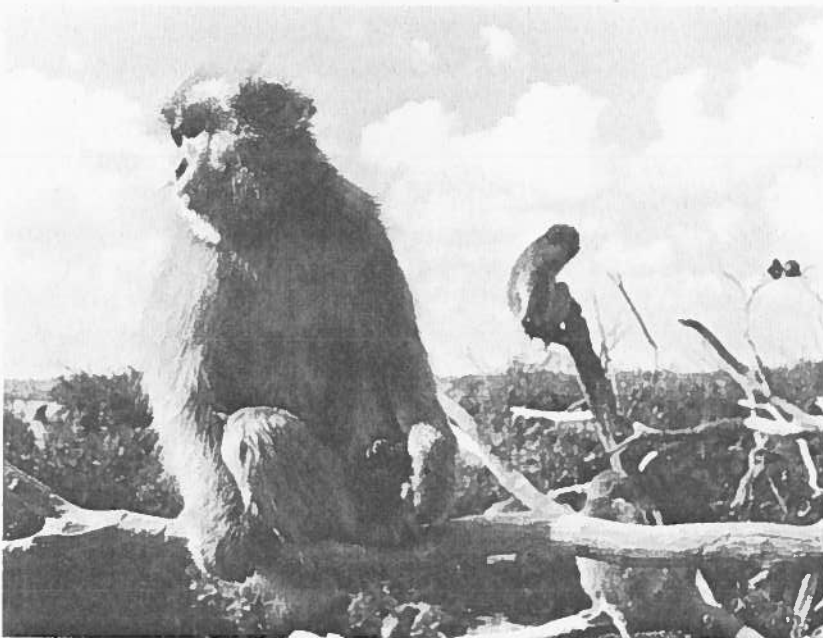


9 *Costs and benefits of old age
reproduction in the Arashiyama West
female Japanese macaques*

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Lady Di (Betta-59-66-78), alpha female of the Arashiyama West troop (photo by the late Karen Dickey, courtesy of Linda Fedigan and Tracy Wyman).

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9.1 Introduction

Do non-human primate females experience menopause? Has natural selection favoured the cessation of reproduction in grandmother monkeys and apes because the benefits of caring for grandchildren outweigh the benefits of continuing to produce more babies? Various attempts to answer these questions have produced a variety of conflicting results based on different interpretations of the significance of a small number of old, mostly captive individual monkeys and apes that appear to have stopped reproducing (Pavelka and Fedigan, 1991; Caro *et al.*, 1995; Fedigan and Pavelka, 2011). The kinds of data that are needed to address these questions are rare: a large sample of individuals of known age at death and reproductive history, living under free-ranging conditions. Fortunately, the maintenance of genealogical records on all members of the Arashiyama monkey group since 1954 has provided us with just such a database and thus the opportunity to shed light on ageing and reproduction in non-human primates and to highlight some of the unique characteristics of human ageing. In this paper, we review the results of a series of studies of ageing and reproduction, and present new data on the costs of old age reproduction utilising the Arashiyama West monkey database. Many of the individual monkeys in this database were ones that we each knew personally due to years of behavioural study on the colony.

Early descriptions of ageing monkeys and apes were surprisingly familiar to those living in conditions of modernisation, at least in the west. Old monkeys were described as socially withdrawn and peripheral, less active and socially disengaged (Waser, 1978; Hrdy, 1981; Hauser and Tyrell, 1984; Huffman, 1990). Indeed these reports of isolated monkeys paralleled what had long been proposed (and hotly debated) in social gerontology: that successful ageing in humans would be characterised by social disengagement, a mutual withdrawal of the individual and society in preparation for the ultimate withdrawal of the individual through death (Cumming and Henry, 1961; Cumming, 1975). However the early reports of old monkeys were based on descriptions of small numbers of individuals whose exact ages were not known. Identifying individuals as old because they look and act the way one expects an old monkey (or human) to act, and then using them to describe what old animals look and act like leaves open the strong possibility for circularity, subjectivity and human bias in descriptions of ageing in non-human primates.

A year long study of a large sample ($n = 20$) of old female Japanese monkeys of known age, compared with the same number of younger adults, was conducted on the Arashiyama West colony in the mid 1980s. This study (Pavelka, 1991) showed that old females in general were not less socially integrated than younger adult females. And they did not fall in rank. In retrospect, why would we expect them to? Japanese monkey society, especially in large provisioned

groups, is organised into matriline. Kinship and the number of available close female relatives, regardless of age, will determine the size of the social network, and likely the time spent in social contact (Pavelka, 1994). Simply getting older did not trigger changes in social relationships, as one might argue it can in humans. When comparing old female Japanese monkeys to old female humans, a striking contrast emerged: most of the old monkeys were still producing babies. There did not appear to be a class of females that were post-reproductive, as all elderly human females are.

