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Managing the Cayo Santiago Rhesus Macaque Population: The Role of Density

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Abstract

Cayo Santiago is the oldest continuously operating free-ranging rhesus monkey colony in the world. Population control of this colony has historically been carried out by periodic live capture and removal of animals. However, the effect of such a strategy on the size, growth rate, age structure, and sex ratio of the population has not been analyzed. This study reviews past removal data and uses a population projection model to simulate the effects of different removal schemes based on Cayo Santiago demographic data from 2000–2012. The model incorporates negative density-dependence in female fertility, as well as male and female survival rates, to determine the population-level effects of selective removal by age and sex. Modeling revealed that removal of sexually immature individuals has negligible effects on the population dynamics explaining why with an initial population of 1309 in 2000 and annual removals of immature monkeys a mean annual population growth rate of 12% and a final population size of ~1,435 individuals by 2012 (~ 0.009 animal/m²) was observed. With no removals, the population is expected to exhibit dampened oscillations until reaching equilibrium at ~1,690 individuals (~ 0.0111 animal/m²) in 2100. In contrast, removal of adult females (> 4 yrs) would significantly reduce the population size, but would also promote an increase in population growth rate due to density feedback. A maximum annual production of 275 births is expected when 550 adult females are present in the population. Sensitivity analyses showed that removing females, in contrast to controlling their fertility through invasive treatments would contribute the most to changes in population growth rate. Given the density compensation on fertility, stabilizing the population would require removing ~80% of the current population of adult females. This study highlights the importance of addressing the population-level density effects, as well as sensitivity analyses, to optimize management strategies.

Keywords

Macaca mulatta; culling; density-dependence; population viability

INTRODUCTION

Cayo Santiago is the oldest free-ranging rhesus monkey colony managed under minimal intervention for support of investigations on the behavior, physiology, demography, ecology and naturally-occurring diseases of this species, as well as to supply monkeys for biomedical research [Carpenter, 1972; Rawlins & Kessler, 1986a]. Maintaining long-term viability of this population allows for the continuation of studies of primate populations which are difficult or impossible to address in the wild [Southwick, 1989]. These include studies on post-partum mating control [Johnson et al., 1993], age-related differences in vital rates [Bercovitch & Berard, 1993; Hoffman et al., 2010; Hoffman & Maestripieri, 2012], sex-related differences in vital rates [Manson, 1994; Hoffman et al., 2008], social ranking-related demographics [Blomquist et al., 2011], and density-dependent dynamics [Hernández-Pacheco et al., 2013]. Maintaining the long-term viability of the Cayo Santiago rhesus macaque population requires development of modeling tools that will allow the analysis of the effects of management practices on the size, growth rate and structure of the population.

Vital rates at Cayo Santiago are characteristically higher than those of wild rhesus populations, resulting in remarkably high mean annual population growth rates (~12%) [Koford, 1966; Rawlins et al., 1984; Rawlins & Kessler, 1986b; Hernández-Pacheco et al., 2013]. Such demographics forced management efforts towards live capture and removal of individuals (removals from now on) to maintain what was estimated as the optimum size for ongoing research (300 individuals), a size determined principally by cost of colony maintenance (e.g., food supply, staff) and visual census taking efforts [Carpenter, 1972; Rawlins, 1989]. Although different removal schemes have been implemented since then, population dynamics at Cayo Santiago has never been stable [Hernández-Pacheco et al., 2013]. In fact, the colony has been characterized by periods of exponential growth following removal events, raising questions regarding the effects of animal removal on the dynamics of the population [Carpenter, 1972; Rawlins, 1989].

Past management of the Cayo Santiago colony directed at population control has consisted of three forms of selective removal: (1) entire social groups as it is assumed to be less disruptive in terms of population structure and behavior since it is a naturally established social unit [Rawlins, 1989; Widdig et al., 2006], (2) by sex to adjust the adult sex ratio to 1:2 (males:females) to approximate the adult sex ratio of feral populations (J. D. Berard, pers. comm.; C. H. Southwick, pers. comm.), and (3) by age as immature individuals require less trapping effort and are better candidates for the Caribbean Primate Research Center's NIH-supported specific-pathogen-free (SPF) breeding colonies at its Sabana Seca Field Station (SSFS). The observed dynamics from 1973 to 2000 indicate that the colony has exhibited several periods of exponential growth that have been interrupted only by removal events [Hernández-Pacheco et al., 2013] (see also Fig. 1). After 10 years of no intervention from

1973 to 1983, live capture and removal was re-established in 1984 as the principal method of population control with the removal of three entire social groups [Rawlins & Kessler, 1986a] (Appendix A). This event reduced the population size by ~50%, constituting the largest single removal event in the history of the colony (596 individuals). Removal of additional social groups took place in 1985, 1990, 1992, 1994, and 1995 (J. D. Berard, pers. comm.) for a total of 1,416 individuals removed (Appendix A). Yet, by the end of 1995, the population size was still ~1,030 individuals, more than three times the estimated optimum size suggested by Carpenter [1972]. In 1995, the removal of ~40% of adult males (98 adults) was carried out (J. D. Berard, pers. comm.; C. H. Southwick, pers. comm.). Another change in removal practices took place from 1996 to 1999 resulting in the removal of 390 individuals consisting of 370 1- and 2-yr-old monkeys and 20 3-yr old males (Appendix A). But by 1999, the population had again increased to ~1,309 individuals.

