

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

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Received May 22, 1992 / Accepted September 21, 1992

**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 Char-

lesworth 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 that high rank individuals have greater lifetime reproductive success. However, an early age at first birth may not translate into greater lifetime reproductive success (Bercovitch and Goy 1990).

Our aims do not include a complete evaluation of dominance rank, longevity, fertility, offspring sex ratio, offspring survivorship and lifetime reproductive success in the study population, because potential inter-relationships among these parameters are the subject of extensive current analysis. Although we consider the role of dominance rank as a variable, the central problem we evaluate concerns the impact of accelerating the age at first reproduction on lifetime reproductive success. We use longitudinal data to test two competing hypotheses derived from life history theory with regard to the influence of rapid reproductive maturation on lifetime reproductive success. Specifically, we assess whether rapid reproductive maturation *increases* lifetime reproductive success by lengthening the breeding lifespan or *decreases* lifetime reproductive success by imposing survivorship or fertility costs.

## Methods

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 (Altmann 1962; 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, unpubl. data). Female rank among primates is most likely to influence reproductive success when food resources are clumped (Fedigan 1983; Harcourt 1987; Bercovitch 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 Yokata 1991). Any reproductive costs documented in the presence of food-enhancement are likely to be exacerbated under conditions of more restricted food availability.

Rhesus monkeys on Cayo Santiago reside in social groups characterized by female philopatry and male dispersal (Berard 1990). Periodically, monkeys are removed for colony management purposes, but no monkeys have been introduced, or reintroduced, to the island since its initial stocking. Despite the closed nature of this population, a substantial degree of genetic heterozygosity has been maintained (Duggleby et al. 1986; Nurnberg et al. in preparation). In the last 30 years, the island has supported between 3 and 7 troops of monkeys, with each troop containing between 1 and 6 matriline.

Social status among females is determined on the basis of patterns of agonistic interactions. Daughters inherit their mothers relative rank within a group (Sade 1967; Chapais and Schulman 1980; 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.

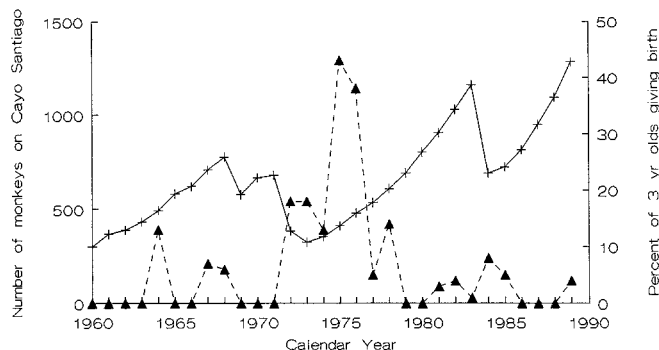
The lifetime reproductive success of each female was defined as the number of offspring produced who survived to the age of sexual maturation (i.e., 4 years in females and 5 years in males). Only females who were both born and died on Cayo Santiago were included in the analysis. Females whose offspring 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  $\pm$  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



**Fig. 1.** Changes in population size (solid line, crosses) and the proportion of fertile 3-year-old (dashed line, triangles) rhesus macaques over 30 years at Cayo Santiago

2.9 years and the oldest was 7.1 years of age. Variation in age at first parturition is quite limited, with nearly 90% of females reproducing for the first time at 4 years of age ( $\bar{x} \pm SD = 4.1 \pm 0.5$  yrs). Only 6.6% ( $n=51$ ) of females first gave birth when 3 years of age and 3.9% ( $n=30$ ) had their first successful parturition at 5 years of age or older. These two subgroups will be referred to as “rapid” and “delayed” reproducers, respectively. In order to more precisely evaluate the role of rapid reproductive maturation on lifetime reproductive success, subsequent analysis is restricted to a direct comparison between these two subgroups.

Since 1960, the proportion of 3-year-olds that have given birth in any one year has altered from year to year (Fig. 1). Because Cayo Santiago has only moderately altered in size over the 30-year period, population size can be considered an accurate index of population density. The probability of rapid reproductive maturation is negatively correlated with population density ( $r = -0.364$ ,  $n=30$ ,  $P < 0.05$ ), but periods of population expansion were not consistently associated with decreases in the proportion of rapid reproducers. The proportion of 3-year-olds who gave birth in a given year was not significantly correlated with the rate of population change from year to year ( $r = -0.101$ ,  $n=29$ ,  $P > 0.50$ ). In addition, the fraction of 3-year-olds who gave birth in any one year was not affected by the sex ratio among reproductively mature animals ( $r = -0.209$ ,  $n=30$ ,  $P > 0.20$ ).

