Chapter 10
Costs of Reproduction Among Rhesus Macaque Females on Cayo Santiago

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10.1 Introduction

Reproduction is energetically costly for mammalian females during the periods of gestation and lactation and, consequently, is likely to be associated with reduced survival (Stearns 1989, 1992; Roff 2002), particularly when maternal condition is poor. Higher mortality may be associated with birth-related complications, but it also may be the consequence of elevated circulating levels of cortisol suppressing immune function (see McEwen et al. 1997, for a review). If the hypothalamic–pituitary–adrenal (HPA) axis is hyperactivated in post-partum females during prolonged periods as a result of either the energetic demands of lactation or the associated psychosocial stressors, immune function may become impaired, potentially making females more vulnerable to diseases and to increased risk of mortality.

Survival costs of reproduction have been documented for a few mammalian species. Among seasonally breeding Columbian and Richardson's ground squirrels (*Spermophilus columbianus* and *Spermophilus richardsonii*), adult female mortality is highest in the birth season and during the period of lactation (Michener and Locklear 1990; Michener 1998; Neuhaus and Pelletier 2001). Among baboons (*Papio* spp.), mortality rates are highest among lactating and pregnant females (e.g., Cheney et al. 2004).

The terminal investment and senescence hypotheses both predict that the costs of reproduction should increase with age. According to the senescence hypothesis,

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physical and physiological deterioration lead to declining reproductive output (Weladji et al. 2002). Evidence for this hypothesis has been documented in many animal populations (e.g., *Parus major*, Bouwhuis et al. 2009; *Arctocephalus tropicalis*, Beauplet et al. 2006; *Ovis canadensis*, Berube et al. 1999). According to the terminal investment hypothesis (Williams 1966), a female's reproductive strategies should change depending upon her likelihood of conceiving and surviving until her offspring reach independence. When she is in poor physical condition or in advanced age, her reproductive effort should increase. This hypothesis has been supported by studies of several avian and mammalian species (e.g., *Passer domesticus*: Bonneaud et al. 2004; *Sula nebouxii*: Velando et al. 2006; *Kobus megaceros*: Bercovitch et al. 2009). Although reproductive output should decrease with age according to the senescence hypothesis, and reproductive effort should increase with age according to the terminal investment hypothesis, these two hypotheses are not mutually exclusive (Weladji et al. 2010). Compared to younger females, older females, for example, may have fewer resources to provide for offspring due to senescence, but they may invest a greater proportion of their available resources in their offspring. Even with such increased investment, however, offspring mass and survival may still decline with maternal age if the effects of senescence outweigh the consequences of increased maternal investment.

Primates are ideal subjects for examining the costs of gestation and lactation and for testing the senescence and terminal investment hypotheses because they tend to be long-lived and their offspring have a prolonged period of dependency, requiring months and sometimes years of maternal care. Although the process of senescence has been documented for primates (Walker and Herndon 2008), evidence for the terminal investment hypothesis is mixed. Studies of several species have demonstrated that interbirth intervals increase with maternal age (e.g., Gagliardi et al. 2007; Robbins et al. 2006), which may suggest slowed reproduction due to senescence or to increased maternal investment. Furthermore, some studies have reported that infants born to older mothers have greater birth weights and survival rates (Dolhinow 1979; Silk et al. 1993; Paul et al. 1993), but this relationship has not been found in other studies (Borries and Koenig 2008; Wright et al. 2008; Fessler et al. 2005). Few studies have taken multiple measures from mothers and their infants to test both hypotheses simultaneously.

The goals of this study are to assess the costs of reproduction for rhesus macaque females and to investigate possible age-related changes in female reproductive strategies and offspring survival, such as those predicted by the senescence and terminal investment hypotheses. Rhesus macaques are an interesting species for studying female reproductive strategies because females have long life spans and infant survival is entirely dependent upon maternal care. Furthermore, dominance ranks are stable for female rhesus macaques (Melnick and Pearl 1987), and studies have generally reported higher cortisol levels in low-ranking than in high-ranking females (e.g., Gust et al. 1993; Maestripieri et al. 2008). Chronic activation of the HPA axis, as evidenced by high levels of cortisol, can impair immune function (Sapolsky 2005) and may contribute to life history differences.

