



# Availability and adaptive value of reproductive and postreproductive Japanese macaque mothers and grandmothers

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(Received 15 October 2001; initial acceptance 12 December 2001;  
final acceptance 14 February 2002; MS. number: A9191R)

Prior tests of the grandmother hypothesis have suggested that postreproductive female Japanese macaques, *Macaca fuscata*, do not significantly improve the survivorship of their descendents. However, not all postreproductive females are grandmothers, and not all grandmothers are postreproductive. In this study we looked at the daughters and grandchildren of 70 female Japanese macaques to assess the availability and adaptive value of reproductive and postreproductive mothers and grandmothers. We found that postreproductive Japanese macaque grandmothers are very rare. Only 2.8% of the sample of daughters had a postreproductive grandmother available when they began to reproduce, and only 4.2% of the reproductive life span of the daughter (less than 6 months for the average female) was spent with a postreproductive grandmother available to help the daughter. Grandchildren who survived to age 5 had a postreproductive grandmother available to them for only 4% of the first 5 years of life (i.e. a couple of months on average). The presence of a living mother, irrespective of her reproductive status, was associated with improved reproduction in her adult daughters, and the presence of a postreproductive grandmother was associated with significantly improved survivorship of grandchildren to age 1. While improved maternal investment does not appear to be the primary explanation for reproductive termination in Japanese monkeys, the few postreproductive females that have unweaned grandchildren available appear to have a positive influence on their survival.

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There is little evidence in animal species for the universal midlife termination of reproduction that is seen in human females. Most reports of the cessation of female reproduction in mammals indicate that the termination of reproductive function is part of the overall advanced ageing of the organism (Pavelka & Fedigan 1991). For example, postreproductive females are not known to occur in baleen whales (Hamilton et al. 1998) nor in most odontocetes, despite age-related declines in fecundity (Marsh & Kasuya 1986). Only phenotypically superior bighorn ewes, *Ovis canadensis*, are said to survive long enough to reach reproductive senescence (Berube et al. 1999). Red deer hinds, *Cervus elaphus*, like other farm animals, show sharp fertility declines only as they approach the maximum expected life span (Fisher et al. 1996). Japanese macaques, *Macaca fuscata*, have been

documented to show population-wide termination of reproduction at age 25, but most rarely survive to this age (Takahata et al. 1995; Pavelka & Fedigan 1999; Fedigan & Pavelka 2001). This also appears to be true for the closely related rhesus macaque, *M. mulatta* (Johnson & Kapsalis 1995, 1998). Few data are available on reproductive performance in later life in birds, but deterioration in performance is generally attributed to degenerative senescence (Newton & Rothery 1997). Short-finned pilot whale, *Globicephala macrorhynchus*, females may be the only exception, in that they cease to breed when they still have a mean life expectancy of 14 years (Marsh & Kasuya 1986; Olesiuk et al. 1990).

According to maternal investment models, menopause originated as an adaptation for postreproductive maternal investment, whether mothering or grandmothering investment (Hill & Hurtado 1991; Hawkes et al. 1998; Peccei 2001). The mothering hypothesis focuses on investment in first-generation offspring, such as increasing the reproductive performance of daughters, whereas the grandmother hypothesis concentrates on the second generation and on the survivorship of grandchildren

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(Peccei 1995a, b). Human females are hypothesized to stop reproducing at midlife because there are greater fitness benefits to be had by contributing to the production and/or survival of their children's offspring than there are from continuing to produce their own. By virtue of being unencumbered by the demands of their own infants, these women are thought to be in a position to direct helpful behaviour towards their children or grandchildren, behaviour that has an effect on reproductive success.

Some researchers have argued that postreproductive female animals other than humans may also have a positive influence on the survivorship of existing descendants, particularly in species such as cetaceans and primates, who bear one young at a time, have low lifetime productivity, nearly exclusive maternal care and lengthy periods of offspring dependence (Marsh & Kasuya 1986). However, reports on the behaviour and adaptive value of grandmothers in other species are rare. This was noted by Borries (1988) and continues to be true nearly 15 years later. To our knowledge, only Packer et al. (1998), who tested the grandmother hypothesis in olive baboons, *Papio cynocephalus anubis*, and African lions, *Panthera leo*, recognized and measured both grandparental and reproductive status in their subjects. They found that postreproductive females did not enhance the fitness of grandchildren or older children, and that reproductive cessation resulted from the general ageing process, rather than from direct selection favouring postreproductive grandmothers.