Population size has fluctuated from about 320 to over 1200 monkeys (see Fig. 1) since attaining a stable age distribution around 1970. Data were split into two 10-year periods in order to more precisely examine the influence of density on reproductive maturation. The interval from 1970–1979 was considered the low density period and the interval from 1980–1989 was considered the high density period. Between 1970 and 1979, average population size was 512 ( $\pm 142$ ), while between 1980 and 1989, average population size was nearly twice as high (945  $\pm$  195). Females were significantly more likely to initiate reproduction at 3 years of age under low density conditions and to delay first parturition until 5 years of age under high density conditions ( $\chi^2 = 17.00$ ,  $df=1$ ,  $P < 0.001$ ). Of the 248 females who survived to 3 years of

**Table 1.** The effects of population density and dominance rank on reproductive maturation

	Dominance rank		
	High	Middle	Low
A. High density (1980–1989)			
Rapid reproducers	8	2	0
Delayed reproducers	3	5	8
B. Low density (1970–1979)			
Rapid reproducers	17	6	8
Delayed reproducers	0	4	0

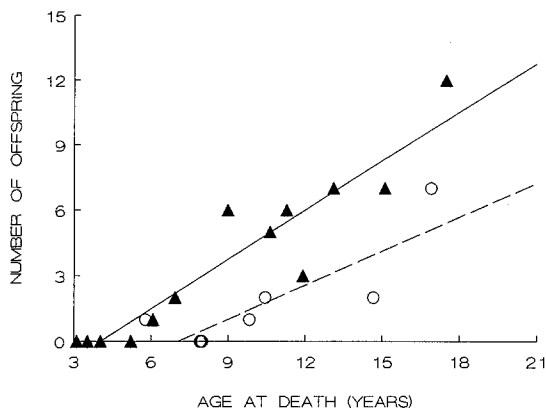
High density and low density refer to 10-year blocks based upon population size during the two intervals indicated. See text for definition of rapid and delayed reproducers and for methods of determining dominance rank among females

age during the low-density period, only 4 delayed the onset of reproduction until after 5 years of age (Table 1). During the high density period, high rank females were more likely than low rank females to reproduce at an early age (likelihood ratio  $G = 13.380$ ,  $df=2$ ,  $P < 0.01$ ), but sample sizes are too small to assess the influence of rank on reproductive maturation during the low density period (see Table 1).

Social status was linked to rapid reproductive maturation, but not to delayed reproductive maturation when the effects of population density were omitted from consideration. Females from the highest ranking matriline were significantly more likely to give birth at 3 years of age than were females from other matrilines ( $\chi^2 = 47.73$ ,  $df=2$ ,  $P < 0.001$ ), but females from the lowest ranking matrilines were not more likely to have their first parturition at 5 years of age or later than were females from the highest or middle ranking matrilines ( $\chi^2 = 3.01$ ,  $df=2$ ,  $P > 0.20$ ). Although high rank females were more likely than middle or low rank females to have their first parturition at 3 years of age, the majority of high rank females had their first parturition at 4 years of age, or the same age as females of other ranks.

#### *Rapid reproductive maturation and lifetime reproductive success*

Rapid reproducers averaged more offspring that survived to the age of sexual maturation ( $3.8 \pm 3.8$ ,  $n=13$ ) than did delayed reproducers ( $1.6 \pm 2.3$ ,  $n=8$ ), but this difference was not statistically significant ( $t = 1.45$ ,  $df=19$ ,  $P > 0.20$ ). If reproductive output is based upon the total number of births recorded over a complete lifetime, regardless of infant survival, then the results do not change ( $t = 0.79$ ,  $df=23$ ,  $P > 0.30$ ). Age at first parturition and number of offspring surviving to reproductive age are not significantly correlated ( $r = -0.349$ ,  $n=21$ ,  $P > 0.10$ ), nor is total number of offspring produced predicted by age at first parturition ( $r = -0.252$ ,  $n=25$ ,  $P > 0.10$ ).



