

Sex differences in survival costs of reproduction in a promiscuous primate

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Abstract In sexually promiscuous mammals, female reproductive effort is mainly expressed through gestation, lactation, and maternal care, whereas male reproductive effort is mainly manifested as mating effort. In this study, we investigated whether reproduction has significant survival costs for a seasonally breeding, sexually promiscuous species, the rhesus macaque, and whether these costs occur at different times of the year for females and males, namely in the birth and the mating season, respectively. The study was conducted with the rhesus macaque population on Cayo Santiago, Puerto Rico. Data on 7,402 births and 922 deaths over a 45-year period were analyzed. Births were concentrated between November and April, while conceptions occurred between May and October. As predicted, female mortality probability peaked in the birth season whereas male mortality probability peaked in the

mating season. Furthermore, as the onset of the birth season gradually shifted over the years in relation to climatic changes, there was a concomitant shift in the seasonal peaks of male and female mortality. Taken together, our findings provide the first evidence of sex differences in the survival costs of reproduction in nonhuman primates and suggest that reproduction has significant fitness costs even in environments with abundant food and absence of predation.

Keywords Survival costs of reproduction · Sex differences · Seasonal reproduction · Climate change · Rhesus macaques

Introduction

Two central assumptions of life history theory are that reproduction is costly and that there are tradeoffs between fitness-related traits, so that, for example, investment in reproduction is likely to be associated with reduced survival (Stearns 1989, 1992; Roff 2002). Costs of reproduction and tradeoffs between reproduction and survival have been demonstrated in a number of animal taxa. For example, studies of insects, fishes, reptiles, and birds show that when individuals engage in mating or parental activities, they may expose themselves to increased risk of predation (reviewed by Roff 2002). Studies of mammals have emphasized the energetic costs of gestation and lactation for females and their effects on fitness. For example, a successful breeding event has been shown to be associated with reduced female survival and fecundity during the following breeding season (e.g., red deer, *Cervus elaphus*, Clutton-Brock et al. 1982; European badger, *Meles meles*, Woodroffe and MacDonald 1995). In polygynous or promiscuous mammals, male mating effort can have

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significant costs due to the risks associated with dispersal, energy expenditure for mate attraction displays or intra-sexual competition, fighting, and increased exposure to predation (e.g., see Promislow 1992). Accordingly, male mating effort is often associated with lower survival (e.g., red deer, Clutton-Brock et al. 1982; elephant seals, *Mirounga angustirostris*, Clinton and LeBoeuf 1993; Columbian ground squirrels, *Spermophilus columbianus*, Neuhaus and Pelletier 2001). By contrast, castration can significantly extend male lifespan (e.g., Soay sheep, *Ovis aries*, Jewell 1997). In ground squirrels with seasonal reproduction, male mortality is generally high during or after the mating season, whereas female mortality is high in conjunction with the birth season and lactation (Michener and Locklear 1990; Michener 1998; Neuhaus and Pelletier 2001).

Although the mating strategies and reproductive effort of nonhuman primates have been the subject of a large amount of research, to date no study has systematically assessed and directly compared the survival costs of reproduction in males and females (but see Penn and Smith 2007, for humans). Furthermore, although many species of primates exhibit seasonal reproduction (see Brockman and van Schaik 2005), it is unknown whether the survival costs of reproduction for males and females occur at different times of the year, or the extent to which these costs are accounted for by reproduction-related energy expenditure, predation, or exposure to infectious diseases. There is some evidence in wild baboons (*Papio* spp.) that adult female mortality is highest among pregnant and lactating females (e.g., Cheney et al. 2004), while studies of rhesus macaques have shown that adult males lose 10% of their body weight during the mating season and may suffer serious wounds due to intense fighting with other males (Bercovitch 1997). No study of primates, however, has directly demonstrated that while the costs of reproduction for females are mostly associated with pregnancy, giving birth, and lactation, the costs of reproduction for males mostly result from their mating effort.