9.2 Post-reproductive female Japanese monkeys compared with menopausal women

This observation led to the investigation of the reproductive performance of old female Japanese monkeys in the Arashiyama West colony, using the many decades of genealogical and life-history data that were available. Behavioural observations at the time of the ageing study suggested that most old females continued to produce infants, however the rich database allowed us to investigate the actual relationship between age and reproduction using a large sample ($n = 95$) of completed lives with complete reproductive histories. The first challenge was to find a way to distinguish females who were post-reproductive (presumably no longer able to reproduce, like menopausal women) from those who still possessed these capabilities. In the absence of endocrinological and histological data, which are typically only available for small numbers of captive animals (Atsalis *et al.*, 2008), reproductive termination must be identified from reproductive records. Some studies have assumed that the entire time lag between the birth of the last infant and the death of the mother is post-reproductive; however this is clearly not the case. By this measure, every female would be considered post-reproductive (or menopausal), regardless of the age at which she died. Death within a normal interbirth interval is not evidence of the termination of reproductive abilities, and the time lag between last parturition and death is not necessarily post-reproductive.

Therefore, we used a technique developed by Caro *et al.* (1995) in which 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 categorising females as reproductively terminated simply because they died before having another baby. It also allowed us to explore questions about variation in the age at which reproductive termination can occur.

Using the Arashiyama West genealogical records from 1954–1996, we extracted the data on 95 females whose reproductive histories, along with age at birth and death were known (Pavelka and Fedigan, 1999). 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. In order to use the criteria described above for identifying reproductive termination, a female had to have given birth to at least three infants, which 70 of the 95 had done. Because the 1-year behavioural study had given us the impression that old females continue to reproduce, we were surprised when this analysis revealed that 20 of the 70 females had died after living significantly longer than their own lifetime interbirth interval. In other words, they appeared to have stopped reproducing. Who were these females, and where were they during the 1-year behavioural study?

We investigated the age distribution of these reproductively terminated, or post-reproductive females, and discovered that they were mainly a small group of very old individuals who lived exceptionally long lives. Post-reproductive females ranged in age from 14.5 to 32.7 years, although the vast majority of females under age 25 were still reproducing (Figure 9.1). After age 25, reproductive termination became population-wide, as menopause is for women over age 50. Age 25 appears to be the biological endpoint for parturition in

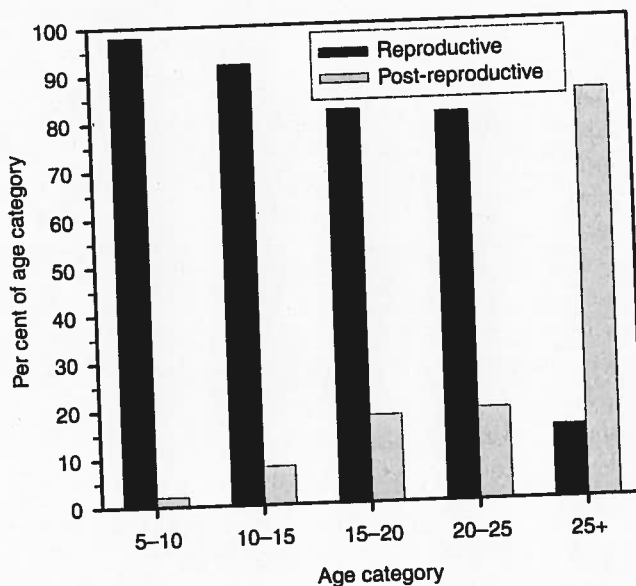


Figure 9.1. Percentage of females in the Arashiyama West population that are reproductive versus post-reproductive in each age category (years).

free-ranging Japanese macaques, as has been shown for the closely related rhesus monkey as well (Walker, 1995; Johnson and Kapsalis, 1998, 2008; Walker and Herndon, 2008). Interestingly, 24 is also the age at which the oldest known male rhesus (Bercovitch *et al.*, 2003; Bercovitch and Harvey, 2004) and Barbary (Kuester *et al.*, 1995) macaque have sired offspring.