**Fig. 2.** The relationship between longevity and lifetime reproductive success. The *number of offspring* refers to the number that survived to the age of sexual maturity (see text). The *solid line* shows the regression between the two variables in rapid reproducers (*triangles*) ( $y=0.754x-3.04$ ;  $r^2=0.88$ ), while the *dashed line* shows the relationship in delayed reproducers (*circles*) ( $y=0.518x-3.65$ ;  $r^2=0.71$ ). For all animals combined, the overall regression between longevity and number of offspring was  $y=0.642x-3.13$ ;  $r^2=0.66$

If rapid reproductive maturation exerts a survivorship cost, then one might expect that the two classes of females would differ in the age at death. However, the two categories of females did not differ in longevity ( $t=1.10$ ,  $df=23$ ,  $P>0.40$ ). On average, rapid reproducers lived to  $9.0 (\pm 4.5; n=14)$  years, and delayed reproducers lived to  $11.0 (\pm 4.5; n=11)$  years. Lifespan is independent of age at first parturition among rapid and delayed reproducers ( $r=0.077$ ,  $n=25$ ,  $P>0.50$ ). Survivorship costs associated with first parturition appear minimal in that 95% of females who reach 3.5 years of age live to be 4.5 years of age (Rawlins and Kessler 1986b). First parturition at age 3 was accompanied by a survivorship rate of 93% ( $n=48/51$ ) to age four.

Longevity was strongly correlated with lifetime reproductive success ( $r=0.812$ ,  $n=21$ ,  $P<0.001$ ; Fig. 2). Among the two classes of females, longevity accounts for 66% of the variance in lifetime reproductive success. The total number of offspring produced is also correlated with longevity ( $r=0.891$ ,  $n=25$ ,  $P<0.001$ ). Covariance analysis between rapid and delayed reproducers, holding age at death constant, revealed that rapid reproducers gave birth to significantly more offspring that survive to the age of sexual maturation than did late reproducers [ $F(1,18)=20.859$ ,  $P<0.001$ , multiple  $r=0.918$ ].

Although rapid reproductive maturation appeared to carry no survivorship costs, a fascinating life history pattern emerged from the data. Among females who were primiparous at 3 years of age the average lifespan was 9 years, while among those primiparous at age 5 the average lifespan was 11 years. Most of the females in this population have their first offspring at 4 years of age and the average age at death for females in this population is 10.5 years (Rawlins and Kessler 1986b). Hence, regardless of age at first parturition, a breeding lifespan that averages 6 years is a characteristic of the females from this population.

Dominance rank did not affect the probability of infant survival among rapid reproducers (likelihood ratio  $G=1.89$ ,  $df=1$ ,  $P>0.10$ ) and infant survival did not influence the probability of subsequent conception among the 3-year-old primiparous females. Of the 29 three-year-old females who gave birth and whose infants survived the first year of life, half of the females ( $n=15$ ) had their second parturition at 4 years of age, and half ( $n=14$ ) failed to reproduce at this age.

Although these results suggest that no fertility cost accompanied rapid reproductive maturation, the chances of bypassing one year of reproduction among the rapid reproducers was influenced by the sex of first offspring. Females rearing male offspring who survived to 1 year of age were significantly more likely than females rearing female offspring to fail to reproduce when four years of age ( $\chi^2=5.99$ ,  $df=1$ ,  $P<0.02$ ). Only 23% ( $n=3/13$ ) of rapid reproducers who had female offspring did not reproduce in the next birth season, whereas 69% ( $n=11/16$ ) of rapid reproducers who had male offspring did not give birth when 4 years of age.

The final assessment of life history consequences of rapid reproductive maturation focused on the role of dominance rank and lifetime reproductive success. The two types of females predicted to show the greatest difference in their total reproductive output would be high rank, rapid reproducers and low rank, delayed reproducers. High rank, rapid reproducers had a lifetime reproductive success of  $4.4 (\pm 4.4; n=7)$  offspring, while low rank, delayed reproducers had a lifetime reproductive success of only  $1.5 (\pm 0.7; n=2)$  offspring, but this difference was not statistically significant (Mann-Whitney  $U=8.5$ ,  $P>0.30$ ). Corroborative evidence concerning the lack of a rank effect emerged in a comparison of the lifetime reproductive success of the same high rank, rapid reproducers with low rank, rapid reproducers ( $n=3$ ;  $\bar{x}=1.7 \pm 1.5$  offspring). Again, the high rank females had a greater output of offspring surviving to the age of sexual maturation, but the difference was not statistically significant (Mann-Whitney  $U=14$ ,  $P>0.20$ ).

