

Rank-Related Fitness Differences and Their Demographic Pathways in Semi-Free-Ranging Rhesus Macaques (*Macaca mulatta*)

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Abstract Researchers have explored the fitness consequences of female dominance hierarchies in many primate populations, with most studies highlighting differences in age of maturation, fertility, and offspring survival. We use resampling techniques and van Tienderen's (2000) elasticity path analysis to identify rank-related differences in finite rate of increase (λ) and their demographic correlates among segments of a semi-free-ranging rhesus macaque population. Higher-ranking population segments grew at greater rates for some portions of the 40-yr study period. The female members of these segments achieved these lifetime fitness differences through higher fertility and especially higher adult survival rates. This is the first clear evidence that social rank influences female primate adult survival, and is a crucial fitness component for any long-lived, slow-reproducing animal. Traditional methods of comparing lifespans, and other life history variables, among rank categories fail to identify most of the rank-related differences primarily because they require completed life histories that are available only on a small number of the females known in the population.

Keywords Demography · Elasticity path analysis · Fertility · Finite rate of increase · Fitness · Reproductive success · Social dominance · Survival

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Introduction

Hierarchies of social rank are important features of many animal social groups and are particularly well studied in primates (Ellis 1995; Fedigan 1983; Harcourt 1987). Evolutionary perspectives on social rank focus on the relative costs and benefits of high rank to individuals or kin networks with the basic prediction that high rank confers fitness benefits, and therefore high rank is worth competing for (Silk 1987; Sterck *et al.* 1997). Testing this prediction has fueled many investigations of primate behavior, demography, and morphology. Further, a great deal of primatological research has focused on explaining why social groups of some species have strong dominance hierarchies and others do not (Kappeler and van Schaik 2002).

Whatever the cause, high rank is expected to confer some net benefit in fitness for female primates (Koenig 2002; Sapolsky 2005). There is growing evidence on this topic, particularly for macaques (*Macaca*) and baboons (*Papio*) (Altmann and Alberts 1987, 2003a, b; Altmann *et al.* 1988; Bercovitch and Berard 1993; Bercovitch and Goy 1990; Berman 1988; Cheney *et al.* 2006; Dittus 1986, 1979, 1998; Fedigan 1991; Fedigan *et al.* 1986; Gouzoules *et al.* 1982; Itoigawa *et al.* 1992; Johnson 2006; Koyama *et al.* 1992; Mori 1979; Packer *et al.* 1995; Paul and Kuester 1990; Paul and Thommen 1984; Rhine *et al.* 2000; Sade 1990; Sade *et al.* 1976; Silk *et al.* 2003; Stucki *et al.* 1991; Takahata 1980; Takahata *et al.* 1999; van Noordwijk and van Schaik 1999; Wasser *et al.* 2004; Watanabe *et al.* 1992; Wolfe 1984). Despite some conflicting results, several generalizations can be made based on this literature. Higher-ranking females frequently give birth to their first offspring at younger ages. However, interbirth intervals are not consistently shorter in higher-ranking females, particularly among macaques. Where information is available, it appears adult body size is not related to rank, but high-ranking females consistently have higher offspring growth rates and tend to have improved offspring survival. This may help to explain the earlier maturation of high-ranking females that reach a threshold mass earlier than their age-mates (Bowman and Lee 1995). Finally, adult survival rates (lifespan) do not appear to be closely tied to rank. One problem often encountered, particularly in wild settings, is low power and lack of statistically significant differences among rank groups for different life history variables or fitness proxies even when there are suggestive trends (van Noordwijk and van Schaik 1999). Currently, this is a powerful argument for the utility of studying primates in free-ranging conditions where samples are typically much larger.