In previous papers, we identified postreproductive female Japanese macaques and performed tests of the mother and grandmother hypotheses by examining the survivorship of offspring and grandoffspring of reproductive versus postreproductive females. Based on those analyses we concluded that reproductive termination in Japanese monkeys is more likely a by-product of longevity, than a trait that was directly favoured by selection (Pavelka & Fedigan 1999; Fedigan & Pavelka 2001). Japanese macaques are an ideal species in which to investigate the adaptive value of reproductive and postreproductive mothers and grandmothers. Reproductive termination, however late in life, has been documented, and these monkeys are long lived and characterized by male dispersal and female philopatry, such that social groups are organized into multigenerational matrilineal lines of related females. Kin selection is believed to be a primary force in shaping behaviour and reproduction in this species, and grandmothers frequently engage in kin-directed cooperative behaviour. Grandmother Japanese macaques could potentially provide substantial assistance, care and protection to their first and second generation of descendants (e.g. through agonistic and social support, and allomothering). In this study we investigated the availability and adaptive value of reproductive and postreproductive mothers and grandmothers. This allowed us to target not just postreproductive females in general (with and without living adult daughters or grandchildren), but the theoretically important subcategories of postreproductive mothers and grandmothers in particular. We examined the availability of

different categories of mothers by measuring the number of females who had a reproductive and postreproductive mother alive when they first give birth, and the proportion of the daughter's reproductive life during which her mother was (1) alive and reproductive, (2) alive and postreproductive and (3) not alive. To examine the availability of reproductive and postreproductive grandmothers we measured the proportion of the first 5 years of the grandchildren's lives spent with each category of grandmother. The adaptive value of reproductive and postreproductive mothers is determined by an examination of the effect of each category of mothers on their daughters' age at first birth and the interbirth intervals, and each category of grandmothers on the survivorship of their grandchildren to age 1 and age 5.

## METHODS

The life-history data for this study were collected on the Arashiyama West population of Japanese macaques, which has been studied over the past 47 years. These monkeys were first found ranging on the outskirts of Kyoto, Japan in 1954 and have been followed ever since. In 1966, the Arashiyama population fissioned into two daughter groups, and in 1972, one of these groups was moved in its entirety to a ranch in south Texas and renamed the Arashiyama West (AW) group. Genealogical records were maintained on each individual born between 1954 and 1997, including date of birth, reproductive history, and date of death or disappearance. These monkeys were minimally provisioned and minimally disturbed by humans throughout the years of this study, and thus they foraged extensively on local flora and encountered local fauna.

AW monkeys have been documented to die of many causes, such as predation (coyotes, *Canis latrans*, bobcats, *Felis rufus*, mountain lion, *F. concolor*), snake bites, infestations of parasites, ingestion of poisonous plants, infectious diseases, noninfectious ailments such as cancer, heart disease and osteoarthritis and social stress (wounding by conspecifics). Although some specific causes of death are native to the south Texas environment, the general categories of mortality are applicable to primates everywhere. The south Texas environment is hotter than their native habitat in Japan, but neither males nor females are more likely to die during the summer months (Fedigan & Zohar 1997).

Once a day, food (monkey chow, grain and/or produce) was spread from a truck along a road bisecting the enclosure and these provisions were usually completely consumed by the monkeys within the hour of feeding. Although the exact effects of food enhancement on demographic patterns in this species are not known, due to the absence of directly comparable data sets from unprovisioned Japanese macaques, Asquith (1989) suggested that an increase in population size due to reduced infant mortality and shortened interbirth intervals occurs in provisioned populations.

Although the AW population is not living in its native habitat and is provisioned, several studies have shown that the demographic profile and life-history pattern of

these monkeys is similar to that observed for provisioned groups in Japan (Fedigan et al. 1986; Fedigan 1991; Fedigan & Zohar 1997). The average age at first birth in Japanese macaques is 5–6 years, with a few outliers first giving birth at age 4 or age 7. Breeding is seasonal, and females can give birth every year, although the average interbirth interval in this population is 2 years (Fedigan et al. 1986). It is also possible that the survivorship of very old females may be increased in provisioned populations, however, we are again lacking comparable data from nonprovisioned groups. For further details of the history, demography, management and environmental setting of the AW population, see Fedigan (1991) and Pavelka (1993).