The rhesus macaques on Cayo Santiago comprise an ideal population for investigating the survival costs of reproduction because colony records spanning more than 50 years exist that include birth and death dates of all females and their offspring who have resided on the island. There is also the opportunity to collect blood samples and morphometric data from this population during the annual trapping period. Blood samples can be assayed for cortisol levels, and morphometric data can be used to characterize the physical conditions of mothers and their infants. Age-related effects on interbirth intervals and infant survival rates can be determined using the long-term database, and age-related changes in maternal care can be studied readily since individuals are tattooed and well-habituated. Given that the rhesus macaques on Cayo Santiago are food-provisioned and reside in a predator-free environment, there may be limitations regarding the generalizability of findings obtained in this population (Maestripieri and Hoffman 2011). If, however, we find variability in maternal physiology, behavior, or survival in relation to reproduction, we can conclude that reproduction is costly even when food is abundant and predators are absent.

In our study, we show that:

1. Breeding on Cayo Santiago is seasonal, and reproduction is influenced by climatic factors, such as rainfall.
2. Female deaths are more likely to occur in the birth season than in the mating season.
3. Plasma cortisol is higher for lactating females than for cycling females.
4. Female body condition and activity levels decline with age in accordance with the senescence hypothesis.
5. Interbirth intervals increase as a function of age in accordance with the terminal investment and senescence hypotheses.
6. Older females, in accordance with the terminal investment hypothesis, invest more resources in their infants even though offspring survival does not necessarily improve with such increases.

10.2   Methods

Cayo Santiago is a 15.2 ha island located 1 km off the southeastern coast of Puerto Rico. The rhesus macaque colony on this island was established in 1938, with free-ranging individuals captured in India (Rawlins and Kessler 1986). Since then, no new individuals have been introduced into the population, except through births. To maintain a stable population size, a fraction of the yearlings and 2-year olds are transferred off the island each year. Monkeys living on Cayo Santiago forage on vegetation and are provisioned with commercial monkey chow. The data for this study came from two different data sets, which will be referred to as "long-term data" and "short-term data," respectively.

10.2.1 Long-Term Data

This data set is comprised of records maintained in the Cayo Santiago database, which includes information on each animal's genealogy and dates of birth and death, as well as a history of each individual's group membership and reproduction. Throughout the periods of interest to this study (1957–2005 for analyses related to female mortality and reproductive seasonality; 1957–2007 for analyses related to maternal age, interbirth intervals, and infant survival), Cayo Santiago staff updated colony records with daily censuses of all animals.

To determine whether there were seasonal effects on reproduction and female mortality, we included in our sample adult females who were born on Cayo Santiago in the period 1957–2001 and died on the island in the period 1961–2005. Only sexually mature females that were at least 4 years old at their time of death were included in the sample. To determine whether rainfall patterns affected the timing of seasonal reproduction, we obtained data on daily precipitations from 1963 to 1996 from the National Oceanic and Atmospheric Administration (NOAA) of the US Department of Commerce station in Humacao, PR (approximately 6 miles from Cayo Santiago). The onset of the spring rainy season was identified as the first day since January 1st in which precipitation was equal to or greater than 1 in.

We calculated median life span, interbirth intervals, and infant survival rates for all reproductively mature females who were born in or after 1957, lived their entire lives on the island, and died prior to May 1, 2007 ($n = 637$). For every age at which a female gave birth to a live infant, we assessed the number of days between that birth and her previous birth. Additionally, we used the long-term database to determine whether or not the female had birth in the previous birth season. After rounding female ages at birth to the nearest year, we calculated the average interbirth interval for females at each age. We included females between 4 and 24 years in these analyses.

We measured the effects of maternal age and offspring sex on average offspring life span and on rates of infant mortality during the first 30 days and 1 year of life. The Cayo Santiago database does not contain accurate information about the animals' dominance ranks; therefore, this variable was not included in analyses using the long-term data set.

10.2.2 Short-Term Data

Approximately 850 animals distributed among six naturally formed social groups resided on Cayo Santiago when the short-term data were collected. This data set is comprised of plasma cortisol samples, morphometric measures, and behavioral data. Between January and March 2007, we collected morphometric measurements and blood samples from females from six social groups who were between 15 and 26 years of age ($\overline{X} = 18.3\,\text{years}$). Between January and February 2008, we collected

morphometric data and blood samples from adult females from four social groups who were between 7 and 26 years of age ($\overline{X} = 15.8$ years). We collected behavioral data between April and December 2007, from subjects ranging between 6 and 22 years of age ($\overline{X} = 15.0$ years).