Models of other harvested macaque populations have assumed density-independence in vital rates on the basis that the population is well below carrying capacity [Crockett et al., 1996]. Although such density-independent models have proven to be accurate in describing Cayo Santiago's dynamics during decadal periods of low density [Rawlins & Kessler, 1986b], the population has recently been found to be regulated by negative density-dependence in female fertility [Hernández-Pacheco et al., 2013]. This finding needs to be incorporated into colony management as the population's vital rates are differentially affected by removal events. The selective removal by age and sex carried out at Cayo Santiago since 1996 was implemented in an attempt to maintain population size at a manageable number (<1000 individuals) while also preserving the colony as a resource for behavioral and biomedical research. Whether such a removal scheme guarantees the long-term viability of the population or not is still unknown.

This study examines the most recent demographic changes in mortality and fertility, which have occurred under the current live capture and removal protocols from 2000–2012, and presents a structured population model that simulates the effects of different removal schemes on the dynamics and structure of the population. This model is novel because it incorporates density-dependence in female fertility, as well as both male and female survival rates. It also establishes the importance of addressing density effects to optimize management strategies for the population. Given the expected reproductive value post-tetanus toxoid inoculation of the colony [Kessler et al., 2014] and density-dependence in fertility among adult females [Hernández-Pacheco et al., 2013], we hypothesize that the annual removal of adult females, and not immature individuals, will have the highest impact on the population growth and that the exponential growth following past removal events is the result of increased female fertility rates.

METHODS

All research procedures were 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 Non-human Primates.

Cayo Santiago is a 15.2-ha island located 1 km off the coast of Punta Santiago, Puerto Rico (18°09'N, 65°44'W) that has served as habitat for free-ranging rhesus monkeys (*Macaca mulatta*) since 1938 [Carpenter, 1972; Rawlins & Kessler, 1986a]. All individuals are descendents of the original 409 Indian-origin founders. Each monkey has a unique identification tattoo on its chest and thigh. Visual census has been conducted since 1956 [Altman, 1962] and information on each monkey includes identity, date of birth, sex, maternity, maternal lineage, natal social group(s), current social group, paternity, and date of death or date of removal from the island. Animals are provisioned with 0.23/kg/animal/day of commercial monkey chow and water is available ad libitum. Veterinary intervention is minimal except during the annual trapping period when yearlings are captured, marked for identification, physical samples are collected (including blood samples for paternity testing), and tetanus inoculation is given [Kessler et al., 2014]. Severely injured animals are either removed from the island for treatment or euthanized in accordance with guidelines of the American Veterinary Medical Association. Animals have been captured alive and removed since the 1940's to the continental USA for laboratory research [Frontera, 1958] and locally to the NIH Laboratory of Perinatal Physiology in San Juan (1956–1970) [Sade et al., 1985] (the term 'culling' is often used). However, only partial information differentiating mortality from live capture and removal data may exist for these periods [Sade et al., 1985]. Thus, removal data prior to 1973 is not described in this study. Since 1973, animals captured during the annual round up are transferred to SSFS. No monkeys return to Cayo Santiago once removed.

Demographic modeling

An age-classified matrix population model was constructed and analyzed as given by the following equation:

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t) - \mathbf{C}(t) \quad \text{Eq.1}$$

$\mathbf{A}$ is a matrix describing the probability transition between different age classes, $\mathbf{n}(t)$ is a vector describing the number of individuals in each age class at time t , and $\mathbf{C}(t)$ is a vector describing the number of individuals removed in each age class at time t . The projection matrix $\mathbf{A}$ is multiplied by the vector $\mathbf{n}(t)$, followed by the subtraction of the vector $\mathbf{C}(t)$ to determine the number of animals in each age class the following year, $\mathbf{n}(t + 1)$ [Caswell, 2001; Hernández-Pacheco et al., 2013]. The real dominant eigenvalue of $\mathbf{A}$ and its corresponding right and left eigen vectors are calculated to obtain the asymptotic population growth rate (λ), the stable age distribution (w), and the reproductive value vector (v), respectively. The sensitivity of λ to changes in probability transitions determined by the prospective perturbation analysis of sensitivity and its proportional values in the form of elasticities were also calculated [Caswell, 2001]. In this way, sensitivity is a prospective perturbation analysis that can be used to determine which life cycle transition should be targeted by managers [Caswell, 2001].

In order to parameterize the model, hypothetical annual censuses from Cayo Santiago daily census data were compiled and a birth-pulse model employing post-breeding censuses was carried out [Caswell, 2001]. A Leslie matrix, incorporating survival (P_x) of males and

females, fertility rates (F_x) of females, and also allowing for stasis of the last age class was constructed. Due to the lack of significant differences in survival among females 4 years, as well as the significant difference in fertility rates between 3 and 4-year-old females and older [Hernández-Pacheco et al., 2013], the population was divided into ten stage classes according to their age and sex: infant [I] (0 to <1-year-old), yearling [Y] (1 to <2-year-old), juvenile [J] (2 to <3-year-old), young adult [YA] (3 to <4-year-old), and adult [A] (4 years) males and females.

