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Demographic variability and density-dependent dynamics of a free-ranging rhesus macaque population

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Abstract

Density-dependence is hypothesized as the major mechanism of population regulation. However, the lack of long-term demographic data has hampered the use of density-dependent models in nonhuman primates. In this study, we make use of the long-term demographic data from Cayo Santiago's rhesus macaques to parameterize and analyze both a density-independent and a density-dependent population matrix model, and compare their projections with the observed population changes. We also employ a retrospective analysis to determine how variance in vital rates, and covariance among them, contributed to the observed variation in long-term fitness across different levels of population density. The population exhibited negative density-dependence in fertility and the model incorporating this relationship accounted for 98% of the observed population dynamics. Variation in survival and fertility of sexually active individuals contributed the most to the variation in long-term fitness, while vital rates displaying high temporal variability exhibited lower sensitivities. Our findings are novel in describing density-dependent dynamics in a provisioned primate population, and in suggesting that selection is acting to lower the variance in the population growth rate by minimizing the variation in adult survival at high density. Because density-dependent mechanisms may become stronger in wild primate populations due to increasing habitat loss and food scarcity, our study demonstrates it is important to incorporate variation in population size, as well as demographic variability into population viability analyses for a better understanding of the mechanisms regulating the growth of primate populations.

Keywords

Cayo Santiago; density-dependence; life table response experiment; population matrix model; primate demography; tetanus

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INTRODUCTION

Density-dependence is understood as a major mechanism of population regulation and, therefore, one of the most important factors to consider when assessing population dynamics and viability [Hassel, 1975; Fowler, 1981; Clutton-Brock et al., 1987; Neubert & Caswell, 2001; Oli & Dobson, 2003]. As populations grow, individuals consume more resources, become more susceptible to predators, perform or receive more aggressive interactions, and find themselves occupying less suitable habitats resulting in a reduction in survival and fertility [Boyd, 1982; Skogland, 1985; Choquenot, 1991; Ha et al. 2011]. This scenario acquires significance when describing the demographics of mammalian populations with complex behavior and social structure, such as primates [Rawlins & Kessler, 1986a; Hoffman et al., 2008; Blomquist et al., 2011; Morris et al., 2011, Blomquist, 2013].

Recently, Morris et al. [2011] explored the consequences of temporal demographic variability on long-term fitness of several primate populations. They concluded that the effects of variation, covariation, and serial correlation in vital rates on long-term fitness were minor and suggested that short-term density feedback, rather than environmental autocorrelation or life history trade-offs, might be the process responsible for the variability observed. Social rank has also been shown to explain demographic differences among primate matrilineal [Blomquist et al., 2011]. Interestingly, during periods of high population density, high-ranking rhesus macaque matrilineal experienced a decrease in population growth rate [Blomquist et al., 2011], suggesting that density feedback mechanisms might be responsible for changes in rank-related fitness. However, both of these studies assumed density-independent vital rates, precluding conclusions about the effects of density feedback in primate demography. Testing for density-dependence, as well as determining how temporal demographic variability affects population growth rate across different levels of density, is required to understand the mechanisms behind the natural regulation and variability of primate populations.

In this study we analyzed the population dynamics of the free-ranging rhesus macaque population, *Macaca mulatta*, of Cayo Santiago from 1973 to 2000 in order to test three hypotheses: that 1) density-dependence in vital rates accounts for most of the long-term dynamics observed in the population, 2) sensitivity in vital rates, not their temporal variation and covariation, contributes the most to the observed variation in population growth rate, and 3) vital rates with higher temporal variability will have less influence in the population growth rate. To test these hypotheses we: 1) parameterized a density-independent, as well as a density-dependent, population projection matrix model and contrasted the projected dynamics of both models against the observed one, 2) determined which vital rate would have more influence in the population growth rate across different levels of density by calculating sensitivity and elasticity matrices, and 3) measured the contribution of temporal variation in vital rates, and covariance among them, to the observed variation in population growth rates across different levels of population density using a life table response experiment of random design. The primate population at Cayo Santiago is ideal for addressing these hypotheses as it is maintained under semi-natural conditions, making it possible to explore the effects of variable density on the population dynamics [Sade et al. 1985; Rawlins & Kessler, 1986]. The general prediction to be tested is that vital rates should decrease during periods of high population density and that such a relationship explains most of the observed population dynamics. We also expected low demographic variability with a negative relationship between the variability in vital rates and their sensitivities, as the variance in population growth rate is minimized by decreasing variation in vital rates [Pfister 1998].