## Discussion

Among female rhesus macaques, rapid reproductive maturation led to neither an increase nor a decrease in lifetime reproductive success. Almost two-thirds of the variance in lifetime reproductive success could be accounted for by differences in age at death, whereas age at first parturition was not correlated with lifetime reproductive success. Variation in longevity ( $V=45.7\%$ ) is substantially greater than is variation in age at first parturition ( $V=12.2\%$ ), yielding a situation where rapid reproductive maturation results in greater progeny output only when survivorship is held constant. Among Japanese macaques, *M. fuscata*, age at first reproduction did not affect lifetime reproductive success, while longevity explained 70% of the variance in lifetime reproductive success (Fedigan et al. 1986). Similarly, longevity accounted for 79% of the variance in lifetime reproduc-

tive success among savanna baboons, *Papio cynocephalus*, living in Kenya (Altmann et al. 1988).

Lifespan among female cercopithecines appears to be independent of dominance rank (Fedigan et al. 1986; Altmann et al. 1988; Cheney et al. 1988; Meikle and Vessey 1988) and our data indicate that high rank female rhesus macaques do not make significantly larger contributions to subsequent generations than do lower rank conspecifics (see also Koyama et al. 1992). High rank females, on average, produced more offspring than low rank females, but the difference was not significant because of the large variation in lifetime reproductive success among females. Lifetime reproductive success was dependent upon length of the breeding lifespan, with this interval much more dependent upon age at death than upon age at first parturition.

Among primiparous 3-year-old rhesus macaques, survivorship of first born young does not result in a fertility cost (see also Sade 1991), but subsequent parturition is delayed among young females who rear male offspring. Fertility costs are defrayed by lengthening the interbirth interval. Both Berman (1988) and Wilson et al. (1983) found that rhesus macaques who gave birth to sons were more likely to fail to give birth the next year than were females who gave birth to daughters. On the other hand, Simpson et al. (1981) noted that female rhesus macaques in their captive colony who gave birth to daughters tended to delay reproduction, but they also commented that their results may be due to the captive nature of their small study groups. Production of male offspring has been linked with fertility costs in a number of studies of free-ranging mammals that regularly have one progeny at birth (Clutton-Brock et al. 1982; Lee and Moss 1986; Wolff 1988; but see Green and Berger 1990).

#### *Resource availability and reproductive maturation*

According to life history theory (Gadgil and Bossert 1970; Stearns 1976, 1977; Pianka 1978; Horn and Rubenstein 1984), individuals are most likely to accelerate the age at first parturition when resource availability is maximal, a condition that can occur when food is plentiful or when population density is low. Increases in population density are predicted to increase intraspecific competition and favor postponement in reproductive effort at the expense of somatic growth (MacArthur and Wilson 1967).

Female rhesus macaques were significantly more likely to reproduce for the first time at young ages under low density conditions. Dominant individuals were able to accelerate reproductive maturation under both low and high density conditions, but rapid reproductive maturation among subordinate females was restricted to low density conditions. Density-dependent delays in reproductive maturation among large mammals have been demonstrated in field studies of northern elephant seals (Reiter and Le Boeuf 1991) and red deer, *Cervus elaphus*, (see Table 11 in Clutton-Brock et al. 1983), and have

been attributed to female competition for breeding sites or food, respectively.

Female rhesus macaques do not have restricted breeding sites, as among northern elephant seals, and food supply was relatively constant because increases in population size were accompanied by increases in the per capita amount of food provisioning supplied to the island. However, the number of feeding sites remained unaltered with increases in population size. Access to the feeding sites was probably hampered among subordinate females under the high population density conditions. Supplementary feeding is believed to hasten the onset of reproduction in female primates, but patterns among two species of macaques (*M. mulatta* and *M. fuscata*) do not provide conclusive evidence in support of this hypothesis (Loy 1988). Food provisioning accelerates age at first birth in high rank female Japanese macaques, but not in low rank conspecifics (Sugiyama and Ohsawa 1982). Although provisioning could accelerate reproductive maturation, the data indicate that enhanced food availability does not alter the variance in age at first parturition. The variance in age at first parturition documented for the study population is comparable to that documented for vervet monkeys, *Cercopithecus aethiops*, living in Amboseli National Park, Kenya (troop range: 12–19%; Cheney et al. 1988) and for savanna baboons residing in Gilgil, Kenya (15%; Bercoitch and Strum in preparation). Density-dependent delays in the onset of first birth among rhesus macaques occurred despite food enhancement of the study population.