The contribution of each life cycle stage at time t to all others at $t+1$ is contained in the 10×10 matrix that projects the population vector between time t and time $t+1$ (Eq. 2)

$$\begin{pmatrix} I(m) \\ Y(m) \\ J(m) \\ YA(m) \\ A(m) \\ I(f) \\ Y(f) \\ J(f) \\ YA(f) \\ A(f) \end{pmatrix}_{t+1} = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & FYA(m) & FA(m) \\ PI(m) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & PY(m) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & PJ(m) & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & PYA(m) & PA(m) & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & FYA(f) & FA(f) \\ 0 & 0 & 0 & 0 & 0 & PI(f) & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & PY(f) & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & PJ(f) & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & PYA(f) & PA(f) \end{pmatrix} \begin{pmatrix} I(m) \\ Y(m) \\ J(m) \\ YA(m) \\ A(m) \\ I(f) \\ Y(f) \\ J(f) \\ YA(f) \\ A(f) \end{pmatrix}_t - \begin{pmatrix} I_c(m) \\ Y_c(m) \\ J_c(m) \\ YA_c(m) \\ A_c(m) \\ I_c(f) \\ Y_c(f) \\ J_c(f) \\ YA_c(f) \\ A_c(f) \end{pmatrix}_t \quad \text{Eq. 2}$$

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 ($t+1$). F_i represents the annual contribution (fertility) of young adult and adult females to male infants, $[Fi(m)]$, and female infants, $[Fi(f)]$ (letter in parenthesis stands for the stage-class sex [m = males; f = females]). Using R.3.0.1 package popbio ([Stubben & Milligan, 2007]; R Development Core Team; <http://www.R-project.org>), an eigen analysis was carried out and the asymptotic λ , w , and v estimated. Male fertility was set to 0 because our model assumes that female life history schedules determine population dynamics as female reproductive success is not limited by

the number of adult males [Caughley, 1980; Caswell, 2001; Lawler, 2011]. However, including male survival data in the model allows for projecting the total number of individuals in the population, as well as the age-specific sex ratio at each time step.

The model was parameterized using data collected during the last decade (2000–2012) in order to capture the dynamics of the population under the current live capture and removal protocol. For this, the following were recorded: (1) the total number of monkeys alive in the population each year, (2) the total number of females that gave birth at specific ages, and (3) the age at death or age when removed from the colony. Age-specific survival of all individuals was estimated by following the fate of 2,046 male and 2,094 female monkeys. 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 $1-q_x$. Age-specific fertility of females (F_x) was estimated by dividing the number of newborns at time t by the number of females of age x alive at time t . Fertility was estimated separately for females giving birth to males and to females. Cohort analysis was used to test for temporal variability in vital rates using nonparametric statistics Mann-Whitney W-test and Kruskal-Wallis test with R.3.0.1 package `pgirmess` (Giraudeau 2013; R Development Core Team, 2007, <http://www.R-project.org>). Such analysis was carried out in order to determine if using a mean matrix parameterized by grouping all years was appropriate for our analysis. A P value equal to or less than 0.05 was considered statistically significant. Tests are two tailed. Each cohort was defined as the total number of monkeys born each year. In order to avoid age classes with insufficient representation for the cohort analysis, males 12 years of age and older, as well as females 14 years old and older were combined into one age class.

Density-dependent effects were incorporated into the model by writing vital rates as a function of the number of mature females in the population [Hernández-Pacheco et al., 2013]. We tested the assumption of linearity by carrying out first and second order linear regression analyses between female fertility and the observed number of mature females each year. Given a higher significance (lowest p-value) in first order linear regression analyses between F of females giving birth to females (fertilities contributing to population growth and fitness in the model) in contrast to their corresponding second order regression, fertility rates are expressed as a linear function of young adult and adult female abundance [$F_i(N_i)$],

$$F_i(N_i)=a+b(N_i) \quad \text{Eq. 3.}$$

where a equals the y-axis intercept, or the expected fertility at minimal female density, and b equals the slope of the regression line, or the rate at which fertility declines as a function of female density [Lyles & Dobson, 1988; Dobson & Lyles, 1989; Hernández-Pacheco et al., 2013]. N equals the number of females in stage i at time t . Linear equations were calculated individually for each F_i entry in Eq. 2. Because Cayo Santiago is an island, it was assumed that any change in the number of individuals was proportional to a change in population density. It was also assumed that the sensitivity of λ to a given transition probability is proportional to the sensitivity of the equilibrium density (N^*) to changes in such transition

probability, the latter being explained by the fact that this macaque population presents equilibrium dynamics, as well as low temporal and demographic variability [Hernández-Pacheco et al., 2013], avoiding significant fluctuations in demographic parameters that might lead to bifurcations of equilibria [Caswell, 2001].

