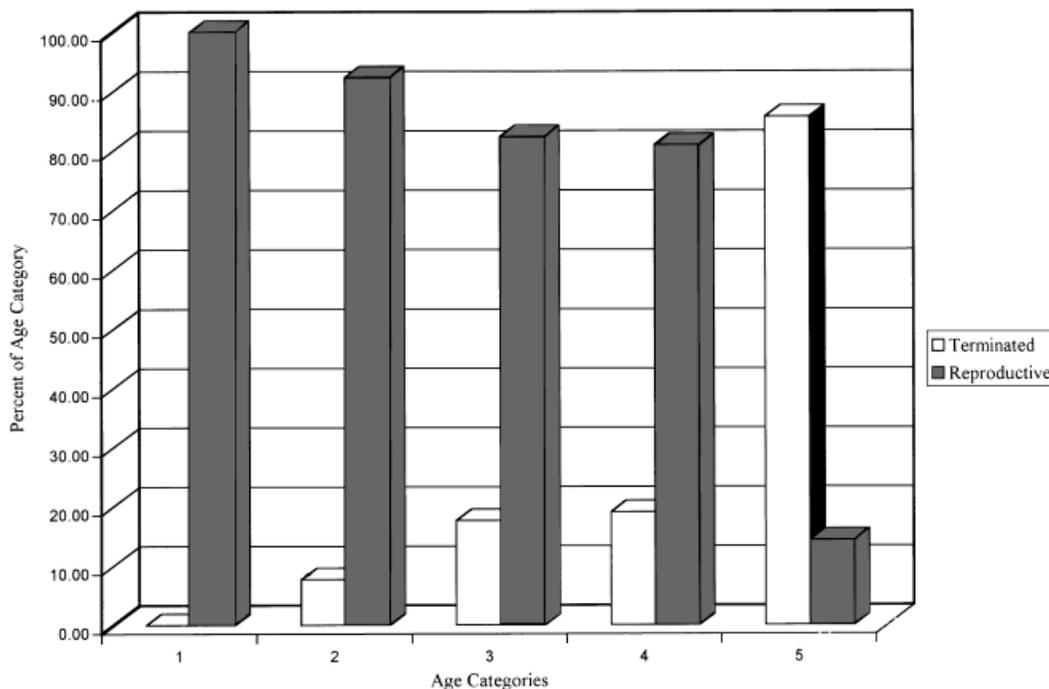


Fig. 1. Age distribution of reproductive and reproductively terminated females.

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 fully 81% of these females were classified as still reproductive, with only 19% showing termination. Old females between ages of 20–25 who became reproductively terminated were thus not representative of their age class. Continued reproduction in these old females is the norm.

This pattern changed with category 5: the vast majority of females over age 25, i.e., 12 out of 14 of the animals in this age category, showed reproductive termination. The other two females in this age category died within the normal range of their own lifetime inter-birth intervals. Betta63 had her last infant at age 23 and died at 25.3 years. The other, Kujiro, had her last infant at age 25 and died, likely of old age, later the same year. The difference in the proportion of terminated females in age categories 4 and 5 is significant ($\chi^2 = 15.004$, $df = 1$, $P < 0.05$).

Table 2 presents life table data showing survivorship of the population to each 1-year age interval and during each age category. According to these data, only 7.9% of the population lived to age 20. The likelihood of living to the start of the subsequent age category (≥ 25 years) is considerably lower than 7.9%. Female Japanese macaques in this population had a 2.9% chance of living to age 25 and a 2.3% chance of living to age 26, the point at which reproductive termination appears to be a certainty.