However, age 25 for a Japanese monkey is much older than is age 50 for a human female, and in fact only a small proportion of the population, less than 3%, ever reach this age (Pavelka and Fedigan, 1999). Most females continue to reproduce until death even if they die in old age. Female Japanese monkeys aged 20 are considered to be old, as they are in the 3rd trimester of the life course, yet most of them were still producing infants, as was observed in the behavioural study. At any one time there might be only one or two of the very old and post-reproductive females in the group, and these females spend less than 10% of their lives in a post-reproductive state, compared with up to 50% of life spent post-menopausal for women. Bercovitch and Harvey (2004) also conclude that very few female non-human primates live long enough to become post-reproductive.

Thus the conclusion from this first set of analyses was that, as a life-history characteristic of the species, in which universality and phase of the life course are important, reproductive termination in Japanese monkeys bears few similarities to human female menopause. Menopause is universal and occurs only half way through the maximum lifespan of humans. It is a feature of healthy middle age (Peccei, 2001; Fedigan and Pavelka, 2011). Reproductive termination in Japanese monkeys is idiosyncratic, characteristic of a very small number of very old individuals, and not distinct from the overall late biological decline of the organism.

9.3 The evolution of menopause in humans and reproductive termination in Japanese monkeys

Menopause in humans is a challenge to explain. How can natural selection have favoured phenotypes that are not reproducing (see van Noordwijk and de Jong, 1986)? One general approach is to view menopause as a by-product of something else, such as the evolution of a long lifespan in humans, rather than as directly adaptive. Data on brain to body ratios in fossil hominids suggest that the maximum human lifespan increased from about 50 years in early hominids to approximately 120 years in *Homo sapiens* (Bogin and Smith, 1996; Hammer and Foley, 1996). However, the age at which human females cease to reproduce appears to have remained stationary at approximately 50 years. Female *H. sapiens* stop reproducing at about the same age as great apes (e.g.

Nishida *et al.*, 2003; Wich *et al.*, 2004; Robbins *et al.*, 2006; Thompson *et al.*, 2007), however 50 years of age is also near the maximum lifespan of great apes. In contrast, women are capable of living for up to another 70 years after the age of 50 in a post-reproductive state! It has been suggested that there may be inherent constraints on the mammalian reproductive system that made reproductive function unable to keep pace with the increase in human longevity (Weiss, 1981; Pavelka and Fedigan, 1991).

The other approach is to view menopause as something that is directly adaptive. Commonly (and collectively) known as the 'grandmother hypothesis', this line of argument is basically that there are greater inclusive fitness benefits to be had by ceasing to produce new infants and instead investing energy in enhancing the survival and reproductive performance of children and grandchildren (e.g. Lancaster and King, 1985; Hawkes *et al.*, 1989, 1997; Alvarez, 2000; Hawkes, 2003). Hawkes *et al.* (1989) provided evidence that post-menopausal Hadza (Tanzanian foragers) grandmothers supply sufficient surplus calories and babysitting services to allow their daughters to successfully raise more offspring. Blurton-Jones *et al.* (1999, 2005) concluded that grandmothing facilitated the evolution of earlier weaning in hominids, and Mace (2000) showed that babies in the Gambia are more likely to survive if their maternal grandmother is alive. Lahdenpera *et al.* (2004) documented that pre-modern Finnish and Franco-Canadian women with a prolonged post-reproductive lifespan had more grandchildren. There is scattered evidence from the ethnographic literature on a variety of societies that older women are a substantial help to their progeny, but whether or not this has a significant effect on inclusive fitness is still a matter of debate (e.g. compare Kaplan *et al.*, 2000 to Hawkes, 2003, 2004). There is a growing body of literature that addresses the costs and benefits of grandmothers in human populations (e.g. see chapters in volumes edited by Volland *et al.*, 2005; Hawkes and Paine, 2006).

While the grandmother hypothesis is still debated as an explanation for human menopause, reports of post-reproductive monkeys and apes (even if they are individual cases) have led to the suggestion that termination of reproduction may have been favoured by natural selection in other primates as well (Hrdy, 1981; Sommer *et al.*, 1992; Paul *et al.*, 1993; Paul, 2005). Here again the Arashiyama West database proved to be invaluable in addressing these questions. Even though the pattern of reproductive termination that we found in this population was significantly different (from a life-history perspective) from human female menopause, we did have lifetime reproductive records on 20 females who appear to have stopped reproducing at some point before death (they did not just die in an interbirth interval) and 50 others who continued to reproduce until death. Female Japanese macaques

Table 9.1. *Offspring survivorship in post-reproductive versus reproductive females*

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

are good candidates for evaluating the grandmother hypothesis because they live in matrilineal societies and engage extensively in kin-directed affiliative behaviours.