In this study, we investigated sex differences in reproduction and mortality in the free-ranging population of rhesus macaques on the island of Cayo Santiago, Puerto Rico (Rawlins and Kessler 1986a). Specifically, we tested the following hypotheses: (1) reproduction has significant survival costs to rhesus macaques, and (2) whereas the probability of mortality of adult males should be highest during the mating season, in conjunction with the peak in male reproductive effort, the probability of mortality of females should be highest in the birth season, in conjunction with the costs and risks of late pregnancy, parturition, and lactation. The rhesus macaque colony on Cayo Santiago is an ideal population in which to investigate the survival costs of reproduction for at least four reasons: (1) predation is absent on the island, and monkeys are food-

provisioned year round, thus simplifying the analysis of the mechanisms through which reproductive effort can affect adult survival; (2) although the population exhibits strong seasonal reproduction, annual climatic changes are minimal (e.g., Rawlins and Kessler 1985), thus minimizing the possibility that climate-related seasonal changes in the environment, rather than reproduction itself, might affect seasonal patterns of mortality; (3) the monkeys are free ranging, do not receive any veterinary care, and are subject to no experimental manipulations; (4) complete and accurate information on births and deaths is available for a large number of individuals over a period of more than 40 years. Therefore, the investigation of relationships between seasonal reproduction and spontaneous occurrence of adult mortality using the large amount of data available for this population could make a significant contribution to our understanding of the survival costs of reproduction in sexually promiscuous nonhuman primates and other animals as well.

Materials and methods

Subject population

The subject population resides on Cayo Santiago, a 15.2-ha island located 1 km off the southeastern coast of Puerto Rico (18° 09' N, 65° 44' W). Cayo Santiago has an average daily temperature of 28°C throughout the year, while relative humidity varies between 60% and 75% (Rawlins and Kessler 1985). Annual variations in rainfall result in a relatively dry winter season, a spring rainy season, and a summer–fall tropical storm season (Rawlins and Kessler 1985).

The rhesus macaque colony on Cayo Santiago was established in 1938, with free-ranging monkeys captured in India (Rawlins and Kessler 1986b). 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 culled each year, and on few occasions, entire matrilineal or social groups have been removed. Although reduction of density through culling of young individuals may reduce social stress within the population, this is unlikely to affect the relation between reproduction and mortality investigated in this study. In 2006, the population included approximately 850 animals distributed among six naturally formed social groups. Monkeys on Cayo Santiago forage on vegetation and are provisioned with rainwater and commercial monkey chow. All individuals are identified by ear notches and a unique alphanumeric name, which is tattooed on their chest and thighs. A census of all individuals in the population is conducted 5 days a week, and accurate records of all births, deaths, and group transfers have been maintained since

1956. Colony records also include information on sex and age of individuals and maternal genealogy. Females give birth for their first time at approximately 3–4 years of age, while the process of male reproductive maturation begins at about 4 years of age (Bercovitch 1997). No information on the precise causes of death is available because in most cases such causes could not be determined.

Procedure

Data for this study were obtained from the colony database and included individuals that were born on Cayo Santiago in the period 1957–2001 and died on the island in the period 1961–2005. Only sexually mature females and males that were at least 4 years old at their time of death (referred to as mature or adult individuals) were included in the sample. Due to unreliable census data prior to 1957 (Koford 1965), individuals born before January 1, 1957 were excluded from analysis, as were all individuals that were culled.

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 consider this a conservative estimate of the beginning and the end of the mating season because it is obtained by only considering mating that resulted in conception and live births.

Seasonal reproduction in the Cayo Santiago rhesus macaque population is associated with climatic factors, particularly the onset of the spring rainy season (Rawlins and Kessler 1985; see more details below). Data on daily precipitations were obtained from the National Oceanic and Atmospheric Administration (NOAA) of the US Department of Commerce. The closest NOAA weather recording station is in Humacao, PR (approximately 6 km from Cayo Santiago), and from this station we were able to obtain data on daily precipitations from 1963 to 1996 (see Rawlins and Kessler 1985, for use of a subset of these data). 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. (see also Rawlins and Kessler 1985).

Similarities and differences in male and female mortality in the population were assessed by comparing monthly mortality probabilities for males and females, as well as by comparing the total number of male and female deaths in the mating and birth seasons. The monthly mortality probability for males was calculated by dividing the number of males that died in a given month by the number of adult males present in the population that month (i.e., all

the adult males that could potentially die). This probability is a number that varies between 0 and 1. The same formula was used to calculate the monthly mortality probability for females. To test statistically for seasonality in the probability of mortality of males and 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*. In a model with both females and males, differences in seasonality between the two sexes were tested via interaction terms between sex and the sine and cosine terms.