The rationale behind these objectives is the fact that studies describing density-dependent population dynamics are scarce, as the large amount of demographic data required to parameterize such models is often unavailable [Morris and Doak, 2002]. The presence of long-term demographic data for only a small number of animal species, such as those of commercial value [Levin & Goodyear, 1980] or those with short generation time (e.g., *Tribolium* spp.) [Bellows, 1981], has confined our knowledge of population growth to a limited number of species, impeding a broader development of density-dependent dynamics theory [Hanski, 1990; Grant & Benton, 2000]. There is a general consensus that matrix models are the best approach to describe the population dynamics of endangered, threatened, and rare species or species that require management of any sort [Alberts & Altmann, 2003; Lawler, 2011a]. Yet, few studies of primates have incorporated them, and none of them have explored density-dependence. This is important as these models are characterized by the equivalence between the dominant eigenvalue of the matrix and the population growth rate (λ), as well as the capability to describe how each of the life cycle transitions contributes to λ via sensitivity analyses [Pfister, 1998].

METHODS

The Cayo Santiago primate population

Cayo Santiago is a 15.2-ha island located 1 km off the south-eastern coast of Puerto Rico (18° 09' N, 65° 44' W). A monkey colony composed of 409 free-ranging rhesus macaques from India was established in 1938 in the island. Since then, the colony has been maintained under semi-natural conditions for behavioral and non-invasive biomedical research [Sade et al., 1985; Rawlins & Kessler, 1986]. Monkeys forage on vegetation and are provisioned with commercial monkey chow (0.23 kg/animal/day). Individuals are identified by ear notches and a unique alphanumeric tattoo. The demographic database is updated with monthly reports since 1956 to include dates of birth, death, group fissions, and group memberships. All monkeys in the colony are descendants of the original 409 individuals and census records include information on sex, age, death, social group, and maternal genealogy of each individual.

Different management strategies have been implemented since 1938 [Sade et al., 1985; Rawlins & Kessler, 1986]. Three major periods can be identified: 1) from 1956 to 1972, random culling was carried out year round to supply animals to the Laboratory of Perinatal Physiology in San Juan, PR, 2) from 1973 to 1983, no culling was carried out, and 3) from 1984 to present, changes in the culling strategy began by removing entire social groups to control population size, followed by random culling of two-year-old males and females to eventually create an adult sex ratio of two females per male to more closely simulate wild populations. Since 1985, individuals have been inoculated against tetanus to eliminate what was the major known cause of mortality in the population [Rawlins & Kessler, 1982; Kessler et al., 1988; Kessler et al., 2006]. All research procedures utilizing the Cayo Santiago monkeys are approved by the Caribbean Primate Research Center and the Institutional Animal Care and Use Committee of the University of Puerto Rico, Medical Sciences Campus, in accordance with USDA regulations and NIH guidelines. This research adhered to the American Society of Primatologists principles for the ethical treatment of primates.

Demographic data collection and parameterization

Age-specific survival and fertility rates of rhesus monkeys were estimated by following the fate of 2796 different female monkeys from 1973 to 2000. Data prior to 1973 were not used for estimating model parameters due to record ambiguities in data from culled versus dead individuals [Sade et al., 1985]. Only female individuals were included in the demographic

model, therefore, the analysis assumes that female life history schedules determine population dynamics given that female reproductive success is not limited by adult males [Caughley, 1977; Rawlins & Kessler, 1986; Lawler, 2011b]. We recorded: 1) the total number of females alive in the population each year, 2) the age of sexual maturity, 3) the total number of females that gave birth to females at specific ages, and 4) the age at death or age when culled (removal from Cayo Santiago as part of the management strategy). Age-specific mortality (q_x) – the probability of dying at a specific age x – was defined as the number of individuals that exited the colony by death (d_x) divided by the number of live individuals in the same age class at the start of the time period. Age-specific survival rate (P_x) – the probability of surviving from one age class to the next – was defined as $1 - q_x$. The

probability of surviving from birth to age x (l_x), equals $l_x = \prod_{i=0}^{x-1} P_i$. Age-specific fertility (F_x) was determined by dividing the number of newborn females at time t by the number of live females of age x during one year. Cohort data was used to test for temporal variability in vital rates using a Mann-Whitney U-test.