The original sample for this study consists of the completed lives of 95 individual females who reached reproductive age and were followed from birth to death. We analysed all possible completed lives from cumulative genealogical records up to the end of 1993. The youngest female in the sample died at the age of 5 years, and the oldest female in the sample lived to 32.6 years. Reproductively terminated females were identified by Caro et al.'s (1995) interbirth interval (IBI) criterion, when  $LP - D / (\bar{X}IBI + 2 SD) > 1.0$ ; that is, when the time lag between last parturition (LP) and the death (D) of the mother ( $LP - D$ ) exceeded two standard deviations of the female's own mean lifetime interbirth interval, she was classified as postreproductive. This use of Caro et al.'s (1995) criterion is important, because many studies regard any time lag between last parturition and death of the mother as postreproductive, without considering how this time lag compares to the normal interbirth interval for the species or for the individual. But death within a normal interbirth interval is not evidence of the cessation of reproductive capabilities, and the time lag between the last parturition and the death of the mother is not automatically postreproductive. The method used requires that an individual female live significantly longer than her own average lifetime interbirth interval, and thus reduces the likelihood of categorizing a female as postreproductive simply because she died before having another infant.

Out of the sample of 95 females, 70 individuals gave birth to at least three infants (the minimum required to calculate a mean interbirth interval and standard deviation). Of these 70 females, 20 were categorized as reproductively terminated and hence living to experience a postreproductive life span, and 50 continued to reproduce until death. Although this method is not direct physiological evidence of ovarian failure, it is a good indicator of reproductive termination for those primate populations in which hormonal profiles, ovarian histology and direct measures of menstrual activity are not available. Eight of the 70 females who could be categorized as reproductive or postreproductive did not produce any daughters (and hence, grandchildren that were known to us), so the present study was based on 62 grandmothers and their 175 daughters and 905 grandchildren. For the analyses in which we needed the daughter's death date we were able to use only 88 of the 175 daughters, and only 74 of these produced infants.

Of the 905 grandchildren born, we had complete information on 886 individuals who 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.

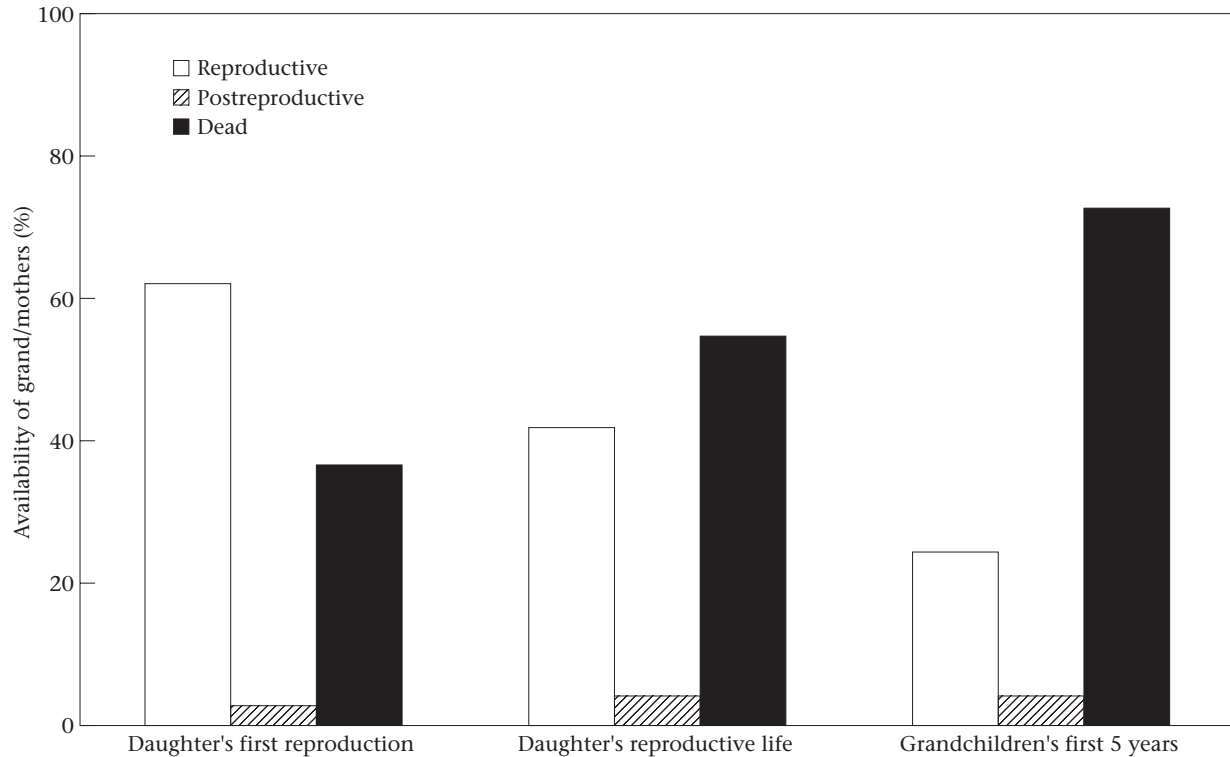
We compared the possible effects of macaque mothers on their daughters' reproduction using independent samples *t* tests to compare daughters whose mothers were dead and alive. We used analysis of variance (ANOVA) tests to compare daughters whose mothers were dead (Dead), alive and reproductive (A-R), and alive and postreproductive (A-PR), with planned comparisons between Dead/A-PR and A-R/A-PR (SPSS-PC; Norusis 1993). We analysed the survivorship of grandchildren whose grandmothers were Dead, A-R, or A-PR using the SPSS-PC program SURVIVAL-Life Tables. This statistical technique employs both uncensored and censored intervals and corrects for censoring. Analyses based only on completed (uncensored) lives are known to create a bias towards shorter intervals. Therefore, SPSS-SURVIVAL incorporates the analysis of completed intervals (e.g. grandchildren with known death dates), and the intervals that are incomplete or censored (because, for example, some grandchildren may not have reached the age of 1 or 5 by the end of our study). Life-table analysis subdivides the period of observation into smaller time intervals (e.g. survival to age 5 can be subdivided into five 1-year intervals) and yields an overall probability of an event (death) occurring during each interval. A Wilcoxon–Gehan test compares the survival distributions of the different groups (Norusis 1993).