In order to collect blood samples and to take morphometric measurements, trained staff members captured adult females and their infants in a feeding corral, approximately 100 m^2, which was provisioned daily with monkey chow. Infants remained with their mothers during the entire trapping and data-collection process. Trapping generally occurred between 8:30 and 12:00. The staff members netted or captured the monkeys by hand in one of three feeding corrals, transferred them to a holding cage ($0.62 \times 0.42 \times 0.62$ m), and moved them to a small field laboratory. The monkeys remained in a standard squeeze cage with their infants for overnight housing. The following morning, veterinary technicians anesthetized the adult females and their infants with ketamine (approximately 10 mg/kg via IM injection).

Veterinary technicians drew blood from the femoral vein of anesthetized females between 7:15 and 10:40 (average time of day: $8:18 \pm 5.0$ min) and, on average, 66.5 ± 5.5 min after the door of the laboratory was first opened (range: 7–213 min) and 22.1 ± 2.7 min after ketamine administration (range 0–127 min). All blood samples were collected into heparin-treated Vacutainer tubes. We refrigerated samples for 20 min and then centrifuged them for 20 min. Following centrifugation, we aliquotted the plasma into microcentrifuge tubes, and stored the tubes at −80°C until we shipped them to the Biomarker Assay Core Lab of the Yerkes National Primate Research Center, where they were assayed for cortisol by radioimmunoassay using a commercially available kit (Diagnostic Systems Laboratories, Webster, TX, USA). The samples collected in 2007 were assayed in April 2007 (see Maestripieri et al. 2008, for some of these data), while the samples collected in 2008 were assayed in July 2008. The assay used has an intra-assay coefficient of variation of 4.90%. Measures of inter-assay variation, assessed by adding low and high concentration standards to each assay, were 15.6% (low) and 13.5% (high). Cortisol concentrations measured the morning after capture presumably reflect the cumulative stressful effects of capture and overnight housing (see Laudenslager et al. 1999; Maestripieri et al. 2008).

To take morphometric measurements, we weighed the anesthetized females and infants separately in a standard hanging scale. We used a large anthropometer (Lafayette Instruments, Lafayette, IN) to measure crown-rump length of each anesthetized adult female while she was placed in a standardized position with her back fully straight. We collected morphometric measurements from 53 adult females from six social groups in 2007 and from 40 adult females and 26 infants from four social groups in 2008. We calculated body mass index (BMI) for each adult female by dividing mass (kg) by the square of crown-rump length (m^2) (Campbell and Gerald 2004).

We collected behavioral data during pre-birth observations (those occurring from April 1, 2007 until a female gave birth) and post-birth observations (occurring from the date a focal female gave birth until mid-December 2007). We determined the proportion of time focal animals spent feeding, resting, traveling, and engaging in grooming interactions by conducting instantaneous sampling at 1-min intervals

during 30-min focal follows. The grooming measure combined grooming given to and received from social partners who were 3 years old and above. During the first month post-birth, we recorded the amount of time mothers and infants were in ventro-ventral contact during 30-min focal follows.

Behavioral data collection initially included 28 females. Each subject was multiparous and belonged to one of three social groups. All 28 females gave birth during the birth season, and we collected behavioral data post-birth on those females that gave birth prior to the termination of behavioral data collection ($n=23$). We conducted focal follows on three additional females, beginning with the week they gave birth. Dominance ranks were assigned on the basis of behavioral data on aggressive and submissive interactions collected by trained observers. Subjects were classified as high-, middle-, or low-ranking depending on whether their rank fell within the top, middle, or bottom third of the dominance hierarchy within their social group.

10.2.3   Data analysis

Seasonality of reproduction and climatic factors affecting seasonality – The first and the last birth in the birth season of any given year were identified as the earliest and the latest birth that occurred within two standard deviations below and above the mean for that year, respectively. Since pregnancy in rhesus macaques lasts about 165 days (Ardito 1976), the beginning and the end of the mating season were identified by counting backward 165 days from the date of the first and the last birth (see also Rawlins and Kessler 1985). We ran Pearson's correlation tests to determine if there was a relationship between birth season year and birth season start date, and if there was a relationship between the onset of the birth season and the onset of the rainy season.

Seasonality of adult female deaths – The monthly mortality probability for adult females was calculated by dividing the number of females that died in a given month by the number of adult females present in the population that month (i.e., all the adult females that could potentially die). To test statistically for seasonality in the probability of mortality of females, we used Poisson regression analysis. Our model included a linear trend in year to capture long-term changes in probability of mortality between 1961 and 2005. Seasonality over the course of the year was captured via a single harmonic sine wave. This was entered in the model using a sine and a cosine term to allow for different phases (timing of the peak), yielding a test for seasonality with 2 df.