Matrix population model

Because the database includes complete individual life histories from 1973 to 2000, hypothetical annual censuses were compiled from the daily census data [Morris et al. 2011], and a birth-pulse model employing post-breeding censuses was carried out [Caswell 2001]. A stage-based matrix, or Lefkovitch matrix, incorporating survival (P_i) and fertility rates (F_i), and also allowing for stasis of the last stage class was constructed. Therefore, the transition matrix contains positive data in the first row, the first sub-diagonal, and the last entry of the matrix [Dobson & Lyles 1989; Caswell, 2001]. Due to the lack of significant differences in survival among individuals four years and older, as well as the significant difference in fertility rates between three-year-old and four-year-old females and older, we divided the population into five stage classes according to their ages: infants [I] (0-1 year old), yearlings [Y] (1 year old), juveniles [J] (2 year old), young adults [YA] (3 year old), and adults [A] (4 year or older) (Fig. 1). The number of females in each of the life cycle stages at time $t+1$ equals

$$\begin{pmatrix} I \\ Y \\ J \\ YA \\ A \end{pmatrix}_{t+1} = \begin{pmatrix} 0 & 0 & 0 & F_{YA} & F_A \\ P_I & 0 & 0 & 0 & 0 \\ 0 & P_Y & 0 & 0 & 0 \\ 0 & 0 & P_J & 0 & 0 \\ 0 & 0 & 0 & P_{YA} & P_A \end{pmatrix} \cdot \begin{pmatrix} I \\ Y \\ J \\ YA \\ A \end{pmatrix}_t - \begin{pmatrix} I_c \\ Y_c \\ J_c \\ YA_c \\ A_c \end{pmatrix}_t \quad \text{Eq.(1)}$$

The contribution of each life cycle stage at time t to all others at $t+1$ is contained in the 5×5 matrix that projects the population vector between time t and time $t+1$ (Eq. 1). P_i are the probabilities of infants (I), yearlings (Y), juveniles (J), young adults (YA), and adults (A), respectively, of surviving to the next year. F_i represents the annual contribution of young adult and adult females to female infants, or fertility. To account for the removal of individuals from the population for management purposes, we incorporated a culling vector to the matrix equation that subtracts the number of females of each stage removed from the colony at time t (Equation 1). For example, I_c represents the number of infants culled at time t . To account for differences in the proportion of adult individuals belonging to different age categories, estimates of adult survival P_A were calculated on the weighted mean based on the number of individuals in each age class. Using Mathcad 13.0, the real dominant eigenvalue and its corresponding right and left eigenvectors were calculated in order to obtain the asymptotic population growth rate (λ), the stable stage distribution (w), and the reproductive value vector (v), respectively.

Density-dependence

To test for density-dependence in survival and fertility, each vital rate was plotted against annual female adult density data, and regression analysis was carried out. Given the significant negative linear relationship found between annual fertility rate and the observed temporal variability in number of adult female individuals in the population (N_A) (See results), fertility (F_i) was expressed as a linear function of female adult abundance ($F(N_A)$),

$$F(N_A) = a + b(N_A) \quad \text{Eq. 2}$$

where a equals the y-axis intercept, or the expected fertility at minimal adult density, and b equals the slope of the regression line, or the rate at which female fertility declines as a function of female adult density [Dobson & Lyles, 1989].

Goodness of fit

Model goodness of fit was tested by projecting the population using the density-independent and the density-dependent model parameters, and plotting both model outcomes against observed data from Cayo Santiago. The total number of female individuals alive in the population from 1973 to 2000, based on census data, was used as $N(t)_{\text{observed}}$. The initial population vector for both model projections, N_{1973} , was determined using the proportion of individuals at each life cycle stage according to the stable stage distribution given by the density-independent matrix model, as no significant difference between this stage distribution and the observed stage distribution of that year was found. The model's goodness of fit was estimated using the correlation coefficient between the observed number of females and the expected number projected by each one of the models, and expressed as the proportion of the observed variability explained (R^2).