## RESULTS

### Availability of Mothers and Grandmothers

Of the 175 Japanese macaque daughters in our sample, 64 (36.6%) had no mother alive, 106 (60.5%) had a reproductive mother and five (2.8%) had a postreproductive mother alive (Fig. 1) at the time they first gave birth. Therefore, the mothers of nearly two-thirds of the daughters in our sample were alive at time of their daughters' first birth, and thus, could potentially contribute to their daughters' production of infants or to the survivorship of those infants, but the vast majority were themselves still producing infants. Very few daughters had a postreproductive mother available to them when they began to reproduce.

To assess the proportion of a daughter's reproductive life that was lived while her own mother was still alive, we used only the daughters for whom we had death dates ( $N=74$ ), and thus, whose entire reproductive lives were known. 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 (Fig. 1). 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 who was herself still reproducing (4.04/9.71 years, 41.6%). Only 0.41/9.71 years or 4.2% of the



**Figure 1.** The availability of Japanese macaque mothers to their daughters at the time of their daughters' first birth ( $N=175$ ) and throughout their daughters' reproductive lives (9.71 years,  $N=74$ ) and the availability of Japanese macaque grandmothers to their grandchildren ( $N=504$ ) during the first 5 years.

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 (Fig. 1), 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 who survived to age 5 had a living grandmother available to them for only 1.4 years, or 28% of that time. During most of that time (1.2 years) the grandmother had an infant of her own to care for. Only 0.2 years, or 4% of the first 5 years of life of the grandchildren in our sample (i.e. 2 months on average) was spent with a postreproductive grandmother available to offer the extra care-giving behaviour predicted by the grandmother hypothesis.

### Adaptive Value of Mothers and Grandmothers

Our next set of analyses explores the possible effects that a female can have on the reproduction of her daughter (Table 1). There was a significant difference in age at first birth between daughters whose mothers were alive versus dead when they began reproducing. The mean age at first birth was 6.0 years (71.7 months) for females whose mothers were dead and 5.6 years (67.11

months) for females whose mothers were alive. As Japanese macaques are annual seasonal breeders, this 4.5-month difference in age at first birth is being driven by a significant difference in the distribution of age at first birth for daughters whose mothers were dead versus alive (Fig. 2; chi-square:  $\chi^2_3=8.942$ ,  $P=0.030$ ). Although there were significant differences in the age at first birth for daughters whose mothers were either dead, reproductive or postreproductive (ANOVA:  $F_{2,172}=3.952$ ,  $P=0.021$ ), there were no significant differences between the daughters of reproductive and postreproductive mothers (contrasts:  $P=0.253$ ).

The presence of a mother also appeared to be of some benefit to females in terms of shortening their interbirth intervals (Table 1), although this tendency was not quite statistically significant. Females, on average, had shorter interbirth intervals when their mothers were alive (18.1 months) compared with when they were dead (19.2 months). This tendency was even greater once mothers became postreproductive, and the average interbirth intervals of their daughters dropped to 16 months.