Macaques have figured prominently in discussions of primate social dominance, in part because of considerable variation within the genus in the strength of dominance hierarchies, kin bias, and patterns of affiliation and aggression (Thierry 2000, 2004). Rhesus macaques (*Macaca mulatta*) have been described as “despotic” and “nepotistic” macaques, and are characterized by unidirectional conflicts in which targets of aggression flee and may be severely injured. Reconciliation after conflicts is rare, particularly across kin boundaries. Kinship networks and dominance hierarchies are a strong determinant of who interacts and in what ways (Datta 1983a, b). They are thus an ideal species to explore the fitness costs and benefits of social rank.

Our goals here are to test the general hypothesis that there are rank-related differences in female primate life history variables and fitness measures and compare 2 methods for gauging this association. The first parallels studies cited in the

preceding text and focuses on standard life history variables, e.g., lifespan, age at first reproduction, and interbirth interval. The second, elasticity path analysis, is a recently developed technique blending matrix models and regressions of the model's constituent fitness components on rank.

Methods

We used demographic data and matriline rank information from a large population of free-ranging rhesus macaques that were transplanted to the 15.2-ha island of Cayo Santiago, Puerto Rico from India in 1938. Monkeys are fed commercial monkey chow and provided water *ad libitum* but forage on natural vegetation and live in naturally formed social groups (Rawlins and Kessler 1986a). At the time of the study in 2005, there were nearly 8000 known individuals that had lived on the island. Reliable demographic records have been maintained since the late 1950s. The population has been managed through the removal of social groups and a random cull of juveniles such that only 34% of the individuals that had exited the population did so because of death.

The population was inoculated against tetanus in the mid-1980s (Kessler *et al.* 2006), and individuals that had been the subjects of medical experiments before the early 1970s (Sade *et al.* 1985) were excluded when necessary from this analysis. Otherwise, there has been a veterinary policy of nonintervention.

Matriline Social Ranks

Social dominance for females of many macaque species follows a clear set of rules whereby daughters occupy a rank in the dominance hierarchy just below that of their mothers and are followed by each of their older sisters (Kawai 1965; Sade 1967; Thierry *et al.* 2004). Daughters typically acquire rank at the time of sexual maturity. These sets of adjacent-ranking female kin that are all descended from a crown female ancestor are called matriline. Because matriline members are generally adjacent to one another, forming blocks within the group dominance hierarchy, the rank of entire matriline can be used as a proxy for individual rank in social groups containing multiple matrilines (Bercovitch and Berard 1993; Stucki *et al.* 1991). Although rank reversals occur, matriline rankings are very stable in rhesus macaques (Hill and Okayasu 1996; Thierry *et al.* 2004).

We indexed social rank information by the rank of a female's matriline within her social group for a given year known from pairwise agonistic encounters (annual rankings for 1960–2000 provided by Donald S. Sade and John D. Berard). Observations result in dominance matrices of individuals or matrilines as published for Cayo Santiago by Missakian (1972). We coded high, middle, and low rank as 0, 1, and 2, respectively. For the analysis reported, this means that an increase in rank is movement from higher to lower rank. Groups in recent years typically have only 1 matriline in each of these categories, and assignment is thus simple because only 2 or 3 matrilines occur in a group. When there were only 2 matrilines they were assigned to high and low. This is a conservative procedure because if being the low-ranked matriline in a 2-matriline group is less detrimental than being the low-ranked matriline in a ≥ 3 matriline group, the effect will be averaged within the category of low rank. In earlier years, there are

$$\begin{pmatrix} 0 & 0 & f_y & f_y & f_y & f_m \\ \sigma_j & 0 & 0 & 0 & 0 & 0 \\ 0 & \sigma_j & 0 & 0 & 0 & 0 \\ 0 & 0 & \sigma_y & 0 & 0 & 0 \\ 0 & 0 & 0 & \sigma_y & 0 & 0 \\ 0 & 0 & 0 & 0 & \sigma_y & \sigma_m \end{pmatrix}$$

Fig. 2 Life cycle model transition matrix containing the survival (σ_i) and fertility (f_i) probabilities calculated from the fitness components. At each stage, i , probability occurs the number of times as the duration of the stage. Stage durations are given with Fig. 1. The subscripts j, y, and m refer to juveniles, young adults, and mature adults, respectively.