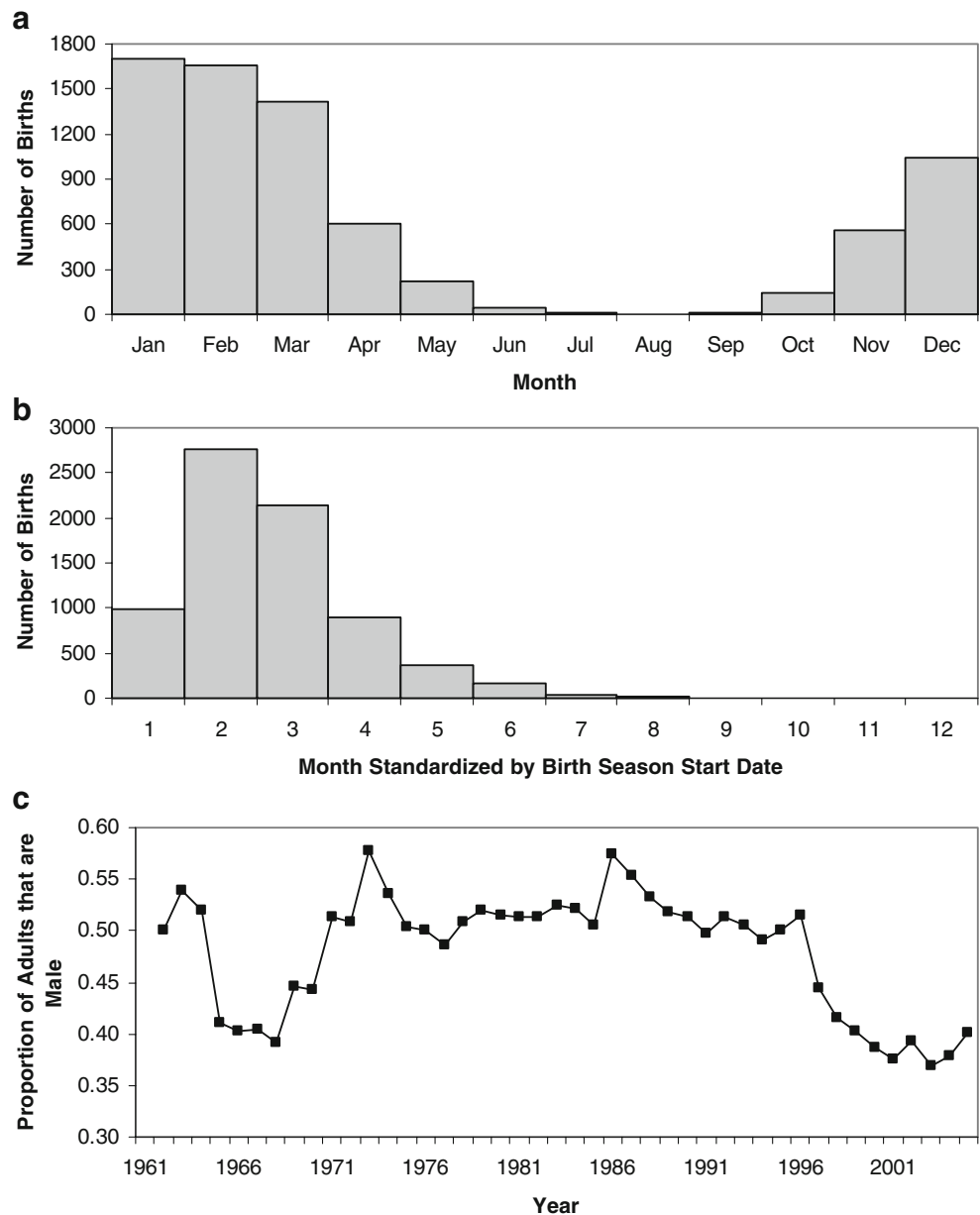
Results

A total of 7,402 live births (males=3,805; females=3,597) were recorded in 45 years (1961–2005). As previously reported for this population (e.g., Rawlins and Kessler 1985), most births (86%) were concentrated in a 5-month period, from November through March (Fig. 1a; the birth season has commenced increasingly earlier over time; see below) whereas, on average, the mating season began in mid-May and ended in October. The mean birth season length was 128.19+16.61 days. Most infants were born in the second and third month of the birth season, with fewer births in the first month and after the third month (Fig. 1b). Although more males were born than females, the percentage of adult males in the population generally fluctuated around 50%, with the exception of the periods 1963–1972 and 1995–2005, when fewer adult males than females were present in the population due to increased culling of males (Fig. 1c; see Rawlins and Kessler 1986c).