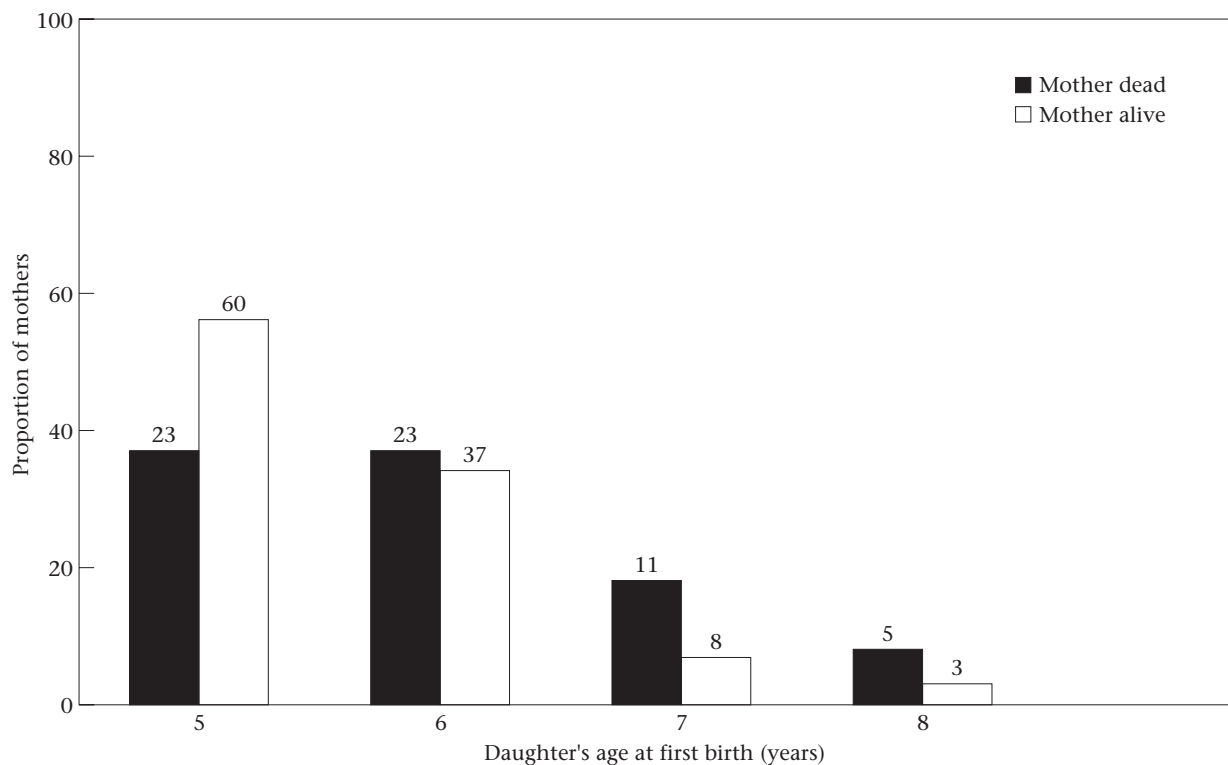
The essence of the grandmother hypothesis is that grandmothers, specifically postreproductive grandmothers, are able to enhance the survivorship of their grandchildren. Thus, we compared the probability of survivorship to age 1 based on the grandmother's status during the first year of the grandchild's life, and the probability of survivorship to age 5 based on the

**Table 1.** Effect of mother status on daughter's age at first birth and interbirth intervals

Daughter's reproduction	Mother's status			
	Dead	Alive	Alive	
			Reproductive	Postreproductive
Age at first birth (years)*				
$\bar{X}$ +SD	6.0+1.0	5.6+0.9	5.6+0.9	6.1+0.7
N	64	111	106	5
Average interbirth interval (months)†				
$\bar{X}$ +SD	19.2+8.5	18.1+7.3	18.5+7.4	16.0+5.7
Number of interbirth intervals	451	273	239	34

\*Independent samples *t* test: dead versus alive:  $t_{173}=2.565$ ,  $P=0.01$ ; ANOVA: dead\*alive-reproductive\*alive-postreproductive:  $F_{2,172}=3.952$ ,  $P=0.02$ .

†Independent samples *t* test: dead versus alive:  $t_{722}=1.702$ ,  $P=0.09$ ; ANOVA: dead\*alive-reproductive\*alive-postreproductive:  $F_{2,721}=2.858$ ,  $P=0.06$ .