Plasma cortisol in relation to reproductive state – We used general linear mixed models (GLMMs) to assess the effects of three categorical variables and three continuous variables on cortisol levels. Dominance rank, social group, and reproductive condition were fixed factors in the models, and female age, female mass, and infant age were continuous factors. We included individual identity and year of sample collection as random factors in the models. One female was excluded from analyses because her cortisol level was more than 2.5 standard deviations below the group average.

   To conduct within-subjects comparisons of 2007 and 2008 cortisol values, we transformed raw cortisol values into *z*-scores because 2007 and 2008 average values differed significantly (for a more detailed explanation see Hoffman et al. 2010a). We used restricted maximum likelihood methods for model estimation and Sattherwaite's *F* tests to gauge fixed effects. We chose the best model using Akaike's information criterion (AIC), starting with all main effects and interactions between each main effect and the random factors "identity" and "year." None of the interactions with identity or year were included in the final model.

Age-related physical and behavioral change – Using the short-term data, we employed general linear modeling (GLM) to test the effects of female age, social rank, and reproductive condition (fixed factors) on BMI (dependent variable). We also used GLM to determine the effects of age and social rank on the proportion of time females spent resting or grooming pre-birth (i.e., when cycling or pregnant) and during the first month post-birth.

Age-related changes in interbirth interval – We performed linear and quadratic regression analyses on data from the long-term data set to determine the influence of female age on interbirth intervals. We conducted linear regression analyses to determine relationships between maternal age and the proportion of offspring surviving to 30 days and 1 year in the long-term database, and we used Chi square analyses to determine if offspring sex influenced offspring survival to these time points.

Age-related changes in maternal behavioral investment and offspring survival – We employed GLM to test the effects of maternal age and social rank on the average number of minutes mother–infant pairs spent in ventro-ventral contact per hour during each infant's first month. We performed linear regression analysis to determine whether infant birth date influenced time in ventro-ventral contact.

   For analyses involving infant mass, we excluded infants younger than 60 days at the time of measurement because rhesus growth is linear only between 2 months and 11 months (Smith and Small 1982). We used GLMM to determine the relationship between infant mass and maternal age, infant age, and infant sex. To determine whether offspring sex ratio changes with age, we calculated from the long-term data set the proportion of offspring that were male born to females at each year of life (years 4–24) and then ran linear and quadratic regressions to determine whether sex ratio changed with maternal age.

   Unless otherwise noted, we conducted two-tailed tests. We considered $p < 0.05$ as significant. We conducted data analyses in SPSS 17.0.

10.3   Results

For females in the long-term data set spanning 1957–2007 who survived to at least 4 years of age ($n = 631$), median life span was 15.0 years and maximum life span was 31.4 years. The oldest female to give birth did so at 24.2 years.

10.3.1 Seasonality of Reproduction and Climatic Factors Affecting Seasonality

Although the rhesus macaques on Cayo Santiago have year-round access to food and water, they continue to breed seasonally, with 86% of births occurring between November and March. Birth records collected between 1961 and 2005, however, indicate that the birth season has commenced increasingly earlier over time ($r = -0.89$; $p < 0.001$; $n = 42$). The shift in the onset of the birth season over the years has corresponded with a shift in the onset of the spring rainy season ($r = 0.43$, $n = 34$; $p = 0.01$), which has begun increasingly earlier in the year over the period of time for which data were available.

10.3.2 Seasonality of Female Deaths

A total of 396 female deaths was included in these analyses. Female mortality probability peaked in February and March (Fig. 10.1a). There was a smaller peak in female mortality in September, but this peak was not statistically significant. The 2-df test for seasonality in the probability of female mortality according to calendar year was significant ($X^2 = 24.91$, $p < 0.0001$). Mortality probability is generally higher in the birth season than in the mating season, but it appears to be more evenly distributed across the first 4 months of the birth season than it is across the first 4 months of the calendar year (Fig. 10.1b). More females died in the birth season than in the mating season (no. of birth season deaths = 198; no. of mating season deaths = 114; $X^2 = 22.08$, df = 1, $p < 0.001$).

10.3.3 Plasma Cortisol in Relation to Reproductive State

Our final model included only female reproductive state as a predictor of cortisol levels (GLMM: $F_{1,58} = 7.86$, $p = 0.007$). Female age, female mass, infant age, dominance rank, and social group were not included in the final model because they were not significant predictors of cortisol concentrations. The model indicated that cortisol levels were significantly higher for lactating females than for cycling females ($t = -2.80$, df = 19, $p = 0.007$).

