Life history costs and consequences of rapid reproductive maturation in female rhesus macaques

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Summary. Life history theory suggests that reproduction at one point in time involves costs in terms of energy, reduced survival, or probability of reproduction at a future point in time. In long-lived iteroparous organisms, initiating reproduction at a relatively young age may exact a cost in terms of reduced survivorship, but an early age of first reproduction could be beneficial if it lengthens the breeding lifespan. Data collected over 30 years from one population of rhesus macaques, *Macaca mulatta*, were analyzed to determine the fertility and survivorship costs of initiating reproduction at a relatively young age. Low population density and high social status increased the chances of accelerating age at first parturition, but high dominance rank was not associated with greater lifetime reproductive success. Rapid reproductive maturation neither reduced short-term survivorship nor decreased lifespan. Fertility costs arose if young females reared a male, but not female, offspring. The fitness consequences of rapid reproductive maturation depend upon longevity, with age at death having a significantly greater impact on lifetime reproductive success than age at first parturition.

Introduction

Life history theory postulates that reproduction involves costs in terms of the probability of future reproduction or survival (Williams 1966a, b; Gadgil and Bosert 1970; Pianka and Parker 1975; Stearns 1976, 1977; Bell 1980; Reznick 1985; Partridge and Harvey 1988), but documentation of a tradeoff between fecundity or mating activity and survival is limited (Bell 1980; Reznick 1985). One problematic area in the literature has been the infrequency with which reproductive costs are distinguished from fitness costs. Fitness costs have most often been measured in laboratory experiments on invertebrates, especially *Drosophila melanogaster* (e.g., Rose and Charlesworth 1981a, b; Rose 1984; Luckinbill et al. 1984) where the ability to measure genetic variation in contributions to future generations are documented. Fitness costs are decrements to future reproductive success accruing from genetic differences among individuals. On the other hand, reproductive costs have most often been assessed in field studies of vertebrates (Bryant 1979; De Steven 1980; Smith 1981; Clutton-Brock et al. 1983; Nur 1984; Ekman and Askenmo 1986; Gustaffson and Part 1990; Reiter and Le Boeuf 1991) where phenotypic effects of present reproduction on future survival or fecundity are measured. Reproductive costs are decrements to future reproductive success accruing from either genetic or nongenetic factors. Fitness costs entail reproductive costs, but the converse is not necessarily true because reproductive costs can arise from nongenetic causes.

Unraveling the life history consequences of rapid reproductive maturation in long-lived, iteroparous organisms is not a subject amenable to laboratory experimentation, and our analysis is confined to documenting reproductive costs and potential fitness consequences associated with rapid reproductive maturation in a population of rhesus macaques, *Macaca mulatta*.

Reproductive costs include both fertility costs, depressing the probability of future reproduction, and survival costs, diminishing life expectancy (Bell 1980). Fertility costs of reproduction in vertebrates are often assessed by experimentally varying litter or clutch size and assessing the impact on future reproductive output (Smith 1981; Reznick 1985; Bryant 1979; Gustaffson and Part 1990), but this technique is not feasible for use in mammals that bear a single offspring (Clutton-Brock et al. 1983; Lee and Moss 1986; Wolff 1988; Green and Berger 1990; Reiter and Le Boeuf 1991). Cercopithecine primates usually give birth to a single offspring (Harvey and Clutton-Brock 1985; Harvey et al. 1987), and removal of offspring is anathema to naturalistic primate field studies. Hence, although correlational studies of life history patterns present some problems (Reznick 1985; Partridge and Harvey 1988), the most
feasible way to assess fertility costs in nonhuman primates is to examine interbirth intervals derived from longitudinal studies. However, this type of naturalistic investigation cannot control for potential covariation in reproductive effort and parental quality. Evaluating survival costs also poses difficulties when attempting to apply life history theory to the evolution of reproductive strategies among nonhuman primates because the maximum lifespan in many species is about 30 years (Harvey and Clutton-Brock 1985; Harvey et al. 1987). Despite these limitations, empirical data obtained from investigations of free-ranging primate populations are an important source of information for providing a critical perspective from which to view models of life history strategies.