**Figure 2.** The proportion of mothers who were alive versus dead at the time of their daughter's first birth. Sample sizes are given above bars.

grandmother's status during the first 5 years of the grandchild's life (see Table 2). There was a significant difference in survivorship of grandchildren to age 1 depending on the grandmother's status (Wilcoxon-Gehan test:  $W_2=6.29$ ,  $P=0.04$ ). Specifically, grandchildren that had a postreproductive grandmother available were significantly more likely to live to age 1 than those without a living grandmother, or a grandmother that was still reproducing ( $W_1=3.99$ ,  $P=0.05$  and  $W_1=6.47$ ,  $P=0.01$ , respectively). There were no differences in the survivorship of grandchildren to age 5 among the three groups of grandmothers ( $W_2=1.272$ ,  $P=0.53$ ).

## DISCUSSION

Grandmother Japanese macaques proved to be less common than we had expected. This study showed that while nearly two-thirds of new mothers had a living mother present when they first gave birth, the mother would probably remain alive for less than half of her daughter's reproductive life. Furthermore, postreproductive grandmothers are exceedingly rare. Only five 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

**Table 2.** Effect of grandmother's status on survivorship of grandchildren to age 1 and age 5

Grandchildren's survivorship	Mother's status			
	Dead	Alive	Alive	
			Reproductive	Postreproductive
To age 1*				
% Surviving	85	89	88	95
N	566	320	281	39
To age 5†				
% Surviving	79	73	72	72
N	745	141	102	39

\*Wilcoxon–Gehan test: dead versus alive-reproductive versus alive-postreproductive:  $W_2=6.29$ ,  $P=0.04$ ; alive-postreproductive versus dead:  $W_1=3.99$ ,  $P=0.05$ ; alive-postreproductive versus alive-reproductive:  $W_1=6.47$ ,  $P=0.01$ .

†Wilcoxon–Gehan test: dead versus alive-reproductive versus alive-postreproductive:  $W_1=1.272$ ,  $P=0.53$ .

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 opportunities for classic maternal investment models to operate.

Despite being somewhat 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 earlier (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 oestrus (one that results in a conception) at age 4.5. The first oestrous 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 they would have had little need or opportunity to interact with previously. The inexperienced behaviour of these young Japanese monkey females increases the likelihood that adult males will target them for aggression (McDonald 1985). In vervet monkeys, *Cercopithecus aethiops*, adult daughters whose mothers are still living in the group receive less aggression and are defended more often than young adult females whose mothers have 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 consort.

Although few, other reports of grandmother animals also suggest the potential for mothers/grandmothers to have an impact on the reproduction of descendants. Fairbanks & McGuire (1986) report that captive vervet monkey females with living mothers produce more surviving offspring. Borries (1988) reports that grandmother langurs (*Presbytis entellus*) do invest behaviourally in their

grandchildren, and old rhesus macaque females are known to defend and protect related infants (Partch 1978). In both African elephants, *Loxodonta africana* (Lee 1987) and Asian elephants, *Elaphus maximus* (Rapaport & Haight 1987), matrilineal relatives display extensive allomaternal care, and grandmothers will allow calves that are their grandoffspring to suckle at their breasts. In African lions and olive baboons, neither the survival of grandchildren nor the reproductive performance of adult daughters is improved by the presence of a post-reproductive grandmother. Lion cubs show higher survival only if their grandmother is herself reproductively active, because female lions only engage in allomothering while tending to their own cubs (Packer et al. 1998). To our knowledge, there are no studies on the availability and adaptive value of grandmothers in whales or other cetaceans.

Evidence for the adaptive value of postreproductive mothers and grandmothers is less straightforward. In a previous test of the grandmother hypotheses (Fedigan & Pavelka 2001), in which all 20 reproductively terminated females were compared with all 50 reproductive females (irrespective of maternal or grandmaternal status), we 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 favouring longevity. Yet in the present study, in which we were able to target the theoretically important postreproductive mothers and grandmothers, we found some tantalizing evidence for the adaptive value of postreproduction, the essence of maternal investment hypotheses. The presence of postreproductive mothers was associated with a tendency towards shorter interbirth intervals in their daughters, and those few grandchildren who had a post-reproductive grandmother present during their first year of life were significantly more likely to survive (95%) than those without a grandmother present (85%), or than those whose grandmother was present but still

reproducing (89%). The first year of life is critical, as most mortality of immatures occurs during this period (Fedigan & 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 restricted to the infant or preweaning stage of life. Recall, however, that by this stage, almost 75% of the grandchildren no longer had 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.