Among the females who provided plasma samples both years, 12 were lactating one year and cycling the other. Within-subjects comparisons revealed that cortisol was significantly higher when females were lactating than when they were cycling (lactating: 0.44 ± 0.29; cycling: -0.26 ± 0.32; $t = 2.98$, df = 11, $p = 0.01$). For the eight females who were in the same reproductive state when trapped in 2007 and 2008, there were no differences in 2007 and 2008 cortisol values (2007: 0.39 ± 0.35; 2008: 0.47 ± 0.36; $t = -0.19$, df = 7, $p = 0.86$). Age did not affect the increase in cortisol
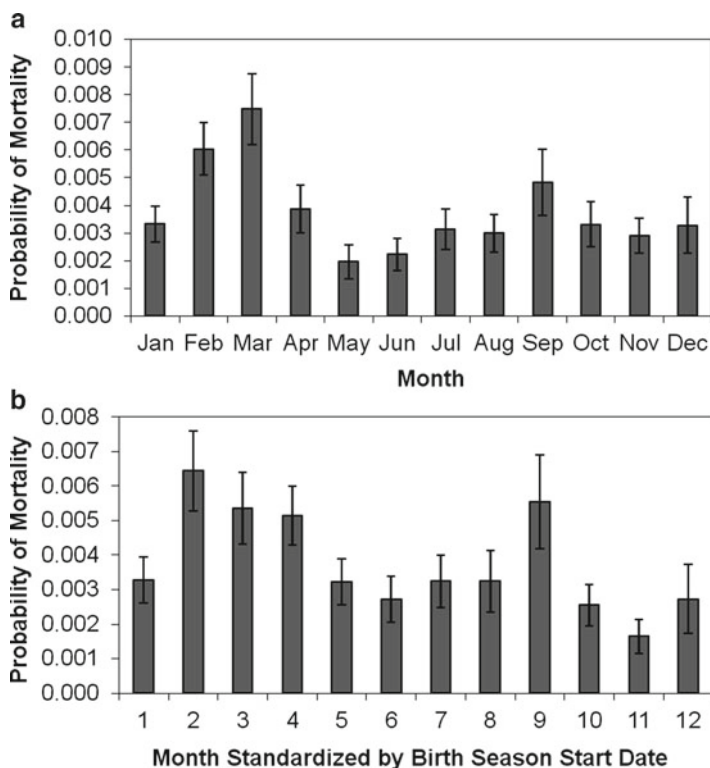
Fig. 10.1 The probability of adult female mortality based on (**a**) the number of months into the calendar year and (**b**) the number of months into the birth season. Modified after Fig. 2a, b in Hoffman et al. (2008)

from the cycling condition to the lactating condition ($n=12$, $r=-0.36$, $p=0.25$), but dominance rank did: low-ranking females had greater increases in cortisol from the cycling condition to the lactating condition than did middle- or high-ranking females ($F_{2,9}=6.99$, $p=0.02$) (Fig. 10.2).

10.3.4   Age-Related Physical and Behavioral Changes

Although we found no association between maternal age and cortisol, we did find age-associated declines in body condition and changes in behavior. In both 2007 and 2008 samples, there was a significant relationship between female age and BMI (2007: $F_{1,51}=5.90$, $p=0.02$; 2008: $F_{1,38}=4.90$, $p=0.03$), with BMI decreasing with increasing maternal age. Social rank and reproductive condition were not significant predictors of BMI. No age-related behavioral differences were observed during the
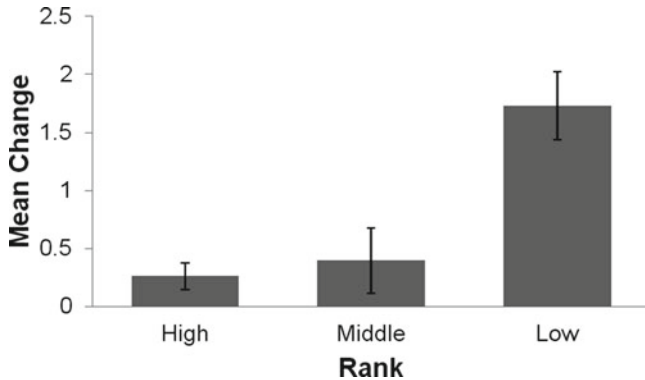
Fig. 10.2 Relationship between social rank and mean change in cortisol from the cycling condition to the lactating condition. *z*-Scores are used here because, as described in the text, mean cortisol values for 2007 and 2008 differed significantly. Modified after Fig. 2 in Hoffman et al. (2010a)