Fitness components in elasticity path analysis must be scored in 2 ways. The first uses the years being analyzed to create the matrix entries for predicting population growth rate (λ) and computing elasticities (right side of Fig. 3). The other scoring is done to derive fitness component values for individuals while they were in each age class. These values are used as dependent variables in regressions with some other independent predictor, such as matriline social rank (left side of Fig. 3). In these regressions, the fitness components are standardized by dividing by their respective means to facilitate comparisons between regressions (van Tienderen 2000).

The same set of life histories is used for generating both sets of scores, but information is pooled differently in each scoring to obtain counts of individuals in

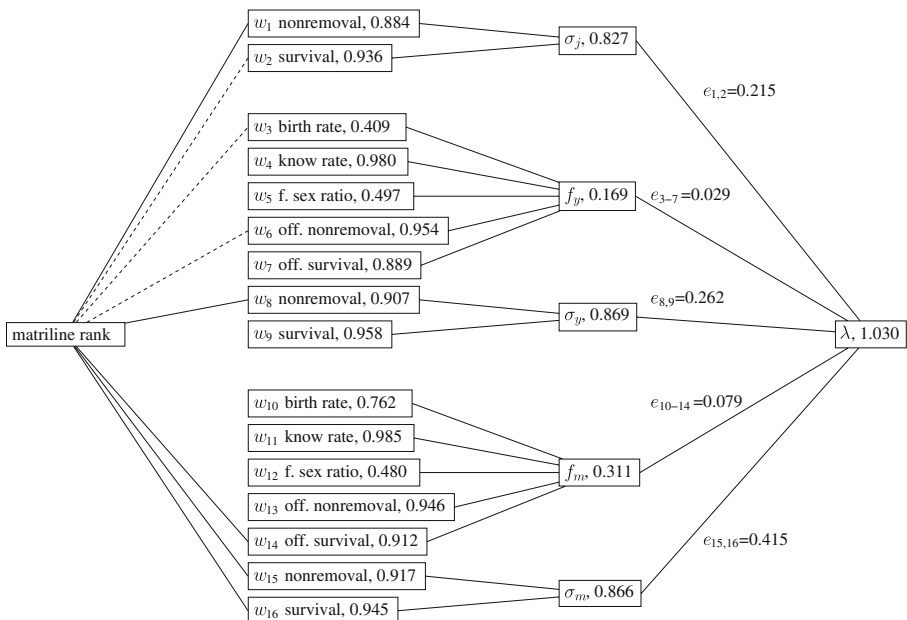


Fig. 3 Elastogram illustrating the connections among fitness components, matrix elements, and λ . Elasticities, matrix values, and fitness components are calculated for all females in the 1960–2000 period. Because the fitness components are multiplied to yield the matrix values, the elasticity of each component being multiplied is the same, e.g., $e_{15;16}$ gives e_{15} or e_{16} , both of which are 0.415. Paths on the left side of the figure indicate significant bivariate regressions between matriline social rank and the fitness components (Table II). Solid lines indicate more highly significant regressions.

different states. In the calculation of the matrix entries, the grouping is done for age 6 class and year, whereas for the construction of fitness components the counts are based on grouping by age class and individual identity. Once the proper counts are made, fitness components are calculated from the same formulae for both sets of scoring. All of the fitness components are probabilities defined such that an increase in any one of them will result in an increase in fitness (λ). This is a common definition of fitness components (Hughes and Burleson 2000). As noted previously, removal of primates from Cayo Santiago has been common practice (Rawlins and Kessler 1986b; Sade *et al.* 1985). This can be accommodated in elasticity path analysis as a separate fitness component that represents the probability of avoiding removal.