The tendency towards shorter interbirth intervals of daughters and the significant difference in survivorship of grandchildren to age 1 both seem to fit one classic premise of maternal investment hypotheses that by ceasing to reproduce, a female can contribute to the production and survival of her children's offspring. What is the proximal mechanism by which postreproductive females could shorten the interbirth intervals of their daughters? Japanese macaque grandmothers do not feed or nurse the offspring of their daughters, but many of them do protect, babysit, agonistically support and retrieve from danger those infants who are their matrilineal descendents, especially the offspring of their daughters (Fedigan 1992). They may do so whether they are postreproductive or still reproducing themselves, but those who are postreproductive and not burdened with their own infants may be better able to assist in the care of the infants of their female kin. The additional mothering/grandmothering care creates sufficient energy and release time for their daughters to mate and conceive again sooner than they would without their mother's assistance, and increases survival of the unweaned grandchildren. Female Japanese macaques with infants from the prior year will mate again in the subsequent season and temporarily leave their infants behind with matrilineal relatives while they mate.

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. We have argued elsewhere that reproductive termination in this population is a by-product of selection favouring longevity rather than a result of direct selection for reproductive termination (Fedigan & Pavelka 2001). 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 who find themselves without an unweaned infant of their own but with a grandchild available to benefit from their free time and energy. Given that females lose their fertility through the ageing process, it would be adaptive to focus their care towards the most vulnerable members of their family. It is also possible that the correlation between the presence of a

postreproductive grandmother and the production and survival of grandchildren may be due to other factors, however, an earlier comparison of females who lived to become postreproductive with those who died while still reproductive revealed no difference in lifetime dominance rank, body weight, or matrilineal affiliation (Fedigan & Pavelka 2001). Still, these and other possible confounding factors, such as kin group size, environmental conditions and heritability, are the subject of ongoing analyses.

### Acknowledgments

We are grateful to the many scientists who have studied the Arashiyama monkeys over the past 45 years for their contributions of life-history data. We especially thank Lou Griffin, the Director of the Texas Snow Monkey Sanctuary and manager of the Arashiyama West population, for the genealogical information that she supplied over many years. Olivia Brusselers and Shannon Digweed assisted with editing. M.S.M.P. and L.M.F.'s research is funded by research grants from the Natural Sciences and Engineering Research Council of Canada (NSERC). Thank you also to the Calgary Institute for the Humanities for support provided to M.S.M.P. for this project, and to two anonymous referees for very thoughtful and helpful comments on the manuscript. The research presented here was described in Animal Care Certification Protocol No. 96004, approved April 1994 by the University of Calgary Life and Environmental Sciences Animal Care Committee.

### References

- Asquith, P. J. 1989. Provisioning and the study of free-ranging primates: history, effects and prospects. *Yearbook of Physical Anthropology*, **32**, 129–158.
- Berube, C. H., Fiesta-Bianchet, M. & Jorgenson, J. T. 1999. The individual differences, longevity, and reproductive senescence in high horn ewes. *Ecology*, **80**, 2555–2565.
- Borries, C. 1988. Patterns of grandmaternal behavior in free-ranging Hanuman langur (*Presbytis entellus*). *Human Evolution*, **3**, 239–260.
- Caro, T. M., Sellen, D. W., Parish, A., Frank, R., Brown, D. M., Volland, E. & Bergerhoff Mulder, M. 1995. Termination of reproduction in nonhuman and human female primates. *International Journal of Primatology*, **16**, 205–220.
- Fairbanks, L. A. 1988. Vervet monkeys grandmothers: effects on mother–infant relationships. *Behaviour*, **104**, 176–188.
- Fairbanks, L. A. & McGuire, M. T. 1986. Age, reproductive value and dominance-related behaviour in vervet monkey females: cross-generational influences on social relationships and reproduction. *Animal Behaviour*, **34**, 1710–1721.
- Fedigan, L. M. 1991. History of the Arashiyama West macaques in Texas. In: *The Monkeys of Arashiyama: Thirty Five Years of Research in Japan and the West* (Ed. by L. M. Fedigan & P. J. Asquith), pp. 54–73. Albany: State University of New York.
- Fedigan, L. M. 1992. *Primate Paradigms*. 2nd edn. Chicago: University of Chicago Press.
- Fedigan, L. M. & Pavelka, M. S. M. 2001. Is there adaptive value to reproductive termination in female Japanese monkeys? A test of maternal investment hypotheses. *International Journal of Primatology*, **22**, 109–125.
- Fedigan, L. M. & Zohar, S. 1997. Sex differences in mortality of Japanese macaques: twenty-one years of data from the