Life Table Response Experiment

A life table response experiment (LTRE) of random design [Caswell 2000; Lawler, 2011b] was performed to quantify the population-level effect of variation in vital rates across different levels of adult density. The LTRE is a retrospective analysis that determines how variation in life-cycle transitions, during a sequence of years, contributed to the observed variation in the population growth rate [Caswell 2000; 2001]. The variation in λ across years, $V(\lambda)$, can be broken down into contributions from vital rates' variances, and covariances among them, in the matrix entries [Caswell, 2000; 2001]:

$$V(\lambda) = \sum_{ij} \sum_{kl} C(ij, kl) s_{ij} s_{kl} \quad \text{Eq. (3)}$$

where $C(ij, kl)$ is the covariance of a_{ij} and a_{kl} , and the sensitivities s_{ij} and s_{kl} are evaluated at the mean matrix ($\bar{A}$), which is the average projection matrix calculated using each of the 28 projection matrices generated from 1973 to 2000. In order to determine how variation in vital rates during periods of low vs high female adult density influenced λ , two separate LTREs of random design were carried out using matrices from 1973-1984 (average female adult density = 165 individuals) and matrices from 1985-2000 (average female adult density = 290 individuals).

RESULTS

Vital rates of rhesus macaques

Temporal variability in annual survival was related to changes in management strategy. Survival of female individuals increased significantly following tetanus toxoid inoculation in 1985 (Mann-Whitney U-test: 11447.0, $P < 0.000$). During the period previous to tetanus

toxoid inoculation, mean survival ranged from 0.84 in 1973 to 0.90 in 1984. After tetanus toxoid inoculation began in 1985, mean annual survival increased significantly to 0.94 in 2000. Because of this, we pooled the survival data into pre- and post-inoculation against tetanus. For both time periods, infants had the lowest survival rate (88%) (Appendix A). Once individuals reached one year of age, survival increased to 96% and 95% in both time periods, respectively. Juveniles showed the highest probability of survival during the entire study period with 98% of them reaching the next stage class. Young adult and adult females exhibited a 95% probability of survival during pre-inoculation years. However, young adult and adult survival increased to 97% following tetanus toxoid inoculation.

A total of 2399 female births were recorded. Sexual maturation was first observed at three years of age. However, the majority of females in the colony gave birth at four years of age or older. Mean fertility of adults was significantly higher (0.370) than that of young adults (0.156) (Mann-Whitney U-test: 32.00, $P < 0.001$). Temporal variation in fertility of young adults and adults was related to adult density. A significant negative linear relationship between young adult and adult fertility rates and the total number of adult females was found ($y = -0.0005x + 0.279$, $R^2 = 0.30$, $df = 26$, $p < 0.01$; $y = -0.0003x + 0.407$, $R^2 = 0.21$, $df = 26$, $p < 0.05$, respectively) (Fig. 2).

Population dynamics and model projections

From 1973 to 2000, the adult female population of rhesus macaques increased from 168 to 695 individuals (Fig. 3, solid line). During the first 11 years, no culling was carried out allowing the population to increase naturally. From 1973 to 1984, the population showed geometric growth for a net gain of 286% in female individuals. In 1984, culling was implemented, and 325 females (50% of the total female population) were removed, this being the largest single culling event in the history of the colony. During the subsequent five years, there were no females culled, and the number of females increased to 766 by 1990. This was the year with the largest number of females in the population. During the next decade, culling was more frequent, causing the observed annual variability in the number of individuals in the population.

The density-independent model was able to predict with some accuracy the observed population dynamics until 1984 ($R^2 = 0.68$) (Fig. 3A). However, by 2000 the model overestimated by more than twice the actual number of females in the population but predicted a stable stage structure similar to the observed one - 17% newborns, 13% yearlings, 11% juveniles, 10% young adults, and 49% adult individuals - during both time periods. In contrast, the density-dependent model projection accurately tracked the observed population dynamics throughout the entire study period ($R^2 = 0.98$) (Fig. 3B). This model overestimated the observed number of females by only 48 individuals at the end of the projection. According to this model, λ declines linearly at a rate of 0.01 as adult density increases by 100 individuals.