pre-birth period of observation, but differences emerged during the first month post-birth. Female age did not affect the proportion of time females spent resting or grooming pre-birth (resting: $F_{1,26}=0.79$, $p=0.38$; grooming: $F_{1,26}=0.26$, $p=0.61$), but during the first month post-birth, the proportion of time females spent resting increased with maternal age ($F_{1,24}=6.24$, $p=0.02$). Furthermore, the proportion of time females engaged in grooming during that month decreased with maternal age ($F_{1,24}=4.24$, $p=0.05$).

### 10.3.5 Age-Related Changes in Interbirth Interval

We found age-related changes in the frequency of reproduction. The interbirth intervals for the 631 females who lived their entire lives on Cayo Santiago ranged from 300 to 2,591 days ($\overline{X}=431.6$ days, SD $=147.4$, $n=1,800$ births) and increased significantly with increasing maternal age ($F_{2,18}=66.93$, $p<0.001$) (Fig. 10.3). Average interbirth intervals of females between 4 and 18 years of age ranged between 392 and 463 days, but the average interbirth interval rose to 541 days at 19 years and was 607 for females 19 years and older.

10.3.6 Age-Related Changes in Maternal Investment and Offspring Survival

Compared to younger mothers, older mothers spent more time in ventro-ventral contact with their infants during the first month post-birth ($F_{1,24}=10.02$, $p=0.004$). Even though we observed age-associated behavioral changes, these changes did not result in greater infant body condition or survival rates. There was no relationship
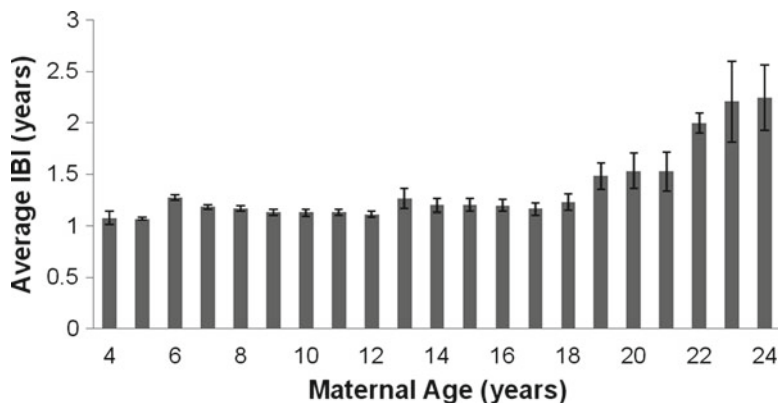
Fig. 10.3 Relationship between female age and interbirth interval. Modified after Fig. 6 in Hoffman et al. (2010b)
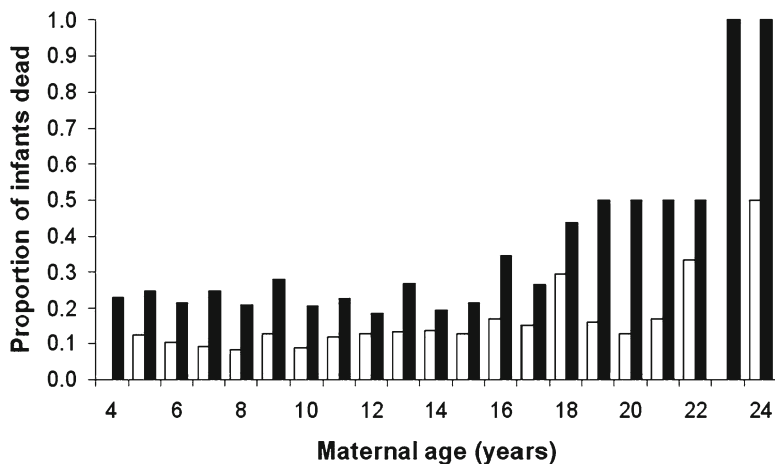
Fig. 10.4 Relationship between maternal age and probability of infant death by 30 days (*white bars*) and 1 year (*black bars*). Modified after Fig. 5 in Hoffman et al. (2010b)

between infant mass and infant age or sex (for both $p>0.10$), but there was a relationship between infant mass and maternal age ($F_{1,17.82}=6.94$, $p=0.02$). Infant mass was lower for those infants born to older mothers. In the long-term data, we found no relationship between maternal age and sex ratio (linear: $F_{1,19}=0.71$, $p=0.41$; quadratic: $F_{2,18}=1.74$, $p=0.20$).