- Arashiyama West population. *American Journal of Physical Anthropology*, **102**, 161–175.
- Fedigan, L. M., Fedigan, L., Gouzoules, S., Gouzoules, H. & Koyama, N.** 1986. Lifetime reproductive success in female Japanese macaques. *Folia Primatologica*, **47**, 13–157.
- Fisher, M. W., McLeod, B. J., Mockett, B. G., Moore, G. H. & Krew, K. R.** 1996. Reproductive senescence in aged red deer hinds. *Proceedings of the New Zealand Society of Animal Production*, **56**, 344–346.
- Hamilton, P. K., Knowlton, A. R., Marx, M. K. & Kraus, S. D.** 1998. Age structure and longevity in North Atlantic right whales *Eubalaena glacialis* and their relation to reproduction. *Marine Ecology Progress Series*, **171**, 285–292.
- Hawkes, K., O'Connell, J. F., Blurton Jones, N. G., Alvarez, H. & Charnov, E. L.** 1998. Grandmothering, menopause, and the evolution of human life histories. *Proceedings of the National Academy of Sciences, U.S.A.*, **95**, 1136–1139.
- Hill, K. & Hurtado, A. M.** 1991. The evolution of premature reproductive senescence and menopause in human females. An evaluation of the grandmother hypothesis. *Human Nature*, **2**, 313–350.
- Johnson, R. L. & Kapsalis, E.** 1995. Ageing, infecundity and reproductive senescence in free-ranging female rhesus monkeys. *Journal of Reproduction and Fertility*, **105**, 271–278.
- Johnson, R. L. & Kapsalis, E.** 1998. Menopause in free-ranging rhesus macaques: estimated incidence, relation to body condition, and adaptive significance. *International Journal of Primatology*, **19**, 751–765.
- Lee, P. C.** 1987. Allomothering among African elephants. *Animal Behaviour*, **35**, 278–91.
- McDonald (Pavelka), M. S.** 1985. Courtship behavior of female Japanese monkeys. *Canadian Review of Physical Anthropology*, **4**, 67–75.
- Marsh, H. & Kasuya, T.** 1986. Evidence for senescence on female cetaceans. *Report of the International Whaling Commission, Special Issue*, **6**, 57–74.
- Newton, I. & Rothery, P.** 1997. Senescence and reproductive value in sparrowhawks. *Ecology*, **78**, 1000–1008.
- Norusis, M. J.** 1993. *SPSS for Windows. Advanced Statistics Release 6.0*. Chicago: SPSS.
- Olesiuk, P. F., Bigg, M. A. & Ellis, G. M.** 1990. Life history and population dynamics of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. *International Whaling Commission Report, Special Issue*, **12**, 209–243.
- Packer, C., Tatar, M. & Collins, A.** 1998. Reproductive cessation in female mammals. *Nature*, **392**, 807–811.
- Partch, J.** 1978. The socializing role of post-reproductive rhesus macaque females. *American Journal of Physical Anthropology*, **48**, 425.
- Pavelka, M. S. M.** 1993. *Monkeys of the Mesquite: the Social Life of the South Texas Snow Monkey*. Dubuque, Iowa: Kendall-Hunt.
- Pavelka, M. S. M. & Fedigan, L. M.** 1991. Menopause: a comparative life history perspective. *Yearbook of Physical Anthropology*, **34**, 13–38.
- Pavelka, M. S. M. & Fedigan, L. M.** 1999. Reproductive termination in female Japanese monkeys: a comparative life history perspective. *American Journal of Physical Anthropology*, **109**, 455–464.
- Peccei, J. S.** 1995a. A hypothesis for the origin and evolution of menopause. *Maturitas*, **21**, 83–89.
- Peccei, J. S.** 1995b. The origin and evolution of menopause: the altriciality–lifespan hypothesis. *Ethology and Sociobiology*, **16**, 425–449.
- Peccei, J. S.** 2001. Menopause: adaptation or epiphenomenon? *Evolutionary Anthropology*, **10**, 43–57.
- Rapaport, L. & Haight, J.** 1987. Some observations regarding allomaternal caretaking among captive Asian elephants (*Elaphus maximus*). *Journal of Mammalogy*, **68**, 438–442.
- Takahata, Y., Koyama, N. & Suzuki, S.** 1995. Do the old aged females experience a long postreproductive life span? The cases of Japanese macaques and chimpanzees. *Primates*, **36**, 169–180.