Finally, in order to make meaningful comparisons to human female menopause as a life history characteristic, the proportion of life span spent in a postreproductive state must be considered. Table 1 shows the length of postreproductive life for the 20 reproductively terminated females and the proportion of the female's life span that it represents. The average time lived postreproductively was 2.1 years, ranging from a minimum of a few days in the case of a female aged 18.7 years (Meme71) to 7.59 years in the case of a

TABLE 2. Life table of Arashiyama West females (1972–1993)

Age interval (in years)	Age category	Number alive at beginning of interval	Percentage of population surviving at each age
0–1	1	618	100.0
1–2	1	563	91.1
2–3	1	530	85.8
3–4	1	481	77.8
4–5	1	416	67.3
5–6	1	364	58.9
6–7	1	320	51.8
7–8	1	287	46.4
8–9	1	243	39.3
9–10	1	200	32.4
10–11	2	174	28.2
11–12	2	146	23.6
12–13	2	128	20.7
13–14	2	116	18.8
14–15	2	101	16.3
15–16	3	93	15.0
16–17	3	76	12.3
17–18	3	67	10.8
18–19	3	59	9.5
19–20	3	56	9.1
20–21	4	49	7.9
21–22	4	41	6.6
22–23	4	38	6.1
23–24	4	28	4.5
24–25	4	20	3.2
25–26	5	18	2.9
26–27	5	14	2.3
27–28	5	9	1.5
28–29	5	4	0.6
29–30	5	1	0.2
30–31	5	1	0.2
31–32	5	1	0.2
32–33	5	1	0.2

female who had her last infant at age 11 but lived to be 22 (Rheus58).

The data presented in Table 1 show a high level of variation in the length of postreproductive life. Based on comparisons with women, we might expect variation in the length of the postreproductive life to be directly related to age at death: the older the woman, the longer she will have lived in a postreproductive state. However, there was no significant relationship ($r^2 = 0.157$, $F = 3.354$, $P > 0.05$) between age at death and length of postreproductive life. This is illustrated in Figure 2.

DISCUSSION

Reproductive termination can occur in female Japanese monkeys between ages 10–25, but its expression in this age group is rare. After age 25, reproductive termination appears to be a certainty for this species,

with 86% of subjects over age 25 becoming reproductively terminated. Given that there are no records of any female in this (or any Japanese macaque) population ever giving birth after age 25, we appear to be dealing with a biologically meaningful cutoff point in the reproductive lives of female Japanese monkeys. This parallels the findings of Walker (1995) and Johnson and Kapsalis (1998), who reported reproductive termination after age 25 for the closely related rhesus macaque.

As Caro et al. (1995) pointed out, the interbirth interval 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, false positives and negatives are possible. 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. Physiological data were not available for the study population, so we cannot speak directly to the question of menopause-like changes in the reproductive systems of our subjects. However, Nozaki et al. (1997) reported that the ovaries of 3 female Japanese monkeys, aged 26–28, showed a thickening and sclerosis of the ovarian surface, no or few primordial, primary, and tertiary follicles, abnormal follicles in the cortex, the development of thick-walled blood vessels, and large luteal-like tissue masses in the medulla. They judge these 3 animals to be perimenopausal.

Only Caro et al. (1995) used a nonclinical measure of reproductive termination that distinguishes reproductive termination from death during a normal interbirth interval. Based on their examination of demographic records from 13 nonhuman primate species, they reported a range of 0% (vervet monkeys) to 60% (chimpanzees) of females terminating reproduction, and 99% of a sample of women. The authors also reported on the percentage of females terminating reproduction for three macaque species: 3.8% for bonnet macaques, 13.2% for rhesus macaques, and 25.6% for pigtail macaques, as compared with the 28.5% of female Japa-