Two fitness components are used to define the survival and graduation probabilities (σ_i) in the transition matrix in Fig. 2 (see also Fig. 1). The annual survival or graduation probability is the product of these 2 components. The probability of a juvenile or adult avoiding removal (nonremoval) is the difference of 1 and the ratio of the number of females that were removed (NR) and the total number that entered the age class (T).

$$\text{nonremoval} = w_1 \text{ or } w_8 \text{ or } w_{15} = 1 - \frac{NR}{T} \quad (1)$$

The annual probability of a juvenile or adult surviving given that she was not removed (survival) is the difference of 1 and the ratio of the number of females in the age class that died during the year (ND) and the number that escaped removal ($T-NR$).

$$\text{survival} = w_2 \text{ or } w_9 \text{ or } w_{16} = 1 - \frac{ND}{T - NR} \quad (2)$$

Five fitness components are used to define the fertility probabilities (f_i) in the transition matrix in Fig. 2. The matrix fertility probability is the product of these 5 components. The annual birth rate (birth rate) is the ratio of the number of offspring of any sex born to females in the desired age class in the year (GN , generic newborns) and the number of adult females alive for any portion of the age class (T).

$$\text{birth rate} = w_3 \text{ or } w_{10} = \frac{GN}{T} \quad (3)$$

The probability of knowing the sex of the infant is used to accommodate the production of infants that were never sexed by population observers, usually due to the young death of the infant. This fitness component (know rate) is largely an infant survival measure, but cannot be interpreted because of variation from year to year in the number of unsexed infants. It is given by the ratio of the number of infants of known sex (SN , sexed newborns) to the total number born (GN).

$$\text{know rate} = w_4 \text{ or } w_{11} = \frac{SN}{GN} \quad (4)$$

The female sex ratio (f. sex ratio) of the infants is the ratio of female infants (FN , female newborns) to the number of infants of known sex (SN).

$$\text{f. sex ratio} = w_5 \text{ or } w_{12} = \frac{FN}{SN} \quad (5)$$

Because a prebreeding census is used the final 2 fitness components that affect the transition matrix entries for fertility (f_i) document infant survival or escape of removal prior to census. These work similarly to the juvenile and adult survival and graduation probabilities (σ_i) described previously. The probability of infants escaping removal (off, nonremoval) is the difference of 1 and the ratio of number of infants removed (NR) and the number of female infants (FN).

$$\text{off. nonremoval} = w_6 \text{ or } w_{13} = 1 - \frac{NR}{FN} \quad (6)$$

Finally, the probability of female infants surviving to census given that they were not removed (off. survival) is the difference of 1 and the ratio of the number of female infants that died (ND) and the number of female infants that were not removed ($FN-NR$).

$$\text{off. survival} = w_7 \text{ or } w_{14} = 1 - \frac{ND}{FN - NR} \quad (7)$$

Elasticity path analysis requires the calculation of several parameters from the transition matrix in Fig. 2. Population growth rate or finite rate of increase (λ) is calculated from the transition matrix as its dominant eigenvalue. Elasticities of the transition matrix entries document the proportional response of λ to a minute proportional increase in a matrix entry (a_{ij}) while all others are held constant. Thus, they document how much fitness responds to changes in each of the matrix entries. Formally, an elasticity is the scaled partial derivative of with respect to the matrix entry.

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} \quad (8)$$

We used the `eigen.analysis()` function of the `popbio` package for R (Stubben and Milligan 2007) to calculate elasticities and λ . Because the fitness components that make up each of the matrix entries are multiplicative, the elasticities of the matrix entries are also the elasticities of each of their constituent fitness components (Caswell 2001, p. 232).