The model's goodness of fit was tested by projecting the population using parameters from the density-independent and density-dependent matrix model, and plotting the models' outcome against the observed data from Cayo Santiago [Hernández-Pacheco et al., 2013]. The total number of individuals alive in the population from 2000 to 2012 was used as $N(t)_{\text{observed}}$. The initial population vector for the models projection, N_{2000} , was determined using the number of monkeys alive at the start of year 2000 ($N=1,309$) distributed according to the stable age distribution of the matrix model. The models' goodness of fit were estimated using the correlation coefficient between the observed number of individuals and the expected number projected by each model, and expressed as the proportion of the observed variability explained (R^2). To further analyze the effect of incorporating density-dependence in the matrix projection model, a Kolmogorov–Smirnov test was carried out between two distributions of λ generated from a density-independent and a density-dependent projection by bootstrapping (Appendix B).

Simulations under different removal schemes

To determine the effect of different live capture and removal schemes on the dynamics and structure of the population, we projected the population using different selective removal strategies. The observed population vector of 2012 was used as the initial vector. The simulations proceeded by manipulating the $C(t)$ vector in Eq. 2 using density-dependent fertilities. Three management scenarios were considered:

1. No removal—Done to estimate the population equilibrium (N^*), the population size at which the number of births equals the number of deaths and the population growth rate (λ) equals 1.0. Equation 2 was iterated setting the $C(t)$ vector to 0 for all age and sex classes.

2. Selective removal by age—Done to determine the effects of removing individuals from different age classes. For each age class, four different simulations were performed until 2035, by removing 70, 100, 130, and 160 monkeys [$C(t)$ vector]. The number of removed individuals was equally divided between both sexes (e.g., 70 infants = 35 male infants + 35 female infants). The values were chosen as they are within the range of past removal strategies on the island. A horizon of 23 years for each simulation was used because longer horizons produce negative numbers in the projected $n(t)$ vector.

3. Selective removal by sex—Done in order to disentangle the effects of removing females versus males. The population was projected using the same removal scenarios used above (i.e. 70, 100, 130, and 160), with the difference that all removed individuals were either males or females. Given the significant effect on population dynamics observed when removing adults exclusively (see RESULTS), we present the selective removal by sex on adults only. The simulations were also carried out with a horizon of 23 years.

Given density-dependence in fertility of adult females, the relationship between adult female removals, total fertility and production of infants was calculated. For this, linear regression analysis between the total mean annual fertility rate of adult females (adults giving birth to males and females) and the number of adult females was carried out. The linear function given by the regression analysis was used to estimate the expected fertility given a 25 increase in the number of adult females removed. This was carried out with a theoretical initial population size of 1100 adult females (a density where $F_A \sim 0.0$). In order to simulate an alternate scenario assuming females were treated against pregnancy (e.g., contraception, sterilization), the population was projected using different annual proportions of adult females *treated* against pregnancy (adult females alive in the population but not contributing to annual births). This alternate strategy was simulated under the assumption that treated adult females will contribute equally, relative to non-treated ones, to the negative density-dependent relationship in fertility. For every time-step of the simulation the density-dependent adult fertility was estimated using the total number of adult females as in the original simulations, however, the number of births was estimated using only the number of *non-treated* adult females.

RESULTS

From 2000 to 2012 a total of 1,744 monkeys were removed from Cayo Santiago, including 10 individuals whose sex was not recorded (Table I). With the exception of 2000 and 2008 when no monkeys were removed from the island, annual removal ranged from 71 to 390 individuals and was targeted mostly to 1-year-old and 2-year-olds (68%) (Table II). In 2002 and 2004 immature individuals were removed together with adult monkeys as six entire sub-groups or matrilineal groups that fissioned from other groups were removed (649 individuals). Random removal of adults was also carried out in 2006, 2009, and 2010, but the total number was small ($n=70$).

No significant temporal variation in annual survival of males was observed (Kruskal-Wallis chi-squared = 6.50, $df = 12$, $P = 0.89$). The same result was obtained for female data after a multiple comparison test. Significant differences in age-specific survival of males and females among infants and adults were found (males: Kruskal-Wallis chi-squared = 51.3, $df = 12$, $P < 0.001$; females: Kruskal-Wallis chi-squared = 65.7, $df = 14$, $P < 0.001$). Infants showed the lowest mean annual survival rate for both sexes (males: 87.7%; females: 88.1%) (Table III). Once individuals reached 1 year of age, survival increased to 91.7% in males and 92.0% in females. Juvenile males exhibited a survival rate of 96.4% while juvenile females exhibited a survival rate of 96.7%. Young adults had the highest mean annual survival rate for males; 99.1%, and for females; 98.5%. Mean annual survival rate of adults dropped to 92.9% and 94.3% for males and females, respectively. A total mean number of annual deaths (89 ± 24 ; mean $\pm$ SD) were recorded.

A total of 1,568 male births and 1,515 female births were recorded. These resulted in age-specific fertility rates of 6.7% for young adult females giving birth to males and 6.0% of them giving birth to females (Table III), for a mean total annual fertility rate of 12.9% among young adults. In the same way, 34.1% of adult females gave birth to males while 33.1% gave birth to females for a mean annual fertility rate of 68.1% among adults. No

significant temporal variation in female fertility was observed (Kruskal-Wallis chi-squared = 6.61, $df = 12$, $P = 0.88$). Significant differences in age-specific fertility between young adults and the rest of adult females was found (Kruskal-Wallis chi-squared = 45.5, $df = 11$, $P < 0.001$). A negative linear relationship between F_{YA} and the number of young adults was found for both females giving birth to males and to females ($y = -0.002x + 0.227$, $F = 8.7$, $P < 0.05$, $R^2 = 0.44$; $y = -0.001x + 0.155$, $F = 1.28$, $P > 0.05$, $R^2 = 0.13$, respectively) (Appendix C). Similarly, a negative linear relationship between F_A and the number of adult females was found for both females giving birth to males and females giving birth to females ($y = -0.0005x + 0.518$, $F = 5.2$, $R^2 = 0.32$, $P < 0.05$; $y = -0.0004x + 0.479$, $F = 4.2$, $P > 0.05$, $R^2 = 0.16$, respectively) (Appendix C).

Using the age-specific and sex-specific mean vital rates from 2000–2012, the density-independent mean matrix projection model was constructed (Table III). The asymptotic population growth rate (λ) equaled 1.12 indicating a mean annual population growth of 12%. The stable age distribution gave a structure dominated by adults with 16.3, 12.8, 10.6, 9.1, and 51.2% of the population in the infant, yearling, juvenile, young adult, and adult stages, respectively. Adults showed the expected biased sex ratio given removal events (female 26.2%; males 24.8%). Reproductive value increased with age, with adult females exhibiting the highest value (1.00, 1.27, 1.54, 1.79, and 1.97, for infant, yearling, juvenile, young adult and adults, respectively). Sensitivity and elasticity analyses revealed that survival of female adults is the life cycle transition that would potentially contribute the most to future changes in λ (Table IV). More than 50% of the relative contribution of vital rates to λ is given by the survival of adult females (Table IV). Incorporating the density-dependence in female fertilities resulted in a model fit of $R^2 = 0.84$, in contrast to the density independent model showing a fit of 0.52, overestimating the population by 401 individuals in 2012. Thus, the density-dependent model was able to predict 84% of the observed variation in the population dynamics from 2000–2012. The Kolmogorov–Smirnov test between the two distributions of λ generated from a density-independent and a density-dependent projection by bootstrapping resulted significantly different (K-S test: $D = 0.086$, $P\text{-value} = 0.001$) (Appendix B).

Simulations

No removal—When the population is projected with density-dependent fertility rates, no removal of individuals resulted in exponential growth until 2020 followed by oscillations of decreasing amplitude around an equilibrium of ~1,690 individuals and a sex ratio m:f of 0.40. Equilibrium is attained after nearly 90 years of projection in 2100 (Fig. 2).

Selective removal by age—Removal of adult individuals had more impact on the population than removal of sexually immature individuals (Fig. 3). With annual removal events of 70, 100, 130, and 160 infants, the population exhibited net changes of 18.8%, 16.2%, 12.5%, and 5.35%, respectively, after 23 years of projection (Fig. 3B). No significant deviations in population dynamics was observed when removing the same amount of individuals from the rest of the age classes, except when reaching the level of 160 individuals (Fig. 3B–F). At this level, yearlings and juveniles exhibited an 8.38% and 2.01% increase, while removing 160 young adults, or adults annually resulted in a 21.1% and 71.1% population decline after 23 years of projection, respectively (Fig. 3).

Selective removal by sex—Removal of adult females had drastically different impacts on the population dynamics than the removal of adult males (Fig. 4). Removing 70 adult females annually resulted in a 66.7% population increase reaching 2,392 individuals and a sex ratio of 1.89 males to females at the end of the projection (Fig. 4A). In contrast, removing 100 adult females annually resulted in a 17.7% population decline and the absence of adult females after 11 years of projection (Note that simulations were carried out until one or more of the stage classes was absent) (Fig. 4A). Removing 130 and 160 adult females resulted in the absence of adult females after only 6 and 4 years of projection, respectively, showing 21.0% and 21.6% population decline. Annual removal events of 70 adult males resulted in the expected oscillations with up to 1,938 individuals and no male births after 12 years due to density effects associated to an increase in the number of mature females (Fig. 4B). At the end of the projection the population had 1,685 individuals exhibiting a sex ratio of 0.31 males to females. Under the 100, 130 and 160 adult male annual removal regimes, the population dynamics followed the same pattern resulting in the absence of adult males at an earlier time (Fig. 4).

The relationship between adult female removal, fertility rate and production of infants indicated that a maximum annual production of 275 births from adult females is expected in a population with 550 adult females (Fig. 5). A number lower or higher from 550 adult females would lead to a lower annual production of infants. This results from the negative density-dependence estimated by regression analysis between the annual number of adult females and their total fertility. This linear relationship indicated that a maximum mean fertility of 0.996 is expected at very low population sizes, and that such fertility would decrease at a rate of 0.0009 as the number of adult females increases ($y = -0.0009x + 0.9964$; $F = 6.02$; $DF = 11$, $P < 0.05$; $R^2 = 0.35$). Substituting this information in Eq. 3, using an initial population size of 1100 adult females resulted in a 0.02 increase in mean total adult fertility with every 25 increase in the number of removed adult females (Fig. 5). Related to this, the simulation using the alternate strategy of birth control indicated that a reduction in population growth will be achieved when nearly 80% of the annual adult female population is treated against pregnancy.

DISCUSSION

Due to their high reproductive rate, low mortality rate and the geographical constraints of the island itself, the size of the Cayo Santiago macaque population should be aggressively reduced to avoid excessively high densities that can threaten the colony's long-term viability, and thus, its contribution to multidisciplinary research. The analysis supports our hypotheses demonstrating that the annual removal of adult females, and not immature individuals, will have the highest impact on the population growth rate and that the exponential growth following past removal events is mostly the result of an increase in the adult female fertility rate given decreased density. As the population is currently growing and the density at the projected population oscillations and equilibrium is extremely high, the colony should be reduced by focusing on the age classes and sex that contribute most to growth.

Cayo Santiago is a provisioned primate population with no natural predators. As such, the population exhibits high survival rates coupled with high fertility rates that result in a high population growth rate, extended life expectancy, higher net reproductive rates, and negligible demographic variability. These represent major challenges for effective management and maintenance of colony stability. The fact that even in the absence of resource limitations, the Cayo Santiago population exhibits density-dependent dynamics has further implications because of the density feedback on vital rates that removal of individuals might have. For example, removing a significant number of sexually mature females decreases population size but it also increases fertility rates, resulting in an increase in the long-term fitness of the population (λ). Ignoring density effects could potentially interfere with, or actually be counter-productive to, long-term management goals and viability of the colony.

According to the density-dependent model, the population would stabilize at ~1,690 individuals (~0.0111 animal/m²), a higher density than the current one (~0.0094 animal/m²). The expected oscillations given the nonlinear dynamics of density-dependent growth further accentuate this situation, producing unprecedented population sizes up to 2,421 individuals (0.0159 animal/m²). Hernández-Pacheco and colleagues [2013] showed that density effects become apparent after the population exceeds ~650 females, suggesting that behavioral aspects such as increasing aggressive interactions are the mechanisms regulating density-dependence in Cayo Santiago. Therefore, it is unlikely that the current mean vital rates will remain the same at the extremely high population density of the projected equilibrium (1,207 females). Allowing the population to increase without intervention could, potentially, allow other issues regarding colony management and viability to emerge, such as: (1) increased maintenance costs, as an increase in population size would require more commercial monkey chow [Carpenter, 1972; Rawlins & Kessler, 1986a] and staff; (2) behavioral artifacts as larger genealogies are more likely to induce group fissions [Chepko-Sade & Sade, 1979; Widdig et al., 2006], as well as increased aggressive interactions [Judge & De waal, 1997]; (3) physiological aspects, such as the stress related alteration of hormone levels associated with high density in primates [Altmann & Alberts, 2003]; (4) epidemiological aspects, as the incidence of infectious diseases could increase [Wolfe et al., 1998]. Destruction of vegetation by high numbers of animals foraging on the island is another potential problem. Finally, a higher density will make ongoing research on the island more difficult. The larger the colony becomes the more time it takes to capture and process animals during the annual round up, in turn affecting social relationships among groups and individuals [Berman, 1989]. It is paramount to implement an effective live capture and removal scheme for controlling the Cayo Santiago rhesus monkey population.

Selective removal by age resulted in a population reduction when 160 individuals were removed. This was expected as the mean net gain in number of monkeys for the study period was 148 ± 21 individuals (mean $\pm$ SD; net increase = #births – #deaths). Thus, removing a larger number of individuals than the annual net gain from births will result in a decrease in colony size. However, the rate of decline depends on the age class being removed. The combined removal of adult males and females resulted in the highest rate of decline. This is because adult females have the highest reproductive value, and thus, they contribute most to population growth. Because this model only utilizes female fertilities, the number of

removed adult females contributed the most to the observed rate of population decline. Annual removals of 80 adult females were sufficient to overcome the increase in mean fertility due to the decrease in female adult density following removal.

Selective removal of adult males resulted in expected population oscillations related to an increase in female density. This would result in a lower level of equilibrium as the number of monkeys exiting the colony by removal and deaths comes closer to the number of annual births. This scenario results in the desired adult sex ratio of males to females <1.00 , but the population is still expected to oscillate at $\sim 2,000$ individuals. In contrast, removal events targeting sexually mature females are expected to always have a positive effect on the long-term population fitness (λ) by increasing fertility rates. However, the total production of infants would decrease at periods of high female density due to very low fertility, or at periods of low female density due to a limited number of mature females available to give birth (Fig. 5). The analysis showed that 550 adult females (0.004 adults/m^2) is the critical size for maximum production of births by adult females. Therefore, the live capture and removal strategy with the most impact is the one that controls the number of adult females in the population (although young adults contributed also to population growth, such contribution is minimal as only $\sim 7\%$ gave birth). In order to approximate the population to stasis, the number of adult females should be maintained at <100 approximately so that the potential maximum number of annual births do not overcome that of annual deaths (89 monkeys die annually on average). Another strategy would be to maintain the number of adult females $>1,000$ so that density effects become stronger allowing a limited number of mature females to give birth (see Fig. 5). Understanding this 'paradox of removal' is critical for evaluating the effects of past and present removal schemes at Cayo Santiago.

Cayo Santiago has been harvested for population reduction since its establishment [Carpenter, 1972; Rawlins & Kessler 1986a]. Yet, even today, overpopulation still represents a threat to the colony's long-term viability. The accumulated knowledge on mechanisms of population regulation at Cayo Santiago can now be used to understand the effects of past removal events directed mostly to males and immature individuals. Removing a higher proportion of males will have negligible effects on female fertility and thus, on the population growth rate. A progressive reduction in the proportion of males to females is not expected to affect female fertility unless the number of males falls below the critical threshold level required to service available females [Caughley, 1980]. For rhesus monkeys, this threshold is expected to be low because they are a promiscuous species and because dominant males can monopolize receptive females. In fact, a ratio of 2 adult males for each group of 40 females in free ranging colonies, such as Cayo Santiago, was once considered optimal [Carpenter, 1972]. Also, removing immature individuals at infant or even at yearling stages could further enhance the availability and viability of the mother to reproduce during the next birth season by eliminating lactational amenorrhea and reducing the inter-birth interval [Johnson et al., 1993].

Alternate management strategies: control of female survival vs control of birth production

An important aim of the Cayo Santiago colony is to simulate, as much as possible, a wild habitat for collecting high-quality behavioral and biometric data for multiple scientific

fields. The management policy at Cayo Santiago since the early 1970s has prohibited invasive procedures on monkeys and there have been no attempts to suppress reproduction because of its confounding effects on the physiology and social behavior of these macaques. For instance, chemical fertility control through progestins [Porton & Dematteo 2005; Shek & Cheng, 2010] and physical fertility control such as ovariectomy [Glatston 1998] or endoscopic salpingectomy have been carried out successfully in primates [Shek & Cheng, 2010]. However, unwanted side-effects of hormone-mediated contraceptives such as diabetes mellitus, Cushing's diseases, osteoporosis, weight gain, increased aggression, as well as suppression of oestrus and proceptive behavior might develop among individuals [Glatston, 1998]. Permanent sterilization has also been associated with negative effects on social behavior and anxiety in macaques [Colemana et al., 2011]. The use of contraceptive vaccines developed for wildlife in monkeys is also controversial as the adjuvants currently used caused skin lesions and infections and the duration of contraception is variable [Dascanio et al., 2014]. Invasive sterilization procedures risk disrupting colony demographics via altered social and reproductive behavior, and health of the animals. Thus, managers at Cayo Santiago have opted for the removal of individuals as the primary means of population control.

The sensitivity analysis demonstrated that the functional dependence of λ on the survival of adult females, in contrast to that on their fertility, is highest for Cayo Santiago macaques. This indicates that the life cycle transition expected to contribute the most to future changes in population growth rate (λ) is the annual survival of adult females. Therefore, simulating a decrease in adult female survival by removal events is expected to be the most efficient method to decrease λ , in contrast to simulating a decrease in fertility with the use of contraception and sterilization methods. Our simulations indicate that nearly 80% of live adult females would have to be sterilized annually in order to significantly reduce the population density over the next decades (80% of adult females in 2012 = 291 individuals). Although this strategy might prove to be successful in other mammal populations [Todd et al., 2008], given the time and effort for trapping, physical contraceptive treatment, re-introduction to the social group, the risk of side-effects, the staff and budget needed, ongoing research and the conclusions of this model, removal of adult females is the best approach to population control on Cayo Santiago. Removing individuals would also allow Cayo Santiago to continue serving as a breeding colony for biomedical research and contribute to the overall sustainability of the Caribbean Primate Research Center.

Live trapping and removal activities can also have adverse effects on biological and behavioral aspects of the colony. Removal of individuals might lead to the extinction of unique genes and gene combinations [Sukumar, 1991; Willis & Wiese, 1993]. Trapping activities also alter mother-infant relationships by increasing the time the mothers are in contact with their offspring [Berman, 1989]. Moreover, reports on other populations of mammals have shown that eliminating individuals by hunting activities have no significant effect on population control as long as the quality of resources is kept constant [Caughley, 1980; Brown et al., 2000]. However, such effects could be reduced significantly as long as the removal of individuals is carried out by maximizing the balance among numbers of members of founding matriline or adding new founders to the population, the trapping activities are kept limited to a short period of the year, and food provisioning is administered

at a per capita rate to prevent a significant boost in the rate of increase of the population after a reduction in the number of individuals. Management at Cayo Santiago have proven to be efficient in ensuring genetic variability is maintained with no necessity of introducing new breeding stock (A. Widdig and others, manuscript), designating a period for trapping activities [Berman, 1989] and administrating commercial food according to population density [Rawlins and Kessler, 1986a].

This study is based solely on estimates of demographic parameters and do not take into account other practical constraints that might limit management practices such as those imposed by not disturbing ongoing behavioral research, lack of space for removed individuals at the SSFS or administrative factors [Rawlins, 1989]. Given that vital rates of the Cayo Santiago macaques have varied only slightly through diverse management programs in the past, confidence in our model is high. As long as the trapping and removal protocols are carried out in a way that related negative effects are kept to a minimum level, it seems to be the most effective and suitable management strategy for the long-term viability of Cayo Santiago as a multidisciplinary research facility.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Fig. 1. Population dynamics (solid line) and annual removal (dashed line) of Cayo Santiago's rhesus macaques from 1973 to 2012.

Fig. 2.
Density-dependent population projection with no removal.

Fig. 3.

Population projections under selective removal by age. Removal of 70 (black), 100 (blue), 130 (red), and 160 (green) individuals were carried out. Projections are presented with no removal (A), and with annual removal of infants (B), yearling (C), juveniles (D), young adults (E), and adults (F). For each quantity of removed animals, 50% were males and 50% were females.

Fig. 4. Population projection based on selective removal by sex. (A) removal of adult males and (B) removal of adult females. Removal of 70 (black), 100 (blue), 130 (red), and 160 (green) individuals were carried out. Note: Projections were carried out with a horizon of 23 years but only years with adults alive are presented.

Fig. 5.
Relationship among annual removal, fertility rate and number of births of adult females.

Table 1

Total number and proportion of individuals removed in Cayo Santiago from 2000–2012.

Year	Removals					
	Males		Females		Total	
	Total	%	Total	%	Total	%
2000	0	0.0	0	0.0	0	0.0
2001	111	15.5	61	7.6	172	11.3
2002	180	27.9	202	25	390	26.9
2003	57	10.6	59	8.6	116	9.5
2004	128	23.3	130	18.5	259	20.7
2005	67	13.9	39	6.1	106	9.5
2006	44	8.7	67	10.3	111	9.6
2007	52	9.7	50	7.7	102	8.6
2008	1	0.2	0	0.0	1	0.1
2009	103	15.4	87	11.3	190	13.2
2010	72	11.2	71	9.7	143	10.4
2011	52	8.3	30	4.1	82	6.0
2012	33	5.1	38	4.9	71	4.9

Note: a total of 10 individuals with no sex recorded were removed.

Table II
Age-specific total and proportion of individuals removed in Cayo Santiago from 2000–2012.

Age	Removals					
	Males			Females		
	Total	%	Total	%	Total	M:F ratio
0	68	4.7	61	3.9	129	4.2
1	287	19.9	197	14.4	484	17.1
2	367	30.1	323	28.2	690	28.9
3	59	5.6	63	6.3	122	7.5
4	25	6.0	16	2.3	41	4.5
5	9	2.5	13	3.1	22	2.8
6	12	4.2	13	3.2	25	3.5
7	9	3.8	21	5.9	30	4.8
8	11	5.2	9	2.7	20	3.5
9	4	2.1	15	5.7	19	3.9
10	13	6.0	17	4.8	30	6.8
11	10	7.0	18	5.9	28	7.2
12	4	8.2	8	9.6	12	3.4
13	5	5.1	14	7.0	19	5.9
14	2	1.9	10	5.0	12	4.2
15	1	1.5	8	4.3	9	3.7
16	2	2.8	10	5.6	12	6
17	3	3.3	9	5.9	12	6.2
18	2	2.9	5	4.9	7	4.8
19	0	0.0	2	3.8	2	1.5
20	4	6.5	2	2.6	6	5.3
21	3	9.6	0	0.0	3	3.6
						-

Note: a total of 10 individuals removed with no sex recorded are not included.

Table III

Mean projection matrix of Cayo Santiago's rhesus macaques from 2000–2012.

	I_m	Y_m	J_m	YA_m	A_m	I_f	Y_f	J_f	YA_f	A_f
2000–2012										
I_m	0	0	0	0	0	0	0	0	0.067	0.341
Y_m	0.877	0	0	0	0	0	0	0	0	0
J_m	0	0.917	0	0	0	0	0	0	0	0
YA_m	0	0	0.964	0	0	0	0	0	0	0
A_m	0	0	0	0.991	0.929	0	0	0	0	0
I_f	0	0	0	0	0	0	0	0	0.060	0.345
Y_f	0	0	0	0	0	0.881	0	0	0	0
J_f	0	0	0	0	0	0	0.920	0	0	0
YA_f	0	0	0	0	0	0	0	0.967	0	0
A_f	0	0	0	0	0	0	0	0	0.985	0.943
Q_x	0.123	0.083	0.036	0.009	0.071	0.12	0.080	0.033	0.015	0.057
N_x	1558	1451	1216	774	2574	1515	1381	1171	852	4405

Note: I , Y , J , YA , and A stand for infants, yearlings, juveniles, young adults, and adults. Subscript m stands for males and f stand for females (See METHODS).

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Table IV
Sensitivity and elasticity matrices for Cayo Santiago's rhesus macaque females from 2000–2012.

Sensitivity	I_f	Y_f	J_f	YA_f	A_f
I_f	0	0	0	0.055	0.309
Y_f	0.125	0	0	0	0
J_f	0	0.119	0	0	0
YA_f	0	0	0.114	0	0
A_f	0	0	0	0.108	0.607
Elasticity	I_f	Y_f	J_f	YA_f	A_f
I_f	0	0	0	0.003	0.095
Y_f	0.098	0	0	0	0
J_f	0	0.098	0	0	0
YA_f	0	0	0.098	0	0
A_f	0	0	0	0.095	0.512