Based on analysis of the long-term data, early offspring survival was not affected by infant sex but decreased as a function of increasing maternal age. The proportion of infants dying by 30 days and 1 year post-birth was greater for older females, even when mothers dying prior to these time points were excluded from analyses (30 days: $F_{2,18}=4.65$, $p=0.02$; 1 year: $F_{2,18}=57.61$, $p<0.001$) (Fig. 10.4).

10.4   Discussion

Even though the Cayo Santiago rhesus macaques are food-provisioned year-round, their reproduction remains seasonal and has significant fitness costs for adult females. Most conceptions in the period 1961–2005 occurred between May and October, and most births occurred between November and April (see also Carpenter 1942; Koford 1965; Rawlins and Kessler 1985, 1986). We confirmed and extended Rawlins and Kessler's (1985) finding that the onset of spring rainfall is a seasonal predictor of reproduction by showing that a gradual shift in the onset of the spring rainy season over the period 1963–1996 was accompanied by a parallel shift in the beginning of the mating and birth seasons.

Our study also provides evidence that not only births but also deaths show significant seasonal fluctuations. Specifically, the probability of mortality for adult females is significantly higher during the birth season than during the mating season. It is possible, especially in wild primate populations, that annual changes in climatic factors may result in seasonal patterns of deaths as a result of changes in food or water availability, but it is unlikely that climatic factors are the direct cause of the observed mortality patterns on Cayo Santiago since this population is food-provisioned year-round and free of predators.

Although our study does not provide direct evidence for a causal relation between reproduction and mortality, the most reasonable interpretation of our results is that mature females are most likely to die when they give birth and rear offspring. Suggestive evidence of a causal link between reproduction and adult female mortality was provided by the finding that as the onset of the birth season shifted gradually over the 45-year period of this study, so too did the pattern of mortality for adult females. Furthermore, our finding that plasma cortisol levels were elevated during the period of lactation also indicates that the period of lactation is energetically taxing for females. Although higher levels of cortisol among mothers may be an artifact of increased glucose production during lactation (Gittleman and Thompson 1988; Bell and Bauman 1997), it is unlikely that the metabolic costs of lactation accounted for the observed differences in cortisol levels since we found no relationships between reproductive condition and body mass or between cortisol and body mass.

The higher cortisol responses to stress exhibited by lactating females may have been the result of concerns about infant safety. Consistent with this explanation, we found that the amount of increase in cortisol from the cycling reproductive state to the lactating reproductive state for females sampled in 2007 and 2008 was significantly higher in low-ranking females than in middle- or high-ranking females. Compared to middle- and high-ranking mothers, low-ranking mothers may perceive their infants to be at greater risk of mistreatment from other group members, and these mothers experience greater constraints in their ability to provide protection for offspring (Maestripieri 1995). Since infant rhesus macaques born to low-ranking females have a lower probability of surviving their first year than infants born to high-ranking females (Drickamer 1974), motherhood may be particularly challenging for low-ranking females. Thus, in addition to the energetic demands of pregnancy

and lactation, the psychosocial stress associated with motherhood can be a significant cost of reproduction for rhesus macaque females. Sustained hyperactivation of the HPA axis during lactation may impair immune function (Sapolsky 2005), increasing the risk of mortality.

By integrating demographic data on survival and reproduction from the Cayo Santiago long-term data set with new morphometric and behavioral data collected from a sample of mothers and infants, we found that older females may increase investment in their offspring, but the increased effort does not result in increased offspring survival. In accordance with the senescence hypothesis, older females had lower body mass indices, were less active post-birth, and had infants with lower masses and survival rates than younger females. Age-associated increases in inter-birth intervals and time in ventro-ventral contact with infants, however, suggest that older females may invest more in their offspring than younger females, providing evidence for the terminal investment hypothesis. Thus, we found strong evidence for senescence and only weak evidence for terminal investment.

As previously observed in a captive rhesus macaque population (Gagliardi et al. 2007), infant survival on Cayo Santiago decreased sharply as females entered their late teens. Our data highlight at least two factors that may lead to this: maternal social behavior and maternal body condition. Though there were no age-related differences in grooming or resting pre-birth, older mothers were involved in less grooming interactions following their infant birth than younger mothers were. Unfortunately, previous studies that have characterized rhesus behavior in wild habitats have not included female age, rank, or infant presence in their analyses (e.g., Teas et al. 1980), preventing comparison of these results with wild populations. Given that cercopithecine non-mothers and mothers with young infants tend to be attracted to females with young infants (e.g., *Papio anubis*: Frank and Silk 2009; *Papio cynocephalus ursinus*: Silk et al. 2003; *Macaca mulatta*: Whitham et al. 2007), this reduced grooming time may mean that the offspring of older rhesus females are less attractive to other females. The observed decrease in sociality may affect the likelihood of infant survival, given the potential links between social support and survivorship in primates (Silk et al. 2006). Strong social bonds may increase infant survival and benefit infants by providing mothers with support in agonistic interactions, lowering mother's basal cortisol levels, increasing infant protection from harassment, or making more resources accessible to mother–infant dyads (Silk et al. 2003).

The low body mass of the older females' infants likely reflects old mothers' diminished abilities to invest energetically in offspring during pregnancy and lactation due to their poor body condition. Although a previous study failed to document direct relationships between maternal body composition or age and lactation performance in captive rhesus monkeys (Hinde et al. 2009), the effects of female age, body composition, and access to resources on lactation performance should be explored on Cayo Santiago due to the amount of variation present within this population. Free-ranging, rhesus females in poor physical condition are expected to produce milk in low quantities or of lower quality since relationships between maternal condition and lactation performance have been reported from studies of human populations (Ettyang et al. 2005; Villalpando et al. 1992). The infants' low masses

also suggest that infants of older mothers may develop more slowly than those born to younger mothers. Slower infant growth rates have also been observed in offspring born to older chacma baboon mothers (*Papio ursinus*, Johnson 2006), and low infant mass is predictive of infant mortality in common marmosets (*Callithrix jacchus*; Tardif et al. 2002). Low body mass may be a major factor contributing to high mortality rates for rhesus infants born to older mothers.

According to the terminal investment hypothesis, increasing interbirth intervals and suckling time may increase infant survival for older females, but this is not the case for females in our study. Consistent with a vast body of literature on primate life history (e.g., Higham et al. 2009; Okamoto et al. 2000; Malik et al. 1992), we might expect interbirth intervals to be shorter for females whose infants die, but we see no evidence of this; whereas infant survival was lower for the older females in our study, their interbirth intervals were longer. These patterns are consistent with general reproductive senescence in these females. Additional data are needed to determine if lengthening interbirth intervals are associated with hormonal or behavioral changes. Hormonal data would indicate whether the increasing interbirth intervals are associated with increasingly irregular ovulatory patterns, as they are in captive rhesus populations (Gilardi et al. 1997). Furthermore, behavioral data collected from mothers and infants between 2 and 8 months post-parturition would reveal whether age-related differences in suckling intensity affect time between parturition and the resumption of mating (see Johnson et al. 1998). If extended interbirth intervals among older females are clearly related to increased lactational effort, this would be consistent with a terminal investment interpretation for longer interbirth intervals. Conversely, if extended interbirth intervals occur among older females even though overall lactational effort is consistent across the adult life span, this would support a senescence interpretation of the effect.

10.5   Conclusion

The rhesus macaques on Cayo Santiago reside in a provisioned, predator-free environment, but they continue to breed seasonally. Furthermore, the population appears to remain sensitive to climatic factors since the onset of the birth season closely tracks the onset of the rainy season. Our findings show that although rhesus macaque females on Cayo Santiago have the physical and physiological ability to conceive and give birth virtually until the end of their life span, they experience increased HPA axis activation during the period of lactation and, perhaps as a consequence, elevated mortality risks. The costs of reproduction increase with female age whereas the benefits diminish since a female's ability to sustain pregnancy and lactation and guarantee infant survival decreases steadily and dramatically in her last 5–10 years of life due to senescence. Extremely old females would fare better if they ceased reproducing and, instead, invested their resources in their existing offspring because even when they increase their investment in new offspring, the probability of their

offspring surviving beyond infancy is low. In wild populations of macaques, predators, disease, and unpredictable food sources make it unlikely that adult females will survive into their third decade (Johnson et al. 1991; Jones-Engel 2006), such that selective pressures for early termination of reproduction are probably negligible or nonexistent in the wild. Thus, our findings regarding the changes in female reproduction and maternal care observed within the oldest residents in the Cayo Santiago population may not generalize to wild populations.

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