Differences in Growth Rate (λ) Among Rank Levels

We relied on a randomization procedure to test for significant differences in λ among population segments of differing social rank (Caswell 2001). We calculated the growth rates of high, middle, and low ranked segments of the population for the entire span of records available (1960–2000) and 3 shorter intervals (1960–1973, 1974–1983, 1984–2000). As it was known that removals have impacted the rank levels differently, the probability of escaping removal was set to 1. The middle timespan (1974–1983) had almost no removals (<5). Calculated λ for this period are thus very close to the realized rate of increase, which was approximately exponential growth. For the other periods, λ will be greater than that actually observed. The first time period also corresponds to a period in which matriline contain fewer individuals and relate more to single females. The construction of matriline rank levels for this period is more subjective and problematic. For most of the final time period, the population was at high density and a regular cull of juveniles was instituted.

The randomization procedure worked by shuffling the rank assignments on the yearly observations for the females within an age class 5000 times. We used the distributions of λ for 1-tailed hypothesis testing, asking whether high-ranked females have higher fitness than middle- or low-ranked ones. We declared a significant difference if the difference between the actual values for λ was exceeded in <0.05 ($=250/5000$) of cases in the difference of randomized rank levels, i.e., $\alpha=0.05$ (Manly 1997).

Differences in Fitness Components Among Rank Levels

Examination of the relationship of fitness components with rank identifies how rank alters the life history of females. We used the 16 fitness components of the life cycle model in linear regression on the ordinally coded matriline rank variable (see also Figs. 1 and 3). We used only components calculated from the entire 1960–2000 timespan for these regressions because of small sample sizes in the shorter time periods.

Because of the 0, 1, 2 coding of rank, it is expected that many of the fitness components will have negative slopes in these regressions. We averaged matriline rank over the period in which we measured the fitness components, which can result in noninteger values, although most fall on 0, 1, or 2. We explored weighted least squares regressions, weighting by the number of observations at each rank value, to accommodate this heteroscedasticity, but these had very minor numerical differences from the unweighted results, which are more conservative. We present only the unweighted results.

Life History Variable Differences Among Rank Levels

To interface with other studies and aid in interpretation of fitness components in the elasticity path analysis, we also analyzed a set of commonly used life history variables. These were age of first reproduction (AFR), lifespan, mean interbirth interval, number of offspring produced (LRS), and a transformation of LRS that is sensitive to the age schedule by which they were born—individual λ (McGraw and Caswell 1996; Sade 1990). To analyze the relationship between rank and these life history variables, we used general linear models including rank and the birth cohort to which females belonged to control for temporal differences in density, weather, and management practices. We treated birth cohort as a categorical variable. We averaged rank over the first 4 yr of life for AFR and over the entire lifespan for the other variables.

Results

Differences in Growth Rate (λ) Among Rank Levels

High, middle, and low-ranking segments of the population on Cayo Santiago grew at different rates for much of the study period (Table 1). Using the entire span of 1960–2000, the high-ranking segment of the population would have grown at a rate of *ca.*

Table I λ for categories of matriline social rank at Cayo Santiago over different time periods and randomization p -values for hypothesis tests on λ differences

	1960–2000	1960–1973	1974–1983	1984–2000
Matriline rank λ s				
λ_{high}	1.148	1.132	1.160	1.145
λ_{middle}	1.135	1.117	1.135	1.138
λ_{low}	1.129	1.149	1.117	1.125
Randomization p -values on λ comparisons				
$\lambda_{\text{high}} > \lambda_{\text{middle}}$	0.058		0.104	0.247
$\lambda_{\text{high}} > \lambda_{\text{low}}$	0.009		0.005	0.030
$\lambda_{\text{middle}} > \lambda_{\text{low}}$	0.239		0.193	0.093

p is the probability the null hypothesis $H_0: \lambda_x = \lambda_y$ is true. Tests are 1-tailed. See text for details of randomization procedure. λ values here are greater than in Fig. 3 because nonremoval probabilities (w_1 ; w_8 ; w_{15}) are set to 1.