In this report, we analyze longitudinal data collected over 30 years from one population of rhesus macaques. Our goals are to assess potential social and demographic factors that could accelerate reproductive maturation in female rhesus macaques and to examine fertility and survivorship costs associated with an early age at first parturition. Among some populations of nonhuman primates, daughters of high rank females tend to give birth at earlier ages than do daughters of low rank females (Drickamer 1974; Roberts 1978; Wilson et al. 1983; Paul and Thommen 1984; Altman et al. 1988; Berman 1988), a pattern lending itself to the conventional viewpoint (Drickamer 1974; Roberts 1978; Wilson et al. 1983; Paul and Thommen 1984; Altman et al. 1988; Berman 1988), and Clutton-Brock 1985; Harvey et al. 1987). Despite these limitations, empirical data obtained from investigations of free-ranging primate populations are an important source of information for providing a critical perspective from which to view models of life history strategies.

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Cayo Santiago (18°09' N, 65°44' W) is a 15-ha island located about 1 km off the southeast coast of Puerto Rico that has been inhabited by rhesus macaques since 1938 (Sade et al. 1985; Rawlins and Kessler 1986a). Births and deaths have been collected on a systematic basis since 1956 (Altman 1982; Sade et al. 1985). Births at Cayo Santiago are confined to the months between December and June, with a peak in February and March (Rawlins and Kessler 1985). The average interbirth interval among the rhesus macaques at Cayo Santiago is 1 year, with about 80% of females giving birth each year (Rawlins and Kessler 1986b). Population size is based upon the total number of monkeys present on 1 July of each year, or at the approximate time that the birth season ends. Although provisioned with commercial monkey chow (ca. 0.23 kg/monkey/day), the rhesus macaques spend half of their feeding time eating the natural vegetation (Marriott 1988). Using data from a food-enhanced population to test life history theory has the disadvantage of potentially underestimating reproductive costs if nutritional stress is mitigated by food provisioning, but increased food availability does not necessarily translate into stable food consumption by all individuals. Food provisioning sites constitute restricted resources, and low rank females are regularly chased away from the food bins (Berard, upubl. data). Female rank among primates is most likely to influence reproductive success when food resources are clumped (Fedigan 1983; Harcourt 1987; Bercovitch and Yokata 1991) and food bins provide clumped high quality food resources. We do not know the extent to which food intake is influenced by dominance rank among females in this population. Among females in a free-ranging, provisioned troop of Japanese macaques at Takasakiyama National Park, high rank females ingest more of the provisioned food items than do low rank females (Soumah and Datta 1988) so subject females have been ranked by intragroup matriline status. All females were assigned to one of three ranks: high rank females are those born into the highest ranking matriline within their natal troop and low rank females are those born into the lowest ranking matriline within their natal troop. All other females have been categorized as middle rank. Calculations of expected frequencies for statistical analysis were based upon the number of matrilines in each category, resulting in an equal number of high and low ranking matrilines.

The lifetime reproductive success of each female was defined as the number of offspring produced who survived to the age of sexual maturation (i.e., 4 years in females and 5 years in males). Only females who were both born and died on Cayo Santiago were included in the analysis. Females whose offspring were removed from the island for colony management purposes before attaining the age of sexual maturation were excluded from analyses. These restrictions limit the data set, but they provide complete life history data for the females under consideration. Fertility refers to parturition events, including live births, still births, and probable abortions.

Statistical tests follow procedures set forth in Sokal and Rohlf (1981) and Zar (1974), with rejection of the null hypotheses based upon $P < 0.05$. Unless otherwise noted, two-tailed tests were used. Measures of central tendency report the mean ± SD.

**Results**

**Demography, social status and rapid reproductive maturation**

Of the 769 females for whom the age at first successful parturition was accurately determined, the youngest was