Life table response experiment

From 1973 to 2000, the population exhibited a mean annual population growth rate of 1.06 ranging between 0.99 and 1.11 (Fig. 4). These values were calculated from the 28 matrices generated from the annual census data. The variation in λ indicates the population experienced growth periods of up to 11% per year, as well as periods of stasis ($\lambda \approx 1.0$) - with the exception of 1983 in which the population decreased by 1% (Fig. 4). Years of population growth coincide with years of low adult density, and years of population stasis coincide with years of high adult density. For the entire period, infants constituted 17.7% of the population, while yearlings and juveniles constituted 13.9% and 11.7%, respectively. Young adults were the least represented stage class, constituting 9.4%. Adult individuals

constituted 47.4% of the population and their survival had the highest sensitivity and elasticity, increasing during high adult density (Fig. 5).

Vital rates' variances contributed the most to the variation in λ , as covariances were weaker (Fig. 6). The largest variation among the a_{ij} entries was exhibited by P_{YA} , followed by P_I and P_Y (Fig. 6A). Survival of adults resulted in the life cycle transition that contributed the most to variation in λ , followed by F_A and P_{YA} (Fig. 6B). For the low density period, F_{YA} exhibited the largest variance (Fig. 6C). The variation and covariation among life cycle transitions that contributed the most to variation in λ were P_A , F_A , and P_I/P_A (Fig. 6D). During the high adult density period, P_{YA} exhibited the largest variation among the a_{ij} entries (Fig. 6E) and variation in life cycle transitions P_{YA} , P_Y , and F_A contributed the most to variation in λ .

DISCUSSION

This study demonstrates that an increase in the abundance of adult females causes a decrease in female fertility rates and that incorporating this negative density-dependence into the demographic model resulted in a more accurate projection of the long-term dynamics observed in the population of rhesus macaques on Cayo Santiago. This is confirmed by the close fit of the density-dependent model, in contrast to the density-independent model. After 1984 - a year of unprecedented number of adult females - the density-independent model projection starts deviating from the observed number of females. Following 1990 - the year with the highest number of adult females after the peak in 1984 - the density-independent model projection dramatically and consistently overestimates the total number of observed females, whereas the density-dependent model closely tracks the observed changes in female population size.

Because the population at Cayo Santiago lived under semi-natural conditions with a well-known monitoring program and management regime, it is possible to evaluate the role that several factors had on the regulation of the population vital rates. First, no significant temporal variability in vital rates was related to climatic events, such as hurricanes. Two major hurricanes significantly impacted the island (Hurricane Hugo in 1989 and Hurricane Georges in 1998) but no effect on survival or fertility due to these events is evident. Second, predation can be ruled out as a factor affecting vital rates as no predators are present in the island. Third, secondary sex ratio adjustment explaining a decrease in females born as the population grew was not observed in previous reports [Rawlins & Kessler, 1986b] nor in our data. Finally, Cayo Santiago represents an abundant-resource environment as increases in population size are accompanied by increases in the amount of food supplied to the population, calculated on a per capita basis [Bercovitch & Berard, 1993]. Although access to feeding sites by subordinate individuals might be restricted at higher densities, even high-ranking females have shown negative density feedback in the age of first parturition in Cayo Santiago [Bercovitch & Berard, 1993] suggesting that food limitation is not the principal density-dependent mechanism affecting vital rates.

Density-dependence of demographic rates is expected in species with complex social systems [Saitoh et al., 1997]. Social interactions resulting in behavioral and physiological changes of individuals, rather than direct competition for food, have been described previously as mechanisms of density-dependence in primate populations. Increasing aggressive interactions among kin and non-kin adult female macaques at high densities has been found [Judge and De waal, 1997]. Altmann and Alberts [2003] reported longer inter-birth intervals in female baboons belonging to larger groups and suggested that the effect of high density on female fertility might be partially mediated through altered hormone levels. High numbers of females have been found to impair each other's fertility by aggressively