14.8% per year ($\lambda=1.148$). Middle- and low-ranking fractions would have grown at 13.5% and 12.9%, respectively. Randomization tests indicate the difference between high- and low-ranking segments is greater than that expected by chance ($p=0.009$). The differences between high and middle, and middle and low are no greater than expected by chance.

However, examining shorter spans of time demonstrates important temporal differences in this pattern. For the earliest years of records 1960–1973, we did not find the expected pattern of high > middle > low ranking. In fact, the low-ranking segment of the population had the highest expected λ for this period. In contrast, the 2 later time spans (1974–1983 and 1984–2000) do have the expected high > middle > low pattern in λ . The difference in λ between high and low is highly significant for 1974–1983 and 1984–2000 periods ($p \leq 0.03$). The difference for 1974–1983 is important because these are nearly realized rates of increase rather than ones predicted by setting the probabilities of escaping nonremoval to 1.

Differences in Fitness Components Among Rank Levels

There are also important relationships between fitness components and rank that we identified by the regression of individualized fitness components. These demonstrate the life history pathways by which rank influences fitness (Table II). Inclusion of data from 1960–1973, when rank and fitness did not have the expected association, will make these regressions more conservative. Regression slopes in Table II indicate high rank provides both survival and fertility benefits for female macaques. Higher ranked mature females (≥ 6 yr old) have greater survival probabilities ($p < 0.01$), as do their infants ($p < 0.001$) and juvenile offspring ($p < 0.05$). There is also a nonsignificant trend for higher ranked young females (3–5 years) to have higher survival rates ($p=0.20$).

Higher ranked young females have higher birth rates when only females that reproduced are analyzed ($p < 0.01$), and there is the suggestion of this trend,

Table II Bivariate regressions of fitness components from elasticity path analysis (1960–2000) on matriline social rank categories for Cayo Santiago females

Fitness component		<i>n</i>	$R^2 \times 100$	Int.	Slope
Juveniles: 1–2 years old					
w ₁	nonremoval	1970	1.01	0.964	0.038***
w ₂	survival	1851	0.31	0.020	−0.020*
Young adults: 3–5 years old					
w ₃	birth rate	1240	0.01	1.007	−0.008
	birth rate ^a	940	0.94	1.373	−0.057**
w ₄	know rate	940	<0.01	1.000	−0.001
w ₅	f. sex ratio	925	0.29	0.945	0.059
w ₆	off. nonremoval	557	1.10	0.975	0.026*
w ₇	off. survival	535	0.02	0.994	0.006
w ₈	nonremoval	1240	4.65	0.927	0.080***
w ₉	survival	1160	0.15	1.010	−0.10
Mature adults: ≥ 6 years old					
w ₁₀	birth rate	754	0.06	1.010	−0.011
	birth rate ^a	698	0.49	1.100	−0.022
w ₁₁	know rate	698	0.05	1.003	−0.003
w ₁₂	f. sex ratio	693	0.35	1.042	−0.046
w ₁₃	off. nonremoval	575	0.60	0.981	0.021
w ₁₄	off. survival	556	2.46	1.045	−0.050***
w ₁₅	nonremoval	754	1.24	0.963	0.041**
w ₁₆	survival	707	1.16	1.027	−0.030**

^a Regression only using values for females that had ≥1 births.

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

though it is not significant for mature females ($p=0.07$). Including females that did not reproduce obscures these relationships. This is particularly true for the young adults; almost one-fourth of the females that entered the age class died or were removed before reproducing. Finally, high rank seems to place females and their infants at greater risk for removal via population management in all phases of life ($p < 0.01$). Management practices thus have balanced the rank-related tendencies of the population by differentially excising high-ranked females.

Elasticities for fitness components in which there are significant rank differences can be quite large (Fig. 3). Components with large elasticities are the survival and removal probabilities. Any change in these components, while holding all others constant, will have a large effect on fitness (λ). Mature adult survival has the largest elasticity ($e_{16}=0.415$). The fact that it is significantly related to rank means that rank differences in adult survival will greatly affect fitness. The birth rate and infant survival or removal rates have much smaller elasticities, implying that rank-related differences in them will not have as large an impact on fitness.

Life History Variable Differences Among Rank Levels

Of the 5 life history variables analyzed, only 1 has a significant relationships with rank (Table III). As was previously known for this population, higher ranked individuals mature earlier (Bercovitch and Berard 1993; Sade *et al.* 1976; Sade 1990), which is also found here ($p < 0.001$). Mean interbirth interval may also be shorter in higher ranked individuals, but this does not reach statistical significance ($p = 0.06$). Lifespan appears to be unrelated to rank, though its estimated regression coefficient implies higher rank may yield longer lifespan ($\beta = -0.321$, $p = 0.51$). Neither of the individual fitness surrogates (LRS or individual λ) is significantly related to rank, though their coefficients are also in the predicted direction ($p > 0.24$).

Discussion

The analyses presented here demonstrate fitness differences among rank levels in the Cayo Santiago females. This is true for the entire period of study (1960–2000), and for years in which there were nearly no removals and the population was allowed to grow unmanaged (1974–1983). Sade *et al.* (1976) and Stucki *et al.* (1991) identified this pattern from their analysis of several years in the 1970s. Here, the expected pattern of rank-related fitness differences was not found in the earliest years of the study period (1960–1973). This could be due to regular removal of individuals for experimental purposes that disrupted social relationships; the relatively low density of the population during this period; or the subjective nature of assigning the many matriline to high, middle, and low categories.

Fitness component differences among rank levels identify how this disparity in λ arises. Three processes are primarily responsible. First, the most important effect rank has on female life histories is to elevate the survival rate of mature adults. Using mean values for each of the 3 rank categories, high-ranking females have mature adult survival rates of 0.94 vs. 0.86 for middle and 0.89 for low-ranked females

Table III Differences in life history variables among rank categories

Variable	<i>n</i>	Model $R^2 \times 100$	Mariline rank β
<i>AFR</i>	1033	21.63***	0.095*
Lifespan	248	10.25	-0.321
Mean IBI	210	24.74	0.047
<i>LRS</i>	248	9.01	-0.448
Individual λ	248	9.29	-0.013

Regression models include the continuous effect of rank level and categorical effect of birth cohort. Data from 1960 to 2000 are used. Birth cohort was not significant in models for lifespan, number of offspring, or individual λ . Dropping it did not change the significance of rank. For age of first reproduction, rank is the average rank over the first four years of a female's life. For the other variables it is the average over her entire lifespan.

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

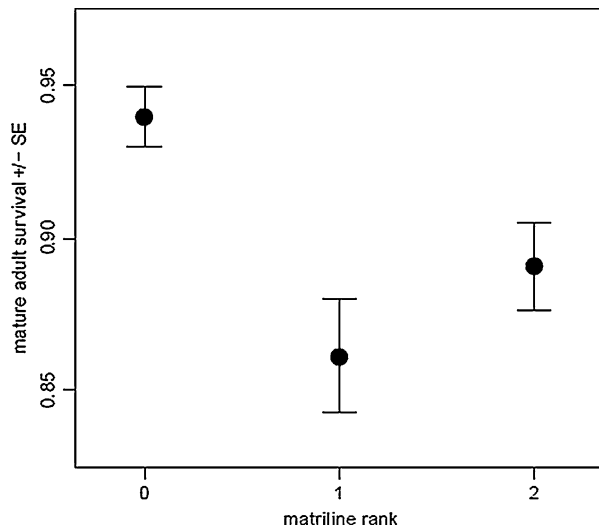
(Fig. 4). Converting the rates to life expectancies illustrates their importance. A 6-yr-old high-ranking female can expect to live another 7.8 yr on average vs. 3.1 for a middle- and 4.1 for a low- ranking female (from $e_x = \sum_{x=6}^{\infty} l_x$ wherein x is age, l_x is the probability of survival from initial age (6) to age x , and e_x is the life expectancy at age x . For simplicity, $l_6=0.5$ for all rank categories).

These are key differences because λ will respond the most to changes in mature adult survival (Fig. 3). Many previous researchers have implicated lifespan or adult survival as the critical variable to explaining variation in reproductive success in long-lived mammals such as primates (Altmann *et al.* 1988; Bercovitch and Berard 1993; Cheney *et al.* 1988; Heppell *et al.* 2000), but no relationship between variation in lifespan or adult survival with rank has yet been documented. These results for the Cayo Santiago females are important, because they are the first clear demonstration that social rank affects adult survival in female primates.

Second, rank strongly affects the infant survival rate of mature adult females. Fitness component regressions predict female offspring survival rates for mature females of 0.953 for high rank, 0.907 for middle, and 0.861 for low rank. The small elasticity on this fitness component (0.079) implies these differences among rank levels will not have strong effects on lifetime fitness; it is only about one-fifth of the size of the elasticity on mature adult survival. However, results with infant survival may be important for methodological reasons. Attempts to identify rank-related differences in numbers of offspring born to a female (a common fitness surrogate), or short-term reproductive success within a breeding cycle will not pick up on this effect of rank.

In contrast, infant survival of young adults is unrelated to rank. This is likely due to the inexperience or inadequate body condition, of all young females in rearing offspring that elevates infant death rates (Altmann *et al.* 1988; Bercovitch *et al.* 1998; Koyama *et al.* 1992; Paul and Kuester 1996; Smuts and Nicolson 1989; Wilson *et al.* 1978). This age difference may contribute to the mixed results on offspring survival noted in the Introduction.

Fig. 4 Mean (\pm SE) of individual mature adult survival rates (w_{16}) plotted by rank category (0 = high, 1 = middle, 2 = low). Points with noninteger values for rank are omitted from the plot (39 of 707). They are included in the mean-standardized regression of fitness components reported in Table II.



Finally, and more specific to the Cayo Santiago data, the management practices of the colony have clearly worked in opposition to the rank-related differences in survival and fertility. The signs of the regression coefficients of the survival and nonremoval probabilities in each age class are different, implying that at all ages the selection operating through management is differentially removing higher ranked individuals from the population.

The life history variables provide far less in the way of insights into rank-related differences among female macaques. Indeed, the analysis of the life history variables takes one no further than the existing body of literature on the life histories of the Cayo Santiago females. As has already been identified, higher ranking females mature earlier (Bercovitch and Berard 1993; Blomquist 2009; Drickamer 1974; Sade *et al.* 1976), which is consistent with the significant regression of young adult birth rate on rank. The only other suggestion of a relationship between rank and these life history variables is in the average interbirth intervals, which may be longer in low-ranked females. As in other analyses of the Cayo Santiago females and other primate populations, we found no connection between lifespan and rank. This may seem odd given the striking relationship between survival rates and rank just discussed. However, the sample available for assessing the lifespan-rank relationship is less than half of that in each of the age classes in the survival rate-rank regression. This lost information is effectively utilized in elasticity path analysis (Coulson *et al.* 2003; van Tienderen 2000). This advantage of the method, particularly in situations with data censored for various reasons, argues for its future application in animal demography.

In conclusion, 3 major results of this article address the magnitude and demographic pathways for fitness differences in long-lived female primates. First, there are clear differences in fitness among high, middle, and low-ranking population segments of females at Cayo Santiago. Second, these fitness differences are accomplished through differences in survival and fertility, though it is the differences in survival—particularly of mature adults—that have the greatest effect on fitness. Finally, elasticity path analysis is an excellent tool for assessing the relationship between variables such as social rank and fitness, particularly in the context of incomplete records such as those for removed Cayo Santiago females and their infants where sample sizes of standard life history variables are limited.

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