A total of 922 deaths (males=526; females=396) were included in data analyses. Deaths for both sexes occurred throughout the year, but male mortality probability peaked in August, September, and October, whereas female mortality probability peaked in February and March (Fig. 2a; a second, smaller peak in female mortality in September was not statistically significant). The 2-*df* test for seasonality in the probability of mortality was significant in both males ($\chi^2=11.49$, $p=0.0032$) and females ($\chi^2=24.91$, $p<0.0001$). The 2-*df* test comparing patterns of seasonality for male and female mortality was also significant ($\chi^2=35.44$, $p<0.0001$). Therefore, both males and females exhibited significant seasonal fluctuations in their probability of mortality, and these fluctuations were significantly different between the sexes.

Figure 2b presents the same data as Fig. 2a, but the data are realigned in relation to the beginning of the birth season

Fig. 1 **a** Total number of births on Cayo Santiago from 1961 to 2005 by month of calendar year. **b** Total number of births standardized by the beginning of the birth season. **c** Proportion of males in the adult population from 1961 to 2005



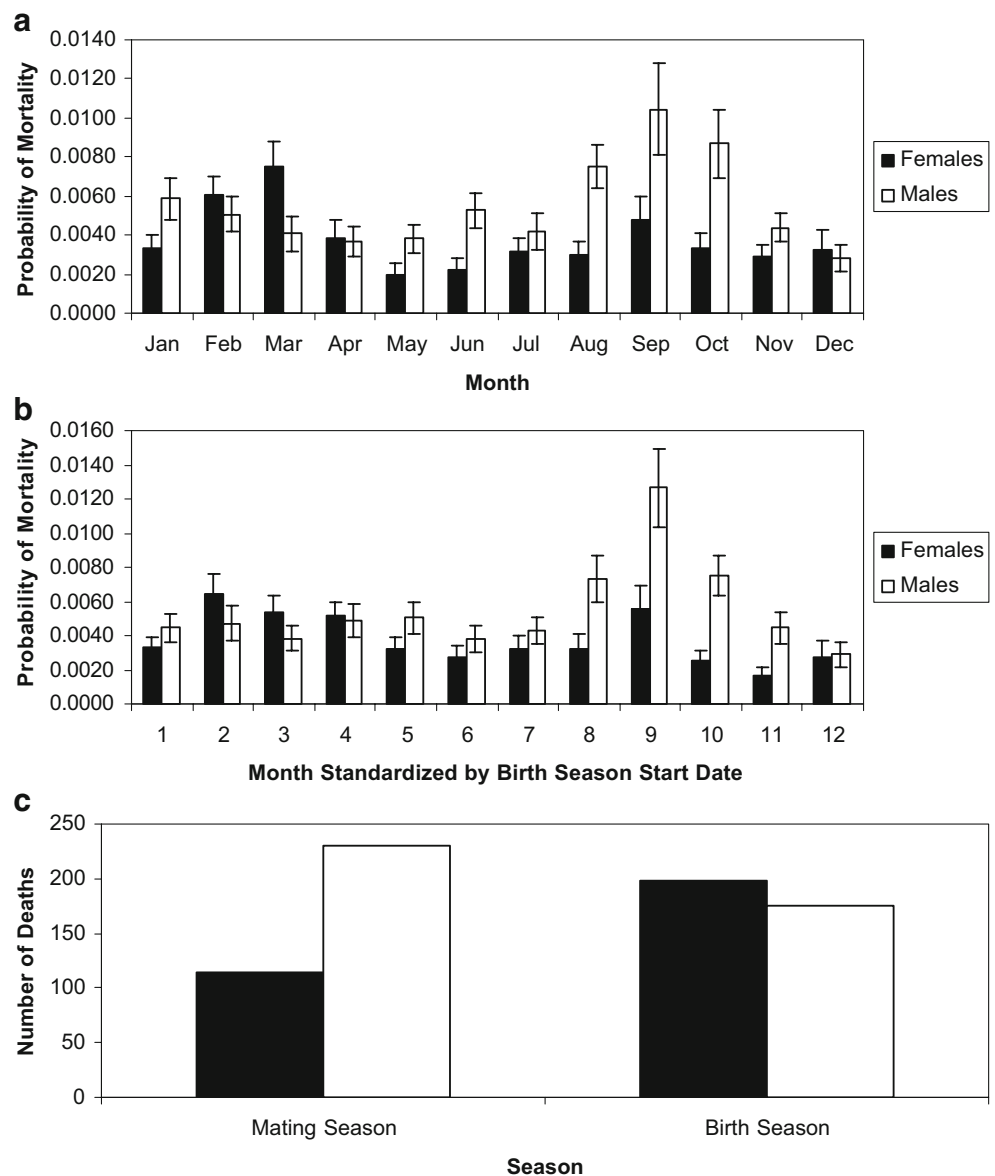
rather than in relation to calendar year. Although the graphs appear very similar, Fig. 2b depicts a clearer peak in male mortality probability in the three central months of the mating season, suggesting that male mortality is affected by seasonal reproduction to a greater extent than by calendar year. For females, 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, suggesting that the effect of seasonal reproduction may not be as strong as for males.

As a further test of the relation between mortality and seasonal reproduction, male and female deaths in any given year were classified as birth season deaths if they occurred

in the time interval between the first and the last birth for that particular year and as mating season deaths if they occurred in the mating season that preceded the birth season for a given year (thus, the mating and the birth season were of equal length). The difference between the number of male and female deaths in the birth and mating season was statistically significant ($\chi^2=28.59$, $df=1$, $p<0.001$; Fig. 2c). Specifically, more females died in the birth season than in the mating season ($\chi^2=22.08$, $df=1$, $p<0.001$), whereas more males died in the mating season than in the birth season ($\chi^2=6.92$, $df=1$, $p<0.01$).

Further evidence that seasonal reproduction is associated with seasonal patterns of mortality would be provided by demonstrating that changes in the timing of

Fig. 2 **a** Mean (and SEM) monthly mortality probability for males and females in the study period. **b** Mean (and SEM) monthly mortality probability for males and females in relation to 12 1-month blocks, from the beginning of the birth season. **c** Total number of male (white) and female (black) deaths in the birth and the mating seasons

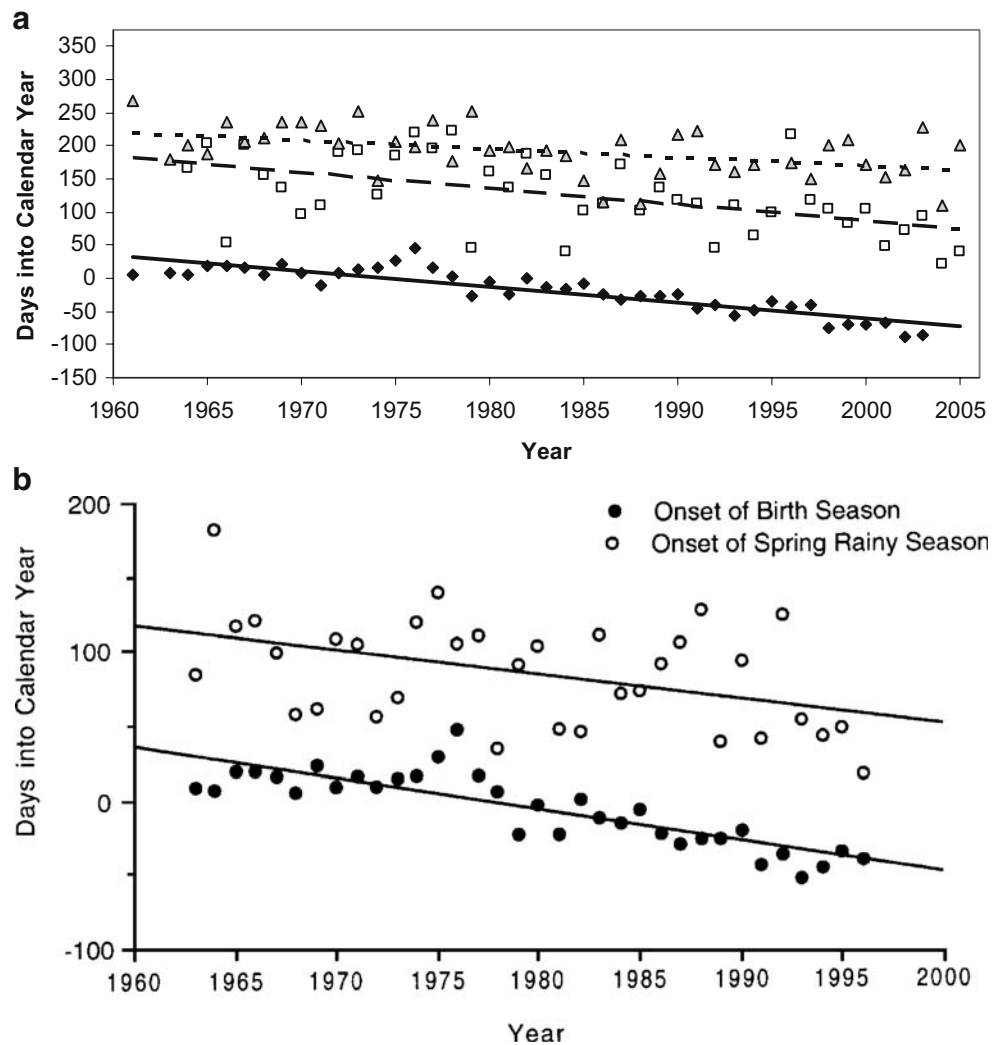


the onset of the birth season from year to year are mirrored by concomitant changes in mortality. In the period between 1961 and 2005, the birth season on Cayo Santiago has commenced increasingly earlier over time ($r=-0.89$; $p<0.001$; $n=42$, Fig. 3a), and the average dates of female and male deaths have steadily shifted as well (females: $r=-0.53$; $p<0.001$; males: $r=-0.45$; $p=0.002$). Females died, on average, 135 ± 70 days after the birth season started, whereas males died, on average, 189 ± 40 days after the birth season started (Fig. 3a). The shift in the onset of the birth season over the years, in turn, was predicted by a shift in the onset of the spring rainy season ($r=0.43$, $n=34$; $p=0.01$), which has begun increasingly earlier over the period of time for which data were available (Fig. 3b).

Discussion

Our study provides empirical evidence in support of two of the most basic assumptions of life history theory and parental investment theory, namely that reproduction has significant fitness costs and that these costs are different for males and females. Although sex differences in the survival costs of reproduction have been documented in some mammals (e.g., Clutton-Brock et al. 1982; Michener and Locklear 1990), our results provide the first evidence for these differences in nonhuman primates. Our study also sheds light on the fitness consequences of seasonal reproduction and some of its underlying mechanisms. These findings can probably be generalized to a number of other vertebrate taxa with seasonal reproduction.

Fig. 3 **a** Regression of time of onset of birth season (*diamonds*), average death date for females (*squares*), and average death date for males (*triangles*) in relation to calendar year. **b** Regression of time and onset of spring rainy season and time and onset of birth season in relation to calendar year



Rhesus macaques are a primate species with a promiscuous mating system and seasonal reproduction. In the rhesus macaque population on Cayo Santiago, most births in the period 1960–2005 occurred between November and April and most conceptions between May and October (see also Carpenter 1942; Koford 1965; Rawlins and Kessler 1985; 1986c). Our study provides the first evidence that not only births but also deaths are seasonal and that the seasonal patterns in the probability of mortality are significantly different between adult males and females. Specifically, adult male mortality was highest in the mating season while adult female mortality was highest in the birth season.

Seasonal reproduction in rhesus macaques and other primates is probably regulated by environmental factors such as photoperiod, temperature, and humidity, and/or rainfall (e.g., Vandenberg and Vessey 1968; Vandenberg 1969; Riesen et al. 1971; van Horn 1980; Herndon 1983; Cozzolino et al. 1992; Sharma et al. 2006). Previous studies of the Cayo Santiago population concluded that annual

changes in daylength or fluctuations in average daily temperatures and relative humidity are too small to act as proximate cues for the regulation of seasonal breeding in this particular population (Koford 1965; Rawlins and Kessler 1985). Rawlins and Kessler (1985), however, provided evidence that the onset of spring rainfall was a strong predictor of seasonal reproduction, as the date of onset of the spring rainy season was significantly correlated with both the median birth date and the median conception date in the period 1976–1983. We confirmed and extended this finding 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 birth season. Previous studies have also suggested that social stimulation may modulate seasonal reproduction in the Cayo Santiago population (Vandenberg 1969), but these social influences are unlikely to change over time in the absence of changes in climatic factors.

Although it is possible, especially in wild primate populations, that annual changes in climatic factors may

result in seasonal patterns of deaths, it is unlikely that climatic factors are the direct cause of the observed mortality patterns on Cayo Santiago for at least two reasons. First, seasonal changes in climatic factors generally affect the mortality patterns in wild populations through changes in food or water availability or the occurrence of predators or parasites (see Brockman and van Schaik 2005). The rhesus macaques on Cayo Santiago, however, are food- and water-provisioned year round and relatively free from predators and parasites. Second, it is very unlikely that the same seasonal changes in climatic factors could result in different seasonal mortality patterns for adult males and females or that male and female deaths could be independently affected by different climatic changes in an environment in which these changes are generally minimal.

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 males are most likely to die in conjunction with their mating effort, whereas mature females are most likely to die when they give birth and rear offspring. Suggestive evidence of a causal link between reproduction and adult 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 did the pattern of mortality for males and females. Females died, on average, 135 days after the birth season started, whereas males died, on average, 189 days after the birth season started.

Previous studies of the costs of reproduction in seasonally breeding species have emphasized the role of seasonal fluctuations in food availability or predation pressure as determinants of reproduction-related mortality (see Promislow 1992). Our results suggest that reproduction can have significant survival costs even in populations without predators and with abundant food supply. Although we have no accurate information on the causes of death in our rhesus macaque population, there is strong evidence that infectious diseases such as tetanus caused significant mortality in the past, before the monkeys received tetanus vaccination (Kessler et al. 2006). Therefore, it is reasonable to suggest that adult males may be more vulnerable to death from infectious diseases during the mating season due to their high rates of aggression and wounding. In addition, both males and females may be more vulnerable to infectious diseases in conjunction with their maximal reproductive effort due to suppression of immune function. Studies in a wide range of animal species have shown that elevated testosterone levels in breeding males can directly suppress the immune system (see Roberts et al. 2004, for a review). Suppressed immune function can also result from elevated circulating levels of glucocorticoid hormones associated with reproduction-related energetic and social stress in both males and females (see McEwen et al. 1997,

for a review). Finally, it is possible that females may be at higher risk of death during the birth season also due to pregnancy or parturition complications.

Future studies of the Cayo Santiago rhesus population as well as other primate populations can address the mechanisms underlying the survival costs of reproduction by gathering accurate information on the causes of adult mortality and quantifying the behavioral, energetic, and risk-related aspects of reproductive effort in males and females. A full understanding of the tradeoffs between reproduction and survival in primates may also require measurements of hormonal variables such as testosterone and glucocorticoid levels and assess how these variables affect immune function and vulnerability to disease.

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References

- Ardito G (1976) Check-list of the data on the gestation length of primates. *J Hum Evol* 5:213–222
- Bercovitch FB (1997) Reproductive strategies of rhesus macaques. *Primates* 38:247–263
- Brockman DK, van Schaik CP (eds) (2005) Seasonality in primates: studies of living and extinct human and nonhuman primates. Cambridge University Press, Cambridge
- Carpenter CR (1942) Sexual behavior of free-ranging rhesus monkeys (*Macaca mulatta*). *J Comp Psychol* 33:113–162
- Cheney DL, Seyfarth RM, Fischer J, Beehner J, Bergman T, Johnson SE, Kitchen DM, Palombit RA, Rendall D, Silk JB (2004) Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana. *Int J Primatol* 25:401–428
- Clinton WL, LeBoeuf BJ (1993) Sexual selection effects on male life history and the pattern of male mortality. *Ecology* 74:1884–1892
- Clutton-Brock TH, Guinness FE, Albon SD (1982) Red deer: behavior and ecology of two sexes. University of Chicago Press, Chicago
- Cozzolino R, Cordischi C, Aureli F, Scucchi S (1992) Environmental temperature and reproductive seasonality in Japanese macaques. *Primates* 33:329–336
- Herndon JG (1983) Seasonal breeding in rhesus monkeys: influence of the behavioral environment. *Am J Primatol* 5:197–204
- Jewell PA (1997) Survival and behaviour of castrated Soay sheep (*Ovis aries*) in a feral island population on Hirta, St. Kilda, Scotland. *J Zool* 243:623–636
- Kessler MJ, Berard JD, Rawlins RG, Bercovitch FB, Gerald MS, Laudenslager ML, Gonzalez JM (2006) Tetanus antibody titers and duration of immunity to clinical tetanus infections in free-

- ranging rhesus monkeys (*Macaca mulatta*). *Am J Primatol* 68:725–731
- Koford CB (1965) Population dynamics of rhesus monkeys on Cayo Santiago. In: De Vore I (ed) *Primate behavior: field studies of monkeys and apes*. Holt, Rinehart & Winston, New York, pp 160–174
- McEwen BS, Biron CA, Brunson KW, Bulloch K, Chambers WH, Dhabhar FS, Goldfarb RH, Kitson RP, Miller AH, Spencer RL, Weiss JM (1997) The role of adrenocorticoids as modulators of immune function in health and disease: neural, endocrine and immune interactions. *Brain Res Rev* 23:79–133
- Michener GR (1998) Sexual differences in reproductive effort of Richardson's ground squirrels. *J Mammal* 79:1–19
- Michener GR, Locklear L (1990) Differential costs of reproductive effort for male and female Richardson's ground squirrels. *Ecology* 71:855–868
- Neuhaus P, Pelletier N (2001) Mortality in relation to season, age, sex, and reproduction in Columbian ground squirrels (*Spermophilus columbianus*). *Can J Zool* 79:465–470
- Penn DJ, Smith KR (2007) Differential fitness costs of reproduction between the sexes. *Proc Natl Acad Sci USA* 104:553–558
- Promislow DEL (1992) Costs of sexual selection in natural populations of mammals. *Proc R Soc Lond B* 247:203–210
- Rawlins RG, Kessler MJ (1985) Climate and seasonal reproduction in the Cayo Santiago macaques. *Am J Primatol* 9:87–99
- Rawlins RG, Kessler MJ (eds) (1986a) *The Cayo Santiago macaques: history, behavior and biology*. SUNY, Albany
- Rawlins RG, Kessler MJ (1986b) The history of the Cayo Santiago colony. In: Rawlins RG, Kessler MJ (eds) *The Cayo Santiago macaques: history, behavior and biology*. SUNY, Albany, pp 13–45
- Rawlins RG, Kessler MJ (1986c) Demography of the free-ranging Cayo Santiago macaques (1976–1983). In: Rawlins RG, Kessler MJ (eds) *The Cayo Santiago macaques: history, behavior and biology*. SUNY, Albany, pp 47–72
- Riesen JW, Meyer RK, Wolf RC (1971) The effect of season on occurrence of ovulation in the rhesus monkey. *Biol Reprod* 5:111–114
- Roberts ML, Buchanan KL, Evans MR (2004) Testing the immunocompetence handicap hypothesis: a review of the evidence. *Anim Behav* 68:227–239
- Roff DA (2002) *Life history evolution*. Sinauer, Sunderland
- Sharma AK, Singh M, Kaumanns W, Krebs E, Singh M, Kumar MA, Kumara HN (2006) Birth patterns in wild and captive lion-tailed macaques (*Macaca silenus*). *Int J Primatol* 27:1429–1439
- Stearns SC (1989) Trade-offs in life-history evolution. *Funct Ecol* 3:259–268
- Stearns SC (1992) *The evolution of life histories*. Oxford University Press, Oxford
- Vandenbergh JG (1969) Endocrine coordination in monkeys: male sexual responses to the female. *Physiol Behav* 4:261–264
- Vandenbergh JG, Vessey S (1968) Seasonal breeding of free-ranging rhesus monkeys and related ecological factors. *J Reprod Fert* 15:71–79
- Van Horn RN (1980) Seasonal reproductive patterns in primates. *Progr Reprod Biol* 5:181–210
- Woodroffe R, MacDonald DW (1995) Costs of breeding status in the European badger, *Meles meles*. *J Zool* 235:237–245