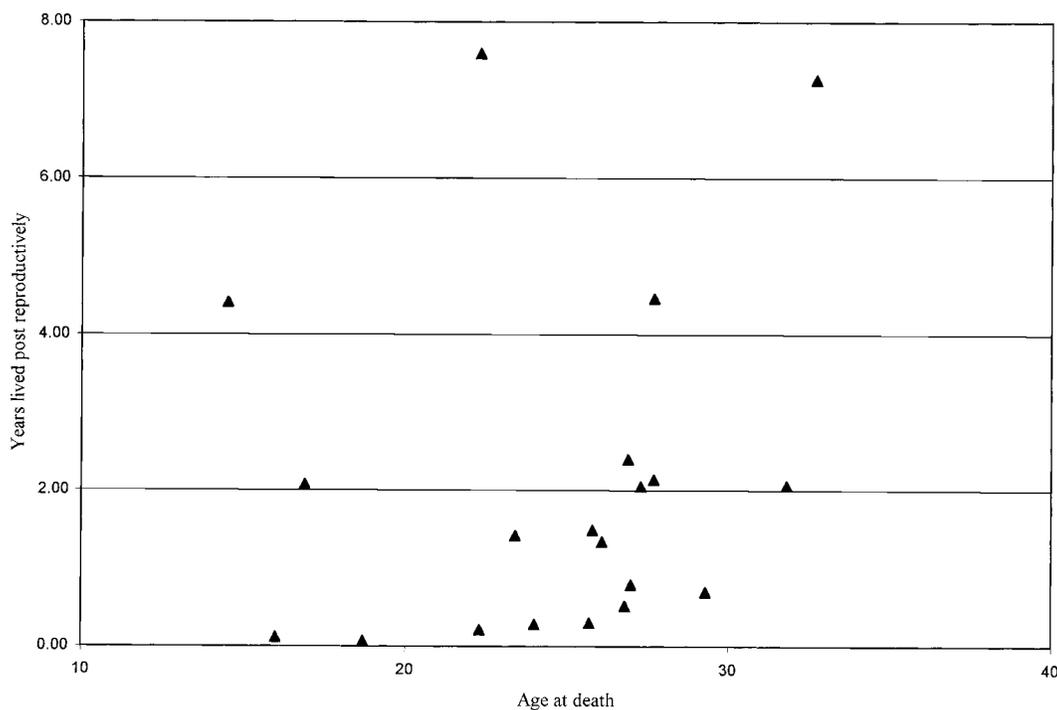


Fig. 2. Scatterplot of age and years lived postreproductively.

nese macaques exhibiting reproductive termination in this study.

Caro et al. (1995) did not present data on the age of females showing reproductive termination, and the age at which reproductive termination became population-wide. Although 28.5%, or 20 of our sample of 70 females, were identified as reproductively terminated, 8 of these 20 females were under age 25. These 8 were not representative of their age class, since prior to age 25, the majority of females are still reproducing. Only 12 reproductively terminated females, or 17% of the sample, were 25 and older: the age at which population-wide termination occurs. Note that survivorship in our sample is higher than survivorship of the general population, in part because our sample of females included only those who had lived to reproductive age. Most mortality occurs in the first 5 years of life (see Table 2 in Fedigan and Zohar, 1997). Population survival values (Table 2) suggest that a much lower number of females, only 2.9% of those born, can expect to live to the age of popula-

tion-wide reproductive termination. Johnson and Kapsalis (1998) found that no more than 10% of rhesus macaque females can be expected to live beyond age 25 and thus to undergo the "climacteric."

Our finding that reproductive termination occurs at a low frequency in female Japanese monkeys between the ages 10–25, 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 human female menopause, other factors must be considered. Human female menopause is a form of reproductive termination that is distinctive in its ubiquity and timing in the life span. Menopause, the complete cessation of ovulation, menstruation, and reproductive capabilities at age 50 (the me-

dian age for menopause both historically and cross-culturally), is universal, and not idiosyncratic, among women. Further, it occurs only halfway through the species life span of 100 years. While women may experience a variable and gradual slowing of reproductive performance in the decades preceding menopause, at approximately age 50 reproductive capabilities terminate entirely. 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 question: how old is a 25-year-old Japanese monkey, 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) reported a 2% survivorship to age 85 for the Dobe !Kung, a value which is comparable to the 2.3% survivorship to age 26 for the Japanese macaque females (Table 2). 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. Tigges et al. (1988) described wide variation among the survival curves of three groups of rhesus monkeys, all maintained at the Yerkes Regional Primate Research Center. Takahata et al. (1995) reported considerably higher survivorship rates for old female Japanese monkeys at Arashiyama in Japan (41% to age 20) than we report for the sister troop in Texas (7.9% to age 20). One explanation for this difference may be sample size: we were able to use population survival rates, which showed that out of 618 females born, 49 individuals lived to age 20, whereas Takahata et al. (1995) reported survivorship values based on 13 out of 32 females living to age 20. These differences illustrate the tenu-

ous nature of comparisons based on survivorship values.

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

$$\frac{\text{species A age X}}{\text{species A maximum life span}} = \frac{\text{species B age X}}{\text{species B maximum life span}}$$

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 human known to Western science was a woman by the name of Jeanne Calment, who was 122 years of age at the time of her death in 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. Nevertheless, 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 20–25-year-olds are unlikely to experience reproductive termination: 81% of this age group were still reproductive.

Human female menopause occurs in healthy middle age. Unlike a 50-year-old woman, a 25-year-old monkey is part of a tiny surviving cohort whose members are visibly aged and showing signs of frailty and deterioration. Johnson and Kapsalis (1995,

1998) similarly pointed out that reproductive termination in rhesus macaques is not temporally distinct from the advanced aging of the organism, and Nozaki et al. (1997) noted that menopause in macaque monkeys occurs close to the end of the life span.

Other important distinctions between reproductive termination in Japanese monkeys and humans are revealed by looking at the length of postreproductive life, and at the relationship between age and length of postreproductive life. In our sample of reproductively terminated females, the average number of years lived postreproductively (measured as $LP-D - (\bar{x} IBI + 2 SD)$) was 2.08, representing an average 8.7% of the life span of the females. Takahata et al. (1995) reported that, in their sample of 13 female Japanese monkeys who lived beyond age 20, the number of years lived postreproductively (measured as $LP-D - 1.5$) was 4.5 years, representing 16% of the average life span. Caro et al. (1995) regarded the entire time lag between last parturition and the death of their terminated subjects to be postreproductive (years lived postreproductively = $LP-D$), thus yielding much higher values for the proportion of life span lived postreproductively in the species in their sample.

Because human reproductive termination occurs in healthy middle age, women spend a large proportion of their lives in a postreproductive state. A woman who lives to be 65 will spend 23% of her life in a postreproductive state, a woman who lives to be 75 will spend 33% of her life living postreproductively, and an 85-year-old will spend 41% of her life in a postreproductive state. Postreproductive life in humans is lengthy and it is directly correlated with age, since every year of life lived after age 50 is postreproductive for women. In fact, these figures underestimate the postreproductive life span of women by assuming reproduction right up until age 50, when in fact less than 3% of births occur in women aged 40 years and older (Fretts et al., 1995).

In summary, the present study addressed at least two of the common problems in research on the postreproductive lives of nonhuman primate females. We were able to work with a reasonably large (by primate standards) sample of individuals followed

from birth to death, and we applied a criterion that allowed us to distinguish postreproductive life from an interbirth interval. Our findings suggest that age 25 years in a Japanese macaque female is the biological endpoint for parturition. Although individual females may experience reproductive termination at almost any stage of reproductive life, few do so before age 25. Most females go on producing infants right up until death. Furthermore, only 2.9% of the Arashiyama West population lived to age 25 years, and of those females that did terminate reproduction before death, most spent less than 10% of their lives in a postreproductive state. There is great variability in the length of postreproductive life, a variability that is not related to the age of the female at death. All of these features of reproductive cessation in our study population seem to us quite distinct from menopause in the human female, and lead us to conclude that the life history pattern of reproductive senescence in Japanese macaques would not be a good model for that found in humans. Nor would human menopause be a good model for reproductive cessation in macaques.

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