We compared the survivorship of descendants of those females who ceased to reproduce (post-reproductive females or PR) with those who continued to reproduce until death (R), looking at three measures: mean survival of all offspring; mean survival of matrilineal grandchildren (daughters' offspring); and survival of final offspring, using SPSS-SURVIVAL (Fedigan and Pavelka, 2001). We found no significant difference in offspring survivorship between PR and R females. In fact infant survival rates are remarkably similar for PR and R females: 85 versus 83% to age 1, and 71 versus 79% for survival to age 5 (Table 9.1).

Although not statistically significant, the data suggest that survival of the final infant of PR females is actually 13% better than it is for the younger, still reproductive females. However by definition, PR females live significantly longer than their own average lifetime IBI after the birth of their last infant than do R females, which means that PR females live well past the age at which their last offspring is weaned. (This will be discussed further below.) 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 ($F = 12.485$, $df = 68$, $p = 0.001$, $R = 0.394$). Since the longer the mother lives, the more care she will provide, the survivorship of final offspring is strongly related to the length of time the mothers survive after giving birth. This same pattern is probably reflected in the association found between longer interbirth intervals and greater infant survival in mountain baboons (Lycett *et al.*, 1998).

Overall, cessation of reproduction did not result in significantly improved survivorship of offspring or maternal grandchildren. Thus we explored a variety of different variables in trying to determine what was different about PR versus R females. For example, heavier female macaques might continue to cycle and reproduce, since per cent 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 post-reproductive (Caro *et al.*, 1995), perhaps it would occur more often in one matriline than another.

Because the Arashiyama West dataset 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, including dominance rank, matrilineal affiliation, cause of death, body weight, sex ratio of offspring, age at first birth and fecundity rates. We found almost no significant differences in any of these variables. What we did find was that PR females lived significantly longer (24.6 years as opposed to 17.4 years for R females; $t = -5.475$, $df = 68$, $p < 0.001$) and gave birth to significantly more offspring (9.7 compared to 7.7 for R females; $t = -2.157$, $df = 68$, $p = 0.035$).

From these data it certainly seems that natural selection is favouring PR females, however the real benefit is due to longevity. If a female Japanese monkey lives to be over 25 she will have had that many more years to produce infants. Because age at first birth varies little (age 5 or 6) a longer lifespan is the same as a longer reproductive lifespan. So old post-reproductive females live longer and have more offspring; however, neither these offspring nor the maternal grandchildren have better survivorship that can be tied to their post-reproductive status. Likewise the non-significant trend for the last infants of PR females to survive better than the last infants of R females is again due to them living longer after the last baby is born and thus not orphaning it when it is too young to survive.

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 enhanced longevity and its consequences rather than with enhanced investment in care of offspring or any adaptive or genetic package that distinguishes post-reproductive females. Packer *et al.* (1998), who provide the only comparable test of the grandmother hypothesis in non-humans, concluded that post-reproductive olive baboon and African lion females did not enhance the fitness of grandoffspring or older offspring, and that reproductive cessation in these species results from the general ageing process, rather than from direct selection favouring post-reproductive grandmothers.

Why might post-reproductive human females be able to improve survivorship of descendants but monkeys (and other non-human primates) are not?

This difference may be tied to another distinction between human and non-human primate ageing that was highlighted in the behavioural study of ageing in the Arashiyama West female Japanese macaques: the absence of food sharing (Pavelka, 1991). Japanese macaque females extend affiliative and potentially beneficial behaviours 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 behaviour that is described in the human literature on the grandmother hypothesis (Lancaster and Lancaster, 1983; Lancaster and King, 1985; Hawkes *et al.*, 1989, 1997, 1998; Hill and Hurtado, 1991, 1996; Kaplan, 1997; O'Connell *et al.*, 1999).

9.4 How common are post-reproductive grandmother Japanese macaques?

Anthropological research specifically targets post-reproductive grandmothers and in humans, there is a strong correlation between being post-reproductive (menopausal) and being a grandmother. However, in our analyses described above, we did not distinguish the grandmothers from the post-reproductive females. Not all post-reproductive females were necessarily grandmothers, and not all grandmothers were necessarily post-reproductive. Thus we next used the rich Arashiyama West database to target the theoretically important post-reproductive mothers and grandmothers and to find out how common they are, and how great is their potential to have an impact on the reproductive output of their descendants (Pavelka *et al.*, 2002).