#### *Fitness and lifetime reproductive success*

Lifetime reproductive success is not a synonym for fitness. Under conditions of constant population size and a stable age distribution, lifetime reproductive success, as measured by progeny output, will approximate Darwinian fitness, as measured by the relative phenotypic contribution to the next generation (Endler 1986). Numerous discrepancies exist in the use of the term “fitness” (Endler 1986), but at least two common denominators surface from different uses of the term. First, fitness is a relative measure obtained within a single generation, and, second, many fitness components accrue from nonadditive genetic variance (Falconer 1960), with phenotypic plasticity guided by natural selection (Via and Lande 1985). Given the changes in population size at Cayo Santiago over the 30-year study period, assessment of potential fitness consequences of rapid reproductive maturation depends upon a comparison of the lifetime reproductive success of rapid and delayed reproducers born into the same cohort. For purposes of discussion, a generational cohort can be considered to be the average interval between a female’s birth and the birth of her first offspring, or about 4 years.

Only one set of rapid and delayed reproducers could be matched for birth within a 4-year period in order to assess potential differences in fitness due to age at first parturition. Variation in lifetime reproductive suc-

cess among these four females was substantial. One rapid reproducer had seven offspring survive to the age of sexual maturation, but one had only one offspring survive this interval. One delayed reproducer had no progeny survive to the age of sexual maturation, but one had seven offspring survive this interval. The sample is exceedingly limited, but provides evidence that rapid reproductive maturation is not necessarily associated with increased fitness, a finding that concurs with the conclusion that an early age at first parturition is not synonymous with greater lifetime reproductive success (Bercovitch and Goy 1990).

At least four implications emerge from our study for understanding the evolution of life history patterns. First, lifetime reproductive success among females cannot be extrapolated from reproductive rates and age at first parturition. Even in situations where rank-related differences in reproductive rates can be documented, and where rank occupancy patterns are fairly stable throughout life, high rank females may only realize a greater lifetime reproductive success than low rank females if they live longer. Computer simulation models purporting to demonstrate a rank-related fitness advantage to early age at first parturition (e.g., Sade 1991) have neglected to consider variation in longevity as a key factor influencing fitness. Second, the results conform with other studies based upon lengthy field work on large mammals residing in polygamous mating systems that have revealed a substantial degree of variation in lifetime reproductive success among females (Fedigan et al. 1986; Clutton-Brock 1988). The variance in lifetime reproductive success among the females of the study population was considerable given the nature of the research site. Third, natural selection consists of differences in fertility and mortality. Longevity and offspring survivorship exert a stronger impact on lifetime reproductive success in many long-lived, iteroparous organisms than does variation in fecundity (see Clutton-Brock 1988; Newton 1989). Fourth, individuals appear to have evolved mechanisms that can minimize, but not eliminate, reproductive costs (Tuomi et al. 1983). Costs of reproduction include both extrinsic and intrinsic factors (Clutton-Brock et al. 1983; Reznick 1985) and could be minimized under favorable conditions when resources are plentiful because organisms may be able to buffer themselves against excessive expenditures (Horn and Rubenstein 1984; Reznick 1985). Advances in understanding reproductive costs and life history strategies depend upon integrating controlled laboratory experiments with longitudinal naturalistic investigations.

*Acknowledgements.* Research on Cayo Santiago has been funded by NIH, NSF, and the University of Puerto Rico. We thank the many scientists and technicians who have contributed to the census data base since its inception, especially Angel Figuero. Critical comments and detailed critiques have been provided by Jeanne Altmann, Tim Clutton-Brock, John Endler, Marc Hauser, Matt Kessler, David Reznick, and Suzi Schwartz on various versions of this manuscript, but responsibility for the conclusions resides with the authors. Current support is provided by NIH Grant RR03640.

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