disrupting ovarian cycles, inducing abortions, or otherwise making successful conception or implantation more difficult [Sterck et al., 1997; Ha et al., 1999; Ha et al., 2011]. Social harassment by coalitions of relatives is also known to contribute to rank-related variation in reproductive success [Altmann et al., 1995]. On Cayo Santiago, high-ranking matrilineal exhibit higher rates of population growth as a result of differences in survival and fertility [Blomquist et al., 2011]. Such differences seem to decline at high densities where λ of high-ranking matrilineal gets closer to middle and low-ranking matrilineal. Although the study of Blomquist et al [2011] is suggestive of the effect of density on vital rates, their model does not consider density explicitly. A matrix model incorporating social structure and density-dependence remains to be constructed for the Cayo Santiago primate population. We hypothesize that social interactions, such as aggression and harassment, are the principal mechanism acting on the regulation of the population through changes in fertility.

When compared to previous studies of natural rhesus populations, in most cases, the Cayo Santiago population exhibits higher than average vital rates. As reviewed in Dobson and Lyles [1989], an annual birth rate of 0.38 and infant survival of 0.55 were reported for a wild population [(Pakistan) Melnick, 1981]. Mean annual birth rate of 0.77, infant survival of 0.82, and adult survival of 0.83 for a natural population that was provisioned with food have been reported [(India) Southwick et al., 1980]. Our analysis estimated an average adult female fertility of 0.37 (only female births), an infant survival of 0.88, and an adult survival of 0.96. Conversely, other studies on provisioned natural populations have reported higher vital rates than those of Cayo Santiago. Malik et al. [(India) 1984] reported a birth rate of 0.82 and an infant survival of 0.96 during a three-year period. Although adult survival data of natural populations is rather limited, these data suggest that vital rates exhibited by rhesus monkeys at Cayo Santiago might reflect similar values in contrast to natural populations with low food limitation. Also, the relatively large influence of adult survival on λ predicted by the sensitivity analysis is expected of long-lived animals characterized by delayed maturity and low reproductive rates [Lawler et al., 2009]. Thus, our analysis reveals that the population at Cayo Santiago mirrors typical life history traits of wild populations with low reproductive rates and long life-spans.

Identifying which life history traits contribute the most to the temporal variation in population growth brings insights on the selective forces acting on a population, as the temporal dynamics in λ , or long-term fitness, is determined by individual schedules of survival, growth, and reproduction (Lawler, 2011b). The LTRE analysis performed on the Cayo Santiago population shows that most of the variation in population growth rate over the past 28 years is due to variation in life cycle transitions of young adult and adult females. Therefore, in order to understand the temporal dynamics of λ , it is necessary to identify processes that influence these two life cycle stages [Lawler, 2011b]. Young adults (three-yr-olds) in Cayo Santiago represent a stage of potential sexual maturation. Although reproduction at three years of age has been previously reported to have no survival cost [Bercovitch & Berard, 1993], earlier reports have indicated that aggressive behavior leading to death in Cayo Santiago's female macaques is significant during the mating season [Wilson and Boelkins, 1970; Manson, 1994]. Thus, we would expect a higher number of aggressive encounters during years of high population density, increasing the variability in survival rates through time. Moreover, high variability in the survival of young adults is expected as parity – number of previous births – has been shown to correlate with differences in reproductive success, indicating that females giving birth for the first time are physiologically immature [Small, 1982]. We would expect this mechanism to be significant in the Cayo Santiago's macaques as these females reproduce earlier in life than expected in the wild which might contribute to a high variance in survival. On the other hand, P_A had a relatively small temporal variance making its high sensitivity the reason for its large contribution to the variation in λ . The small variance in survival of adults is expected owing

to the fact that Cayo Santiago has been under different management strategies targeted at enhancing survival (e.g., tetanus toxoid inoculation, no predation). Variation in adult fertility also contributed to the variation in λ . Although a significant part of the variation in F_A can be explained by variation in density, most of it remains as undocumented environmental variability.

During the low adult density period, the LTRE indicated that survival of adult females contributes the most to variation in λ . However, this transition did not show high variance indicating that its sensitivity contributed significantly to its overall positive effect on λ . In contrast, during the high adult density period, variance in P_{YA} contributed the most to variation in λ , while the variation in P_A decreased dramatically. The decreased variation in P_A suggests that tetanus toxoid inoculation had a significant effect on adult female survival, resulting in a lower contribution to λ during this period. Another interesting aspect is that the contributions of fertility rates' variances, as well as the covariance between them, to λ were smaller during the period of high adult density. It might be tempting to attribute this reduction in F_A variability to density feedback. However, because the two periods used for this analysis also correspond to the pre- and post-tetanus toxoid inoculation periods, differences in density might be confounded with differences in survival following 1985.

Having described the long-term dynamics of the Cayo Santiago population and being able to model it accurately, we feel confident in concluding that the long-term dynamics in population growth rate of the macaque population is mostly the result of population density affecting fertility and the impact of tetanus prophylaxis on adult survivorship. We found support for Pfister's hypothesis that vital rates with the highest sensitivity show less temporal variability [Pfister, 1998], as survival of adult individuals exhibited low variance and the highest sensitivity (Appendix B shows variance values corrected for sampling variation). Although demographic variability in vital rates was low, our findings suggest that selection might be acting to lower the variance in the population growth rate by minimizing the variation in adult survival.

This study demonstrates that accounting for density-dependence in vital rates was crucial for understanding the dynamics of the Cayo Santiago primate population. Whether such dynamics exist in the wild still remains to be explored, but the fact that the density-dependent model explained 98% of the changes in individual abundance in a provisioned population is important as a high number of wild populations might be experiencing food scarcity, and thus, a more significant decline in vital rates as the population increases. Because nonhuman primates represent one of the groups of animals highly threatened by human activities, the impact of density-dependent mechanisms may become greater as human expansion reduces habitat size, making it imperative to incorporate density-dependence into population viability analyses.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

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Figure 1.

Life cycle of rhesus macaque population in Cayo Santiago. I = infants (0 year-old), Y = yearlings (1 year-old), J = juvenile (2 years-old), YA = young adult (3 years-old), and A = adult (4 years-old). P s represent the survival rates and F s represent fertility rates.

Figure 2. Linear relationship between fertility rate of young adults (A) and adults (B) and the number of adult females.

Figure 3.

A) Density-independent, and B) density-dependent model projection of female rhesus macaques at Cayo Santiago from 1973-2000. Solid lines depict the observed population dynamics, dotted lines depict model projections, and dashed lines represent the number of culled females. Percent variation of the observed dynamics explained by each projection (R^2) is provided.

Figure 4. Mean annual population growth rate (solid line) and abundance (dotted line) of female macaques of Cayo Santiago from 1973-2000. Error bars represent standard errors.

Figure 5. Deterministic sensitivities (A) and elasticities (B) of rhesus macaque vital rates from 1973-2000 (white bars), from 1973-1984 (low-density period; bars with lines), and from 1985-2000 (high-density period; bars with diamonds).

Figure 6.

Life table response experiment results showing variances and covariances of rhesus macaque vital rates (A, C, and E) and their contributions to variance in the population growth rate ($V(\lambda)$) (B, D, and F) from 1973 to 2000. The first bar in each group is the variance of the specified vital rate, and subsequent bars are covariances between that vital rate and the other rates.

Table 1

Density-independent population projection matrices, stage-specific mortality rates (q_x), and sample size (n) of female rhesus macaques for 1973-1984 and 1985-2000.

	I	Y	J	YA	A
1973-1985					
I	0.000	0.000	0.000	0.220	0.346
Y	0.881	0.000	0.000	0.000	0.000
J	0.000	0.962	0.000	0.000	0.000
YA	0.000	0.000	0.979	0.000	0.000
A	0.000	0.000	0.000	0.951	0.947
Q_x	0.119	0.038	0.021	0.049	0.053
N	805	663	571	485	2164
1985-2000					
I	0.000	0.000	0.000	0.114	0.373
Y	0.884	0.000	0.000	0.000	0.000
J	0.000	0.953	0.000	0.000	0.000
YA	0.000	0.000	0.975	0.000	0.000
A	0.000	0.000	0.000	0.970	0.968
Q_x	0.116	0.047	0.025	0.030	0.032
N	1661	1252	1022	766	4458