Eight of the 70 females who could be categorised as reproductive or post-reproductive did not produce any daughters (and hence grandchildren that were known to us), so these next analyses are based on 62 grandmothers and their 175 daughters and 905 grandchildren. For tests in which we needed the daughters' death dates, we were able to use only 88 of the 175 daughters, and only 74 of these produced infants. Of the 905 grandchildren born, we have complete information on 886 individuals who were included in the survival analyses. Of these, 504 survived to age 5. The probability of survival to age 5 was calculated based on the survivorship of all of the 886 individuals in the sample.

Post-reproductive grandmothers turned out to be very rare (Figure 9.2). Of the 175 daughters in our sample, 37% had no mother (their mother was dead), 60% had a reproductive mother (present but still dealing with infants of her own), and only 3% (five females) had a post-reproductive mother available to help them when they reached reproductive age. We also looked at how much time they would have their mothers available to them and again, it was not

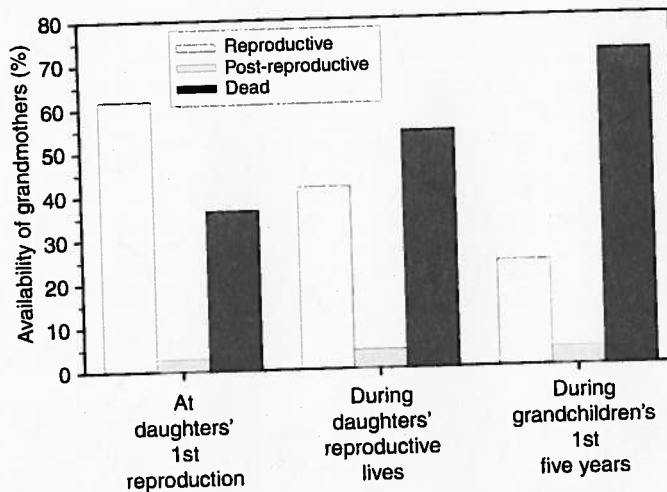


Figure 9.2. The availability (alive versus dead) and reproductive state of grandmothers for daughters at the time of their first reproduction, during their entire reproductive lives and at the time of their daughters' first reproduction.

much. Only 0.41/9.71 years or 4.2% of the reproductive lifespan of the daughters were spent with a post-reproductive mother available to help them. This represents less than 5 months for the average female in the population. This pattern was further reflected in the next generation, in the time available for a post-reproductive 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%), reproductive or otherwise. The grandchildren who lived to age 5 actually had a grandmother available to them for, on average, less than a year and a half. For most of this time, a grandmother had her own baby to care for. The amount of time that these grandchildren had with a post-reproductive grandmother was less than 2 months.

9.5 The value of mothers

This analysis did show some interesting benefits to the 63% of females who had a mother available to them when they reached sexual maturity. Females who had a live mother (regardless of her reproductive status) when they reached reproductive age were significantly more likely to have their first baby at age 5 instead of age 6 (Chi-square: $\chi^2 = 8.942$, $p = 0.030$). How does the presence of a mother result in a significantly earlier age at first birth for her daughters?

Table 9.2. Effect of mother's status on daughter's age at first birth and interbirth intervals (IBI)

Daughter's reproduction	Mother's status			
	Dead	Alive	Alive and reproductive	Alive and post-reproductive
<i>Age at first birth (years)¹</i>				
$\bar{x} \pm \text{s.d.}$	6.0 \pm 1.0	5.6 \pm 0.9	5.6 \pm 0.9	6.1 \pm 0.7
n	64	111	106	5
<i>Average interbirth interval (months)²</i>				
$\bar{x} \pm \text{s.d.}$	19.2 \pm 8.5	18.1 \pm 7.3	18.5 \pm 7.4	16.0 \pm 5.7
No. of IBIs	451	273	239	34

¹ *t*-test: Dead vs. Alive, $t_{173} = 2.565$, $p = 0.01$; ANOVA: Dead/Alive-R/Alive-PR, $F_{2,172} = 3.952$, $p = 0.02$.

² *t*-test: Dead vs. Alive, $t_{722} = 1.702$, $p = 0.09$; ANOVA: Dead/Alive-R/Alive-PR, $F_{2,271} = 2.858$, $p = 0.06$.

It may be that 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 oestrus period for female Japanese monkeys requires that these young females venture out of their tight female kinship units for the first time in order to establish contact with unrelated adult males. Most young females would have had little need or opportunity to interact with unrelated adult males 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, adult daughters whose mothers were still living in the group received less aggression and were defended more often than were young adult females whose mother had died (Fairbanks, 1988). Thus, the mother of the young 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. As Bercovitch and Harvey (2004) pointed out, it is important to note that although life-history theory proposed that lifetime reproductive success is improved with earlier age at first birth (Stearns, 1992), this has not been shown to be the case in female primates (cf. Fedigan *et al.*, 1986 for Arashiyama West Japanese macaques).

The presence of a live mother also appeared to be of some benefit to females in terms of shortening their interbirth intervals (Table 9.2), although this trend

was not quite statistically significant. Females had, on average, shorter inter-birth intervals when their mothers were alive (18.1 months) compared with when they were dead (19.2 months). This trend became even greater when the mother became post-reproductive, and the average interbirth intervals of her daughter dropped from 19 to 16 months.

9.6 The adaptive value of grandmothers

The essence of the grandmother hypothesis is that grandmothers – specifically post-reproductive grandmothers – are able to enhance the survivorship of their grandchildren. Thus we compared the probability of survivorship to age 1 and to age 5 by status of grandmother during first year of the grandchild's life (Dead, Alive R, Alive PR). Here we found a somewhat surprising significant difference in survivorship to age 1 depending on the status of the grandmother (Wilcoxon–Gehan test, $W_2 = 6.29$, $p = 0.043$). Specifically, grandchildren with a living post-reproductive grandmother were significantly more likely to live to age 1 than were grandchildren with either a dead grandmother or a live one who was herself still reproducing ($W_1 = 3.99$, $p = 0.046$ and $W_1 = 6.47$, $p = 0.011$, respectively).

Nakamichi *et al.* (2010) described two instances of grandmother Japanese monkeys, without dependent young, providing essential care to their two granddaughters (one aged 2 months, the other aged 14 months). Whatever the PR grandmother was doing to help her grandchild reach age 1 at Arashiyama West did not extend to helping it reach age 5: there were no differences in the survivorship of grandchildren to age 5 among the three groups of grandmothers ($W_2 = 1.272$, $p = 0.53$). But recall that on average, most grandchildren had a post-reproductive grandmother for only a couple of months, so clearly whatever she was able to do was centred on the first year, in the pre-weaning stage of the grandchild's life.

9.7 Costs of old age reproduction

All of the analysis and discussion so far has focused on the possible benefits that might accrue to females who ceased reproducing. However, in order for natural selection to favour cessation of reproduction over continued reproduction, there would not only have to be benefits to the former, but costs to the latter. All other things being equal, continued reproduction, which we know to be the norm for Japanese macaque females until well into old age, is what we would expect, unless continuing to produce babies were to become too costly.

In humans the latter may well be the case, given the difficulties in labour and delivery that are side-effects of the evolution of bipedalism and encephalisation. Giving birth to a large-brained infant through the narrow pelvis of a biped puts human females of all ages at considerable risk, and perhaps these risks increase as women get older. We certainly know that children born to older human mothers carry a significant risk of genetic defects, although these are likely a by-product of the same constraints on the mammalian system mentioned earlier: a fixed number of eggs are available at birth and these are suspended in anaphase. The older the woman, the longer the eggs have been suspended and the greater the chance of chromosomal mutation.

Are there costs associated with continued reproduction in older Japanese monkeys that might tip the balance in favour of caring for descendants instead? It is generally recognised that reproduction, particularly lactation, is energetically costly for primate females (e.g. Altmann, 1983; Lee, 1996a; Dunbar *et al.*, 2002; Miller *et al.*, 2006), and these costs would be greater for females in poorer overall body condition (Lee, 1996b) as ageing and/or post-reproductive females might be expected to be. Thus first, we looked at weight loss. Lactation in females is associated with loss of body mass in chacma baboons (Barrett *et al.*, 2006) and this is an effect which might be more pronounced in older individuals.

In the Arashiyama West females, we compared the body weights of reproductive and post-reproductive females, the latter being significantly older than the former, and found no difference. Both weighed close to 8 kg. PR females ($n = 19$) who were weighed at least once in adulthood weighed on average 7.96 kg (s.d. = 1.81), and R females ($n = 32$) weighed on average 8.15 kg (s.d. = 3.7; $t = -0.392$; $df = 49$; $p = 0.697$).

Secondly, the most obvious way to diminish future reproduction would be for the female herself to die. For example, there may be a cost to a fast pace of reproduction (Bercovitch and Berard, 1993). Females who produce infants in close succession might be expected to pay a price in terms of their own lifespan. However, this was not the case with the Arashiyama West females. We calculated the average interbirth interval for all females in our sample and ran a regression of interbirth interval on age at death, and found no relationship ($F_{1,72} = 0.776$, $p = 0.381$). There appeared to be no trade-off for females who had infants more closely spaced than those who did not. This result may be tied to the fact that the Arashiyama West monkeys were provisioned and the artificially food-enhanced environment may have permitted enhanced reproduction as well. Asquith (1989) argued that an increase in population size occurs in provisioned populations due to reduced infant mortality and shortened interbirth intervals.

Do females who continue to reproduce when they are old pay a cost in terms of their own survival? We addressed this question by first running a logistic

regression to determine whether maternal survival for 12 months subsequent to parturition declines with age. We found that if a female gave birth, her age did not affect her probability of surviving for 12 months after parturition. Older females were no more likely to die after giving birth than were younger females ($Wald = 0.409$, $df = 1$, $p = 0.520$). However, for females who failed to give birth, their probability of surviving for 12 months subsequent to a given age (e.g. 6 years, 7 years, 8 years) did decline as they got older ($Wald = 66.1$, $df = 1$, $p < 0.001$). Furthermore, we used a logistic covariance analysis to compare females who gave birth versus those who did not give birth at ages 4–25 and found that at every age (except age 5), the probability of survival was greater for those females that gave birth than those that did not give birth. This result suggests that it is not costly to give birth, rather it is beneficial.

However, another explanation could be that healthy females are the ones giving birth, and thus also the ones likely to survive. This pattern too might be related to the specific conditions at Arashiyama West where the animals were provisioned and predation was minimal. In wild baboons, females with small infants were more vigilant and spent less time feeding (Barrett *et al.*, 2006), and again, this effect might be expected to be more pronounced in older females who might be more vulnerable to predation and weight loss.

Thirdly, is there a cost to old age reproduction in terms of infant survival? Do older mothers provide less or lower-quality infant care? For the most part, the literature suggests not. Quite a few studies have shown that older females experience higher offspring survival, especially in birds (e.g. Crawford, 1977; De Steven, 1977; Blus and Keahey, 1978; Curio, 1982; Pugsek and Diem, 1983) and also in some mammals (e.g. Ozoga and Verme, 1986; Festa-Bianchet, 1988; Green, 1990; Hastings and Testa, 1998; but see Ericsson *et al.*, 2001).

Reproductive costs are generally assumed to be highest in primiparous females due to inexperience, small body size and infant suckling patterns (Bercovitch *et al.*, 1998). Not surprisingly, when we ran survival analyses, we found no significant differences in infant survival to 1 year comparing mothers grouped into four age classes ($n = 474$ infants born to mothers 5–10 years; 257 infants to mothers 11–15 years; 132 infants to mothers 16–20 years; 30 infants to mothers 20–25 years, $W2 = 1.670$; $df = 3$, $p = 0.644$). Likewise there was no effect of maternal age on survival of offspring to age 5. The survival rates were very high in all cases: 85% of infants survive to age 1, regardless of their mother's age, and 77–83% survive to age 5 regardless of their mother's age.

Overall infant survival may be unaffected by mother's age, or indeed be enhanced by it because older mothers have more experience. But no amount of maternal experience is going to help the last infant if its mother dies. A fourth obvious cost of old age reproduction would be the greater likelihood

that a female would die and leave behind an unweaned orphan. One might suggest that the death of a final infant due to being orphaned is a waste, rather than a cost, however it is a cost if those females could have had a significant impact on the survivorship of a grandchild, had they not had that last baby. We know that the presence of a post-reproductive grandmother does significantly improve the survival to age 1 of their grandchildren.

In the data presented above comparing the survivorship of the last infant of post-reproductive (older) and reproductive (younger) females, we in fact found the opposite trend: post-reproductive females had a significantly higher survival of their last offspring than did reproductive females. However, keep in mind that post-reproductive females were identified by the fact that they lived a long time after the birth of their last baby, so by definition these females were not dying and leaving unweaned orphans. Only reproductive females, by definition, could do that.

We looked more closely at all cases of infants who died in their first year of life. Weaning is typically completed when the infant is 1 year of age. We divided the data into individuals who died before reaching age 1 ($n = 196$) and those who did not ($n = 438$) and found that the average age of the mothers of those who died unweaned was younger (10.8 years) than those whose offspring lived longer than 1 year (18 years). Again, losing infants appeared more characteristic of younger adult females than of older ones. We ran a logistic regression to test the effect of maternal age on the likelihood of an offspring dying young (less than 1 year of age versus more than 1 year of age), and neither the first ($Wald = 135$; $df = 1$, $p = 0.245$) nor the second ($Wald = 2.25$; $df = 1$; $p = 0.135$) order term was significant. In other words, there was no effect of maternal age. Infant mortality was 13% and it was unrelated to the age of the mother. Indeed whatever trend there might be, the data suggest that infants of young mothers are more likely to die than offspring of older females (Figure 9.3).

Finally, arguments have been made that the sex of offspring may confer different costs on the mother. For example Bercovitch *et al.* (2000) and Mueller (2001) have suggested that male infants are more costly to their mothers, especially in dimorphic species, and production of more sons than daughters has been shown to affect the longevity of women in premodern human populations (Helle *et al.*, 2002a, 2002b; but see Beise and Voland, 2002). Takahata *et al.* (1995) and van Schaik *et al.* (1989) however have argued that macaque daughters are more costly.

Thus we investigated whether mothers who produced more sons than daughters during their reproductive lives experience shorter lifespans. We ran a survival analysis on females categorised into those that had more sons than daughters during their lifetimes ($n = 47$, $\bar{x}_{\text{lifespan}} = 270$ months), those that produced more daughters than sons ($n = 67$, $\bar{x}_{\text{lifespan}} = 245$ months) and those

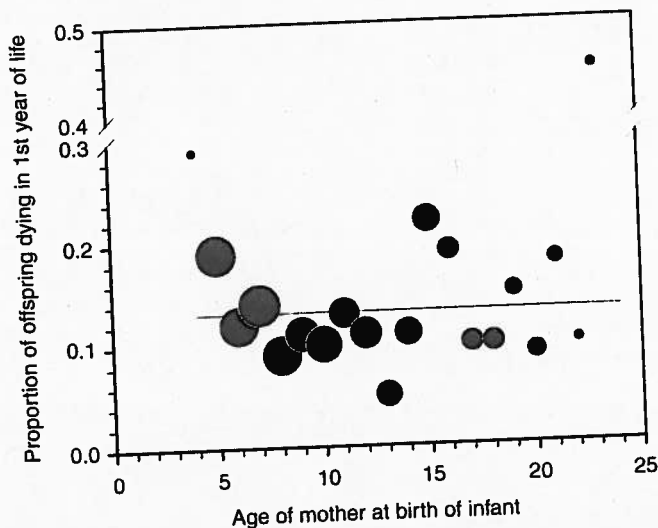


Figure 9.3. The proportion of infants born to mothers of different ages that died at younger than 1 year of age.

that produced equal sex ratios of offspring ($n = 23$, $\bar{x}_{\text{lifespan}} = 293$ months). We found no significant differences in longevity among these three categories ($W_2 = 3.225$, $df = 2$, $p = 0.1194$).

9.8 Closing comments

The maintenance of long-term reproductive records on the large sample of Arashiyama West females resulted in a rich database that has allowed us to gain considerable insight into ageing in old females and the possible evolution of post-reproductive lifespans in monkeys and humans. In the Arashiyama West population, as is the case for most published accounts of free- and semifree-ranging primates (Bercovitch and Harvey, 2004; Fedigan and Pavelka, 2011) most females continue to give birth until the end of their lifespans and few will live to reach a post-reproductive stage of life.

The age at which termination of reproduction occurs in Japanese monkeys is 25 years, although this is very close to the maximum lifespan for the species, with few individuals living past it. Reproductive termination was characteristic of only a small cohort of very old females and post-reproductive females who were significantly older at time of death than were reproductive ones. When we investigated post-reproductive grandmothers specifically, we found them to

be extremely rare. However, in the rare cases in which a female found herself post-reproductive and with a grandchild, she did appear to be able to increase its chance of surviving to age 1.

Nonetheless, 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 descendant's lives, to have sufficient inclusive fitness effects to compensate for the loss of the grandmother's direct reproductive output, as theorised by the grandmother hypothesis. Reproductive termination in this population appears to be a by-product of selection favouring longevity rather than as a result of direct selection for reproductive termination (Fedigan and Pavelka, 2011). This conclusion is further supported by the new data presented here in which there do not appear to be reproductive costs that increase with age. Continuing to reproduce until death is beneficial, not costly, to the fitness of Arashiyama West female Japanese macaques.

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