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Research Article

Population Estimate and Management Options for Introduced Rhesus Macaques

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ABSTRACT Approximately 12 rhesus macaques (*Macaca mulatta*) were introduced to the forests along the Silver River, central Florida, USA, between 2 introductions in the 1930s and 1940s to increase tourism; this land is now Silver Springs State Park (SSSP). By the mid-1980s the population along the Silver River reached nearly 400 individuals. Approximately 1,000 animals were trapped and removed from 1984 to 2012 to reduce population growth and mitigate negative macaque-human interactions. This practice was halted due to extensive public controversy, and consequently no population management has been implemented since 2012. To aid in informing management decisions related to rhesus macaques, we estimated the fall 2015 population size within SSSP, developed an age-structured matrix model to estimate the population growth rate, and examined the efficacy of 4 management strategies to regulate this population, including culling (50% or 80% of subadults and adults) and sterilizing adult females (50% or 80% ≥3 years old). Our assessment suggested there were 176 macaques among 5 social groups within SSSP in fall 2015. We estimated this population was growing and will likely double in size by 2022 without management intervention. Management actions designed to eradicate the macaque population would be most effective by removing ≥50% of subadults and adults at least biennially. The population could be reduced to about a third of the fall 2015 size by sterilizing ≥50% of adult females annually or ≥80% biennially. The rhesus macaque population extends outside of our study site, and thus our results are a proxy for management implications in the region. Managers tasked with rhesus macaque management must carefully weigh the trade-offs of these options in future management of this charismatic, invasive species. © 2018 The Wildlife Society.

KEY WORDS culling, Florida, invasive, *Macaca mulatta*, matrix model, primate, rhesus macaque, sterilization.

Humans have intentionally or unintentionally relocated non-human primates (i.e., primates) to novel habitats for ≥5 centuries (Long 2003). Rhesus macaques (*Macaca mulatta*) are successful invaders when introduced into novel habitats in the United States. Introduced rhesus macaques on Desecheo Island National Wildlife Refuge, Puerto Rico, decimated bird populations through nest predation (Evans 1989). Rhesus macaques and patas monkeys (*Erythrocebus patas*) unintentionally released in southwest Puerto Rico caused millions of dollars in crop losses and management costs (Engeman et al. 2010). A population of rhesus macaques raised on Morgan Island, South Carolina, USA, for biomedical research caused increased levels of fecal coliform bacteria and *Escherichia coli* in surrounding tidal creeks (Klopchin et al. 2008). Rhesus macaques raised on Key Lois and Raccoon Key in the Florida Keys, USA, from the 1970s to 2000 caused extensive environmental damage to the islands, including the destruction of ≥0.12 km^2 of red mangroves (*Rhizophora mangle*; Kruer 1996).

The ability of rhesus macaques to thrive in novel environments is likely due to their plasticity in habitat requirements. This species has the largest native range of any non-human primate (Southwick et al. 1996), spanning elevations from sea level to 4,000 m (Fooden 2000). They are arboreal and terrestrial. They forage primarily on plants and supplement their diet with small vertebrates, invertebrates, eggs, and honeycomb (Fooden 2000). Rhesus macaques live

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in social groups consisting of adult females and her offspring, an adult alpha male, and subordinate adult males. Females remain with their natal groups their entire lives. Most males leave their natal group after reaching sexual maturity, then live independently or in bachelor groups until they join a new group (Maestripieri and Hoffman 2012).

Rhesus macaques thrive in human-dominated landscapes (Richard et al. 1989) and select disturbed habitats (Goldstein and Richard 1989); this has led to overpopulation in human-dominated landscapes throughout their native range (Fooden 2000, Wellem 2014). In urban and suburban areas in their native range throughout central and southern Asia, rhesus macaques receive provisional food from human feeding, raiding trash bins, and crop raiding. Provisional food provided from humans is usually calorically rich and more abundant and reliable, and requires less energy expense when compared to natural foods (Sengupta et al. 2015). Consequently, average group size of provisioned rhesus macaque populations is larger (76.9) than non-provisioned groups (32.3; Fooden 2000). Similarly, population densities are 5 times larger on average in human-dominated habitats (201.1/km^2) than forested habitats (37.2/km^2; Fooden 2000).

Increased population growth and density of rhesus macaques and humans have increased interactions and conflict between these species. In native and introduced rhesus macaque populations, population control efforts include trapping and removal (Southwick et al. 1980, Malik et al. 1984), lethal culling (Wang and Quan 1986, Saraswat et al. 2015, López-Ortiz 2016), and sterilization (Wellem 2014, OPCF 2016). Variation in anthropogenic sentiment towards this species complicates and influences management strategies. Human-macaque conflict (e.g., crop-raiding, aggression) is not uncommon, yet this species is also considered sacred to many humans in parts of its native range (Pirta et al. 1997, Radhakrishna et al. 2013, Saraswat et al. 2015). Consequently, rhesus macaque populations surrounding these locations, such as Hindu temples, are among the largest and densest in the world (Fooden 2000, Radhakrishna et al. 2013).

Rhesus macaques were introduced in the 1930s into Silver Springs, a tourist attraction in central Florida, to increase tourism. This area was purchased by the state of Florida in 1985 and became Silver Springs State Park (SSSP; Florida Department of Environmental Protection [FL DEP] 2014). The original rhesus macaque introduction included approximately 6 individuals released on an island in the Silver River. Rhesus macaques are proficient swimmers, which allowed the animals to swim across the Silver River and establish on the river banks. Approximately 6 additional macaques were released around 1948 (Wolfe and Peters 1987, Hammond 1989). By 1968 the population was estimated at 78 individuals between 2 groups (Maples et al. 1976), and by the 1970s had expanded to natural areas beyond the Silver River (Montague et al. 1994). The macaque population grew to >150 individuals along the Silver River by 1979 (Sarris 1980) and reached almost 400 individuals by 1984 (Wolfe and Peters 1987, Wolfe 2002).

Managers of this park have previously attempted population control of introduced rhesus macaques through trapping and removal, but the lack of public support has repeatedly terminated this practice. Beginning in the mid-1980s, negative human-macaque interactions in Florida were increasingly of concern to natural resource managers. Of concern was the risk of exposure of park visitors and staff to the zoonotic herpes B virus carried by macaques and present in the population in Florida (Montague et al. 1994, Wisely et al. 2018). Although transmission of this virus from macaques to humans is extremely rare, it can be fatal (Huff and Barry 2003, Jones-Engel et al. 2006). Concurrently, ecological effects from rhesus macaques, including potential depredation of bird nests (Montague et al. 1994), was also of increasing concern to natural resource managers. In 1984, approximately 225 rhesus macaques were removed from the Silver Springs area and sold to a biomedical research supply company to reduce macaque density and related interactions with people and negative ecosystem effects. The public demonstrated extensive negative feedback over the removal of the rhesus macaques, which led to the elimination of the removal program (Wolfe 2002). Over the next decade, additional animals were removed through lawful and unlawful efforts, with removals approaching 500 individuals in 1984–1993 (Wolfe 2002). From 1998 to 2012, an estimated 832 rhesus macaques were trapped and removed from SSSP and adjacent lands, approximately 630 of which were from SSSP (Anderson et al. 2017*b*). These animals were also sold into the biomedical research industry. Again, this incited controversy and protest from animal rights groups, leading to termination of the removal effort. Although public sentiment against culling was strong, a 2012 online petition calling for a sterilization program in lieu of a trapping program for the SSSP rhesus macaques received nearly 2,000 signatures (Anderson 2016). Riley and Wade (2016) estimated the spring 2013 SSSP rhesus macaque population, prior to the end of birthing season, included 118 individuals (111 among 4 groups and 7 peripheral males).

Management of charismatic invasive species is difficult and controversial (Verbrugge et al. 2013). Given the potential ecological (Anderson et al. 2016) and human health (Wisely et al. 2018) consequences of this population, we aimed to assess the status of the rhesus macaque population in SSSP and develop a modeling tool to inform population control efforts. We began by estimating the rhesus macaque population size in SSSP in fall 2015. We then used an age-structured matrix population model to explore the efficacy of management options to reduce the population size.

STUDY AREA

The 19-km^2 SSSP is situated along the Silver River, a spring-fed river that flows east into the Ocklawaha River (Fig. 1). The park contains 21 natural communities (Florida Natural Areas Inventory 2016) and provides habitat for 18 endemic and 10 endangered plant species (Hubbard and Judd 2013). The lands along the Silver River are floodplain swamp with canopies dominated by bald cypress (*Taxodium*

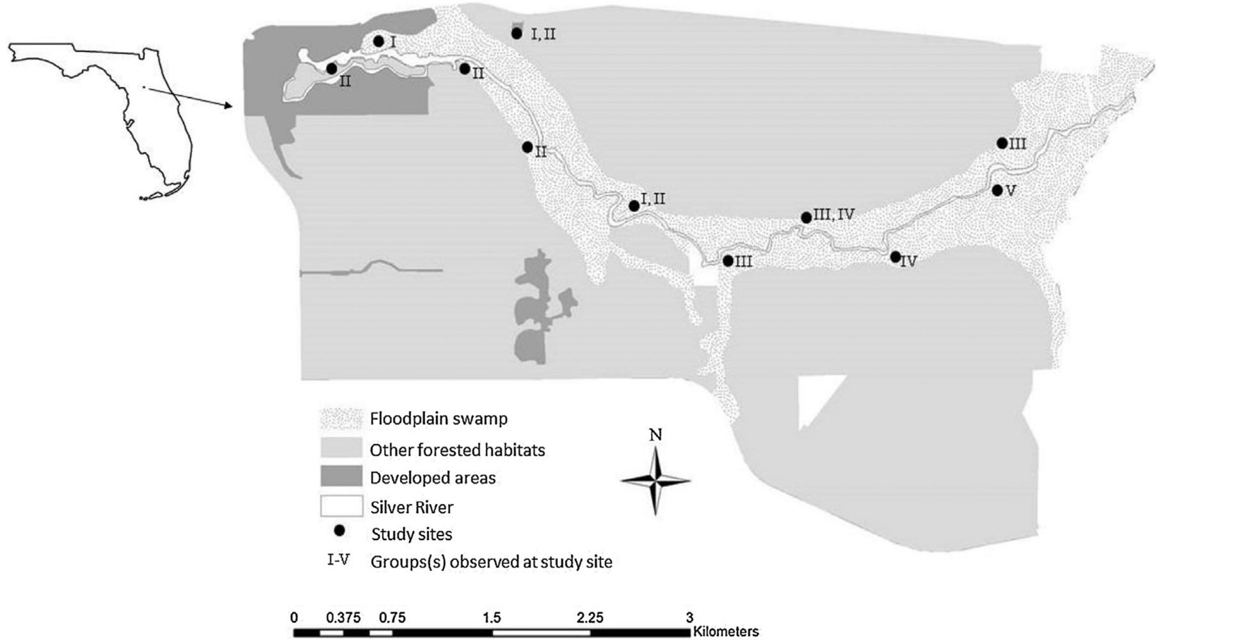

Figure 1. Locations of camera-trap stations used to estimate rhesus macaque population size in Silver Springs State Park, Florida, USA, September–November 2015.

distichum) and including pop ash (*Fraxinus caroliniana*), sabal palm (*Sabal palmetto*), red maple (*Acer rubrum*), water hickory (*Carya aquatica*), sugarberry (*Celtis laevigata*), sweetgum (*Liquidambar styraciflua*), sweetbay (*Magnolia virginiana*), and American elm (*Ulmus americana*). The floodplain swamp is predominantly surrounded by upland hardwood forest, comprised of oaks (*Quercus* spp.), hickories (*Cary* spp.), sabal palms, and pines (*Pinus* spp.), including pignut hickory (*Carya glabra*), sugarberry, sweetgum, sweetbay, loblolly pine (*Pinus taeda*), Shumard oak (*Quercus shumardii*), southern live oak (*Quercus virginiana*), sabal palm, and live oak (*Quercus hemisphaerica*; Hubbard and Judd 2013). Classified as subtropical climate (Chen and Chen 2013), November–May includes a cool, dry season that is typically sunny and clear but occasionally includes rainfall and frost. January daily temperatures range from 7°C to 24°C with an average precipitation of approximately 9 cm (Hubbard 2008). June–October marks a hot and humid season, with nearly daily thunderstorms. August daily temperatures typically range from 24°C to 35°C with average precipitation of 15 cm (Hubbard 2008). Elevation within the park ranges from 0.014 km to 0.023 km above sea level; throughout most of the park, the relatively flat uplands slope down to the floodplain along the Silver River (FL DEP 2014).

The lands around the Silver River have been managed as a tourist attraction since the 1870s. The area around the headspring on the northwestern corner of the property is developed for management and tourist use including several buildings, large parking lots, a restaurant, a public canoe and kayak launch, a dock for glass-bottom boat tours, and a waterpark (FL DEP 2014; Fig. 1). The lands along the Silver River in the central and western portions of the property are managed as native forests and public access is largely restricted (FL DEP 2014; Fig. 1). In 2012–2013 the park attracted 243,080 visitors, provided 179 jobs, and was estimated to contribute \$11 million in direct economic input (FL DEP 2014).

METHODS

Population Estimate

We collected data on the rhesus macaque population size within SSSP from 27 September to 14 November 2015. We identified rhesus macaque groups by the number of individuals, age and sex composition, location, and individuals with unique physical features (e.g., visible injuries, scars, unique facial compositions; Hasan et al. 2013, Jaman and Huffman 2013), following a research protocol approved by the University of Florida Animal Ethics Committee (Institutional Animal Care and Use Committee protocol number 201308022). Data collection was approved by the Florida Department of Environmental Protection (permit number 01281413).

The 2 groups of rhesus macaques (i.e., groups I, II) nearest the headspring of the Silver River were habituated to human presence on land because of their proximity to the developed tourist portion of the park. These animals were not fearful of humans approaching them. This allowed us to conduct point count censuses of these 2 groups (Seth and Seth 1983, Imam and Ahmad 2013, Jaman and Huffman 2013) using bait spread in open, grassy areas to attract the macaques. We differentiated groups I and II by spatial separation, individuals with unique characteristics (e.g., scars), and age and sex composition. We counted individuals in 4 age and sex classes: adult males, adult females, subadults, and infants (Southwick et al. 1980, Johnson et al. 1988). We repeated counts with these groups until 2 observers independently counted the same number of individuals $\geq$3 times.

The 3 groups in the central and eastern portions of SSSP (i.e., groups III, IV, V) were not habituated to humans on land because they do not come into contact with the developed, tourist areas of the property. These animals fled the area when we approached them, which prohibited us from conducting point counts with these groups. Thus, we used camera traps to estimate the size of these groups. Camera traps provide an efficient mechanism for studying unhabituated, terrestrial primates (Gerber et al. 2014, Li et al. 2015). We placed 11 camera-trap stations in the floodplain swamp, 5 on the north bank and 6 on the south bank, with approximately 1 km between each station (Fig. 1). We selected the floodplain swamp because rhesus macaques have been observed selecting this habitat during the cool, dry season (Anderson et al. 2017*a*). Each camera-trap station had 4 camera traps facing in opposing directions, with a minimum of 15 m between each.

We placed corn in front of each camera daily to attract the rhesus macaques, either by hand or via automatic dispensers in remote locations that were not accessible daily. We used the camera-trap data to count the number of individuals in the 4 age and sex classes during each minute the rhesus macaques were present in the station. Double-counting of individuals was prevented by the synchronized time stamps of the camera traps and by the distance between the camera traps. Although rhesus macaque groups forage collectively, this method did not allow us to observe every individual in the group simultaneously. We estimated minimum group size as the largest number of individuals simultaneously observed within each respective age and sex class. Sex could not be distinguished in the infant or subadult age classes using the cameras and we assumed it was a 1:1 ratio (Berman 1988, Bercovitch et al. 2000).

We placed 3 camera-trap locations within the range of group 1 as identified by Anderson et al. (2017*a*) and followed identical protocols to those in other parts of the study area. Two of these locations were found to also be within the home range of group II (Fig. 1), although the 2 groups only occurred in the same location simultaneously on 1 occasion during the study period. Groups I and II were easily identified via camera-trap data (based on identifying characteristics) because we had spent substantial time conducting point censuses with these groups. Using camera-trap data, we counted the number of individuals in these groups by the 4 age and sex classes, as we had with groups III, IV, and V. We compared our census data of groups I and II to the counts per age and sex class via the camera-trap data to determine detection probability (Gerber et al. 2014, Mackenzie et al. 2003) of the camera-trap method. We calculated detection probability as the proportion of the number of individuals in each age and sex class observed from the camera-trap data divided by the known number of individuals in each age and sex class from the census data (Rowcliffe et al. 2008). We then used the detection probability to estimate the number of individuals in groups III, IV, and V based on minimum group size observed from the camera-trap data (Table S1, available online in Supporting Information). We calculated the proportion of individuals in each age class. We calculated fertility (F_x) as the ratio of infants to adult females (Wolfe and Peters 1987, Hernández-Pacheco et al. 2013, Tian et al. 2013).

Model Design

We used an age-structured matrix population model to estimate future population growth of rhesus macaques in SSSP using discrete, annual time steps (Caswell 2001, Hernández-Pacheco et al. 2013, Hernández-Pacheco et al. 2016). These models incorporate F_x and survivorship (P_x) by age class to project future population size. Because female rhesus macaques are promiscuous (Wolfe 2002, Maestripieri and Hoffman 2012), reproductive success is not limited by adult males (Rawlins and Kessler 1986, Hernández-Pacheco et al. 2013). We, therefore, created the matrix model based only on females within the population (Hernández-Pacheco et al. 2013).

We classified infants as <1 year old; we assumed equal sex ratio of infants (Berman 1988, Bercovitch et al. 2000) and that infant survival did not vary by sex (Hoffman et al. 2010). We categorized subadults as 1- and 2-year-olds; we therefore assumed half of surviving subadults would become adults each year (Malik et al. 1984; Fig. S1, available online in Supporting Information). Although 3-year-olds are sometimes considered subadults (Southwick and Siddiqi 1977, Johnson et al. 1988), the average age at first birth for female rhesus macaques is 4 (Drickhamer 1974, Tian et al. 2013). We conducted our 2015 population estimate during fall, which is the breeding period of rhesus macaques in SSSP (Hammond 1989), and conducted our population models with annual timespans with respective estimates in fall. Because most females are sexually mature during the breeding season of their third year (Bercovitch and Harvey 2004), adult females were those ≥3 years old. We identified adults through body size and reddening of the of the facial and anogenital skin, which is prominent during the breeding season (Maestripieri 2010). The initial population size within the models was based on the fall 2015 population estimate, with the number of female infants and subadults estimated as half of the number of individuals in these age classes (because we assumed equal sex ratio in these age classes), and the total estimated number of adult females. We multiplied the estimated F_x by 0.5 to include only female offspring (F_f; Hernández-Pacheco et al. 2013, Tian et al. 2013). Because the population was below potential carrying capacity, the model did not consider density dependence (Crockett et al. 1996, Hernández-Pacheco et al. 2016). We conducted all simulations using the popbio package (Stubben and Milligan 2007) in R (version 3.2.5, www.r-project.org, accessed 15 June 2016; code available in Appendix A, available online in Supporting Information).

Model Parameterization

Because survival by age class is unknown in SSSP, we used survivorship rates from published studies of other rhesus macaque populations in our models (Crockett et al. 1996). Two of the studies derived age-specific survivorship from growing populations (Jiang et al. 1998, Hernández-Pacheco et al. 2013), and 2 from stable populations (Southwick et al. 1980, Johnson et al. 1988; Table S2, available online in

Supporting Information). We used the reported age-specific survival rates from each study to predict how long it will take the SSSP population to reach 400 individuals, the population size that incited management efforts in the mid-1980s (Fig. S2, available online in Supporting Information). *A posteriori* observations indicated the models projected population growth using survival rates reported by Hernández-Pacheco et al. (2013; annual population growth rate [λ] = 1.105) and Jiang et al. (1998; $\lambda = 1.153$), and population size was projected to slightly decrease using the survival rates reported by Johnson et al. (1988; $\lambda = 0.969$) and Southwick et al. (1980; $\lambda = 0.936$). The SSSP rhesus macaque population estimates in 1968 ($N = 78$) and 1984 ($N = 400$) suggest λ during this period was approximately 11%. The annual growth rate using the survivorship rates from Hernández-Pacheco et al. (2013) was the closest to previous population growth in SSSP; therefore, we selected this growth rate for further analyses.

Using the popbio package, we calculated sensitivity and elasticity of the model to compare how these parameters influenced λ (Caswell 1978, de Kroon et al. 2000, van de Kerk 2009). Using the survivorship rates from Hernández-Pacheco et al. (2013), we modeled future population size under 4 management scenarios: culling 50% of subadults and adults, culling 80% of subadults and adults, sterilizing 50% of sexually mature females ($\geq$3 yrs old), and sterilizing 80% of sexually mature females ($\geq$3 yrs old). Because the efficacy of management strategies can be influenced by the timing and frequency of implementation (Abrams 2009, Wells et al. 2016), we modeled the 4 management scenarios implemented at 4 timescales: annually, biennially, every 5 years, and every 10 years (code provided in Appendix A).

We estimated the number of individuals in the population at each time based on the predicted number of females (from the models) and the predicted female:male ratio. Because we assumed infants and subadults had a 1:1 sex ratio, we doubled our values from the female-only models. *Post hoc* observations suggested the adult male to adult female ratio was 1:2.3. Therefore, for every adult female projected to be in the population at a given time, we estimated there would be 0.43 adult males. We did not predict population size beyond 400 because the carrying capacity of rhesus macaques in SSSP is unknown.

RESULTS

There were 81 macaques between groups I and II (Table 1). From the camera-trap data, we were able to detect 60 macaques between these 2 groups. Detection probability varied by age and sex class: 83% for adult males and females, 54% for subadults, and 100% for infants (Table 1). Using the camera traps, we observed 78 individuals among groups III–V (Table 2). After accounting for detection bias, we estimated there were 95 individuals among the 3 groups (Table S1). Overall, we estimated 176 individuals among the 5 groups (Table S1).

Sensitivity and elasticity analyses indicated adult survivorship (S_a) was more than twice as influential on λ than any other parameter (Fig. 2). The female population was

Table 1. Number of rhesus macaques observed in 2 habituated groups in Silver Springs State Park, Florida, USA, by census and camera trapping, 2015.

	Adult males			Adult females			Subadults			Infants		
	Census	Observed via camera traps	Detection probability	Census	Observed via camera traps	Detection probability	Census	Observed via camera traps	Detection probability	Census	Observed via camera traps	Detection probability
Group I	6	4	0.67	13	10	0.77	18	9	0.50	12	12	1
Group II	2	2	1.00	10	9	0.90	14	8	0.57	6	6	1
Average detection probability			0.83			0.83			0.54			1

Table 2. Minimum number of animals observed via camera traps and estimated total number of animals using observed age-specific detection probability of 3 unhabituated groups of rhesus macaques in Silver Springs State Park, Florida, USA, 2015.

	Adult males		Adult females		Subadults		Infants	
	Observed via camera traps	Estimated via detection probability	Observed via camera traps	Estimated via detection probability	Observed via camera traps	Estimated via detection probability	Observed via camera traps	Estimated via detection probability
Group III	5	6	8	9	6	9	7	7
Group IV	5	6	11	13	14	21	10	10
Group V	2	2	4	5	2	3	4	4
Total	12	14	23	27	22	33	21	21

projected to reach extinction by 2019 if 80% of subadults and adults were culled annually and by 2024 if 50% of subadults and adults were culled annually (Fig. 3). The population was projected to reach extinction by 2022 if 80% of the animals were culled biennially and by 2032 if 50% of the population was culled biennially (Fig. 3). No other culling models reached extinction by 2035, although the population was estimated to be near extinction in 2031 if 80% of adult females were culled every 5 years (Fig. 3).

Sterilizing adult females was never projected to lead to extinction. Sterilizing 50% or 80% of adult females annually decreased the population size to less than a third of the 2015 size by 2035. Biennial sterilization of 80% of adult females yielded similar results to annual sterilization of 50% of adult females. Sterilizing 80% of female adults every 5 years was projected to stabilize the population. Sterilizing 50% of adult females less frequently than every other year was projected to allow continued population growth; similarly, sterilizing 80% of adult females every 10 years projected population growth (Fig. 3).

DISCUSSION

The estimated age and sex composition of the rhesus macaque population in SSSP was similar to native populations in Asia. The 1:2.3 ratio of adult male to female rhesus macaques was similar to numbers reported in native populations in India (Makwana 1978, Seth and Seth 1983) and previous reports of the SSSP population (Wolfe and Peters 1987). Sexually immature individuals comprised 59% of the population, consistent with native populations undergoing population growth (Southwick et al. 1980). Fertility, the proportion of infants to adult females, was estimated to be 78%; this was consistent with rhesus macaque populations in tropical and subtropical climates (Southwick et al. 1996) and a previously reported fertility rate in SSSP by Wolfe and Peters (1987; 81%).

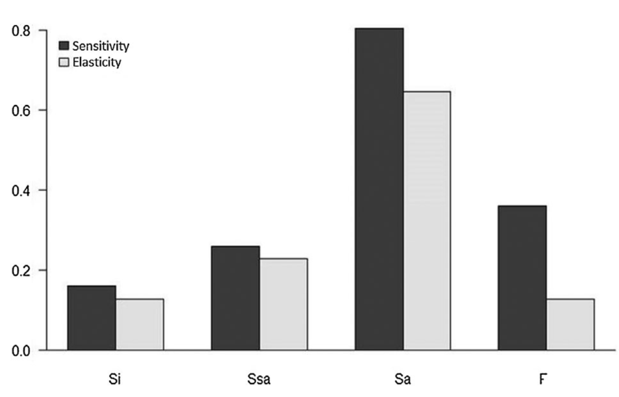

Figure 2. Sensitivity and elasticity measurements of infant survival (Si), subadult survival (Ssa), adult survival (Sa), and fertility (F) of the introduced population of rhesus macaques in Silver Springs State Park, Florida, USA, based on a population estimate from September to November 2015.

Compared to native and other introduced rhesus macaque populations, the 2015 population density and number of groups of rhesus macaques in SSSP was relatively small (Fooden 2000). However, the estimated growth rate from our study ($\lambda = 1.105$) suggests the number of animals within SSSP will approach 400 individuals, the size previously deemed problematic, by the year 2023 without management intervention. Increased density of rhesus macaques in SSSP will likely exacerbate environmental (Anderson et al. 2016) and human health (Wisely et al. 2018) threats of this population. The management plan for SSSP includes the removal of non-native species (FL DEP 2014). Our model suggests eradication may be possible through culling, and population maintenance or reduction is possible through sterilization. The models in this study do not account for sources of variation such as environmental, demographic, or genetic stochasticity, and consequently cannot precisely predict future population sizes (van de Kerk 2009). Further, the number and size of rhesus macaque groups in natural areas adjacent to SSSP is unknown, and therefore the regional population size of rhesus macaques is unknown. Reduction or management of the larger rhesus macaque population would require a better understanding of the number, size, and extent of macaque groups outside of SSSP and coordinated efforts among land managers. Thus, projections from our study are a proxy for management implications for macaques in the region. Further, they can be used by managers to compare tradeoffs between different management strategies as a guideline for decision-making.

Our models indicate the most efficient management action to reduce population size is culling. Prior to a 1978 ban of primate exports, the rhesus macaque population in India dwindled in response to the trapping and removal of animals for sale into the research industry (Malik et al. 1984, Malik 1989); however, the population rebounded quickly after the trapping ban (Southwick et al. 1986, Malik 1989). An introduced population of Japanese macaques (*Macaca fuscata*) in Texas was trapped and moved into a fenced enclosure (Born Free USA Primate Sanctuary 2017), which eliminated a free-ranging and problematic population (Feild et al.

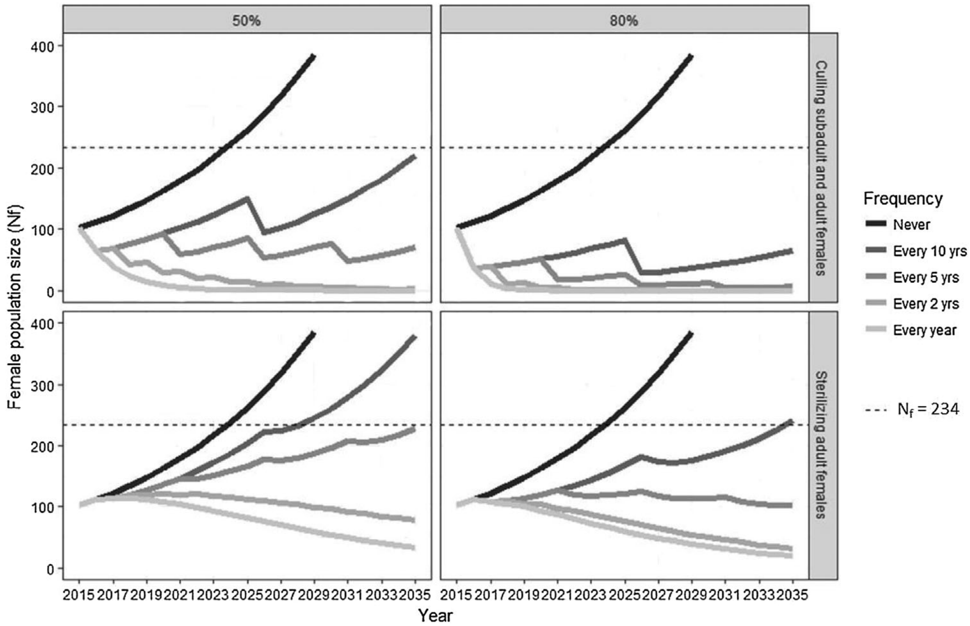

Figure 3. Projected female rhesus macaque population size in Silver Springs State Park, Florida, USA, from 2015 to 2035, using survivorship rates reported in Hernández-Pacheco et al. (2013), under 4 management scenarios: culling 50% of subadult and adult females, culling 80% of subadult and adult females, sterilizing 50% of adult females ($\geq$3 yrs old), and sterilizing 80% of adult females. We provide projections for each scenario implemented at 4 levels of frequency: annually, biennially, every 5 years, every 10 years. We note the point at which the female population (N_f) reaches 234 individuals because this is where total population reaches 400 and carrying capacity beyond this population size is unknown.

1997). Our sensitivity and elasticity analyses indicated subadult survivorship was far less influential on population growth rates than adult survivorship. This is important to consider in any culling program because trapping is typically most successful among subadults owing to trap naivety (Hernández-Pacheco et al. 2016). Our results indicate a culling program would need to remove adult female macaques to hinder or halt population growth. For adult animals, to ensure a removal program is effective, culling via euthanasia may be necessary if traps are avoided. A culling program was implemented for the invasive rhesus macaque and patas monkey populations in Puerto Rico in 2009, and by 2016 both populations were nearly eradicated (R. López-Ortiz, Puerto Rico Department of Natural and Environmental Resource, personal communication).

We cannot state with certainty the population of rhesus macaques in SSSP can be eradicated because our model assumed the population was closed to immigration. If managers successfully removed the current groups of rhesus macaques from SSSP, it is possible the population within SSSP could be restored via immigration from surrounding rhesus macaque groups (Early Detection & Distribution Mapping System 2017). The current size and distribution of rhesus macaques in natural areas adjacent to SSSP is unknown, and the likelihood of immigration cannot be predicted. Maintaining, or reducing, the current population size of rhesus macaques in SSSP without fully eliminating it may prevent rhesus macaques from surrounding areas from immigrating into SSSP, either through aggression or lack of resource availability due to the occupant rhesus macaques (Ciani 1986, Fooden 2000). This could potentially afford researchers and managers additional time to evaluate these surrounding groups and determine effective management strategies for the region.

Maintaining or reducing the current population size of introduced rhesus macaques could be accomplished through sterilization. At least 3 options are available for female contraception. Females in SSSP were previously sterilized via hysterectomy (Hammond 1989); although effective, this invasive procedure cannot be conducted in the field and requires a monitored recovery period. A sterilization program began in Hong Kong in 1998, representing the first large-scale macaque sterilization program (Wellem 2014). Females were initially injected with Spray Vac™, an immuno-contraceptive vaccine; despite initial success in field trials (Wong and Chow 2004), it had limited long-term effectiveness with the macaque population in Hong Kong (K. Martelli, Ocean Park Conservation Foundation [OPCF], personal communication). Since 2009, managers in Hong Kong have used an endoscopic tubectomy procedure to sterilize adult females and vasectomize males (Wellem 2014, OPCF 2016). This program reduced the fertility rate from over 60% in 2009 to less than 30% in 2015 (OPCF 2016).

Reported annual growth rates for increasing rhesus macaque populations range from 3.8% to 26.9% (Fooden 2000). Rhesus macaque populations demonstrate density-dependent biosocial mechanisms of population control. Southwick et al. (1980) suggest this is typically through reduced natality or increased mortality among subadults and adults. The SSSP rhesus macaque population size reached approximately 400 in the mid-1980s, but the potential carrying capacity of this population, or the point at which the population will begin demonstrating density-dependent population regulating mechanisms, is unknown. This study and historical population estimates indicate this population is capable of extensive growth, which may lead to expansion into other areas. Therefore, the growth of the SSSP population is not only of concern within SSSP but rather throughout central Florida.

MANAGEMENT IMPLICATIONS

Our models suggest culling would reduce the rhesus macaque population in Silver Springs State Park, Florida, more quickly and be far more likely to lead to eradication than sterilization. If managers prioritize complete removal of the population, culling via trapping and removal or euthanasia may be viable options. If managers prioritize stabilizing the population or slowing growth, sterilization may be an effective strategy.

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LITERATURE CITED

Abrams, P. A. 2009. When does greater mortality increase population size? The long history and diverse mechanisms underlying the hydra effect. Ecology Letters 12:462–474.

Anderson, C. J. 2016. Ecology and impacts of introduce non-human primate pouplations in Florida. Dissertation, University of Florida, Gainesville, USA.

Anderson, C. J., D. J. Heard, M. A. Andreau, M. E. Hostetler, and S. A. Johnson. 2017*a*. Winter home range and habitat selection of an introduced rhesus macaque group (*Macaca mulatta*) in Silver Springs State Park. Florida Scientist 80(4):159–164.

Anderson, C. J., M. E. Hostetler, and S. A. Johnson. 2017*b*. History and status of introduced non-human primate populations in Florida. Southeastern Naturalist 16(1):19–36.

Anderson, C. J., M. E. Hostetler, K. E. Sieving, and S. A. Johnson. 2016. Predation of artificial nests by introduced rhesus macaques (*Macaca mulatta*) in Florida, USA. Biological Invasions 18:2783–2789.

Bercovitch, F. B., and N. E. Harvey. 2004. Reproductive life history. Pages 61–80 *in* B. Thierry, M. Singh, and W. Kaumanns, editors. Macaque societies: a model for the study of social organization. Cambridge University Press, Cambridge, United Kingdom.

Bercovitch, F. B., A. Widdig, and P. Nürnberg. 2000. Maternal investment in rhesus macaques (*Macaca mulatta*): reproductive costs and consequences of raising sons. Behavioral Ecology and Sociobiology 48:1–11.

Berman, C. M. 1988. Maternal condition and offspring sex ratio in a group of free-ranging rhesus monkeys: an eleven-year study. American Naturalist 131:307–328.

Born Free Primate Sanctuary. 2017. History of the sanctuary. <http://www.bornfreeusa.org/sanctuary/b2_history.php>. Accessed 22 Oct 2017.

Caswell, H. 1978. A general formula for the sensitivity of population growth rate to changes in life history parameters. Theorectical Population Biology 14:215–230.

Caswell, H. 2001. Matrix population models. Sinauer Associates, Sunderland, Massachusetts, USA.

Chen, D., and H. W. Chen. 2013. Using the Köppen classification to quantify climate variation and change: an example for 1901–2010. Environmental Development 6:69–79.

Ciani, A. 1986. Intertroop agnostic behavior of a feral rhesus macaque troop ranging in town and forest areas in India. Aggressive Behavior 12:433–439.

Crockett, C. M., R. C. Kyes, and D. Sajuthi. 1996. Modeling managed monkey populations: sustainable harvest of longtailed macaques on a natural habitat island. American Journal of Primatology 40:343–360.

de Kroon, H., J. M. van Groenendael, and J. Ehrlen. 2000. Elasticities: a review of methods and model limitations. Ecology 81:607–618.

Drickhamer, L. C. 1974. A ten-year summary of reproductive data for free-ranging *Macaca mulatta*. Folia Primatologica 21:61–80.

Early Detection & Distribution Mapping System. 2017. Rhesus monkey. The University of Georgia—Center for Invasive Species and Ecosystem Health. <https://www.eddmaps.org/distribution/viewmap.cfm?sub=18336>. Accessed 13 Sep 2016.

Engeman, R. M., J. E. Laborde, B. U. Constantin, S. A. Shwiff, P. Hall, A. Duffiney, and F. Luciano. 2010. The economic impacts to commercial farms from invasive monkeys in Puerto Rico. Crop Protection 29:401–405.

Evans, M. A. 1989. Ecology and removal of introduced rhesus monkeys: Desecheo Island National Wildlife Refuge, Puerto Rico. Puerto Rico Health Sciences Journal 8(1):139–156.

Feild, J. G., S. E. Henke, and J. G. McCoy. 1997. Depredation on artificial ground nests by Japanese macaques: the unspoken exotic in Texas. Pages 151–155 *in* C. D. Lee and S. E. Hygnstrom, editors. Great Plains Wildlife Damage Control Workshop Proceedings. Kansas State University Agricultural Experiment Station and Cooperative Extension Service, Manhattan, USA.

Florida Department of Environmental Protection [FL DEP]. 2014. Silver Springs State Park Draft Unit Management Plan Amendment. <https://floridadep.gov/sites/default/files/SilverSprings_2014_ApprovedPlan%26Amendment.pdf>. Accessed 13 september 2016.

Florida Natural Areas Inventory. 2010. Guide to the natural communities of Florida. <http://fnai.org/PDF/FNAI-Natural-Community-Classification-Guide-2010_20150218.pdf>. Accessed 13 Sep 2016.

Fooden, J. 2000. Systematic review of the rhesus macaque, *Macaca mulatta* (Zimmermann, 1780). Field Museum of Natural History, Chicago, Illinois, USA.

Gerber, B. D., P. J. Williams, and L. L. Bailey. 2014. Primates and cameras. International Journal of Primatology 841–858.

Goldstein, S. J., and A. F. Richard. 1989. Ecology of rhesus macaques (*Macaca mulatta*) in northwest Pakistan. International Journal of Primatology 10:531–567.

Hammond, J. 1989. A comparison of the social and sexual behavior of sterilized and nonsterilized females in a troop of free-ranging rhesus monkeys (*Macaca mulatta*) at Silver Springs, Florida. Thesis, University of Florida, Gainesville, USA.

Hasan, M. K., M. A. Aziz, S. M. R. Alam, Y. Kawamoto, L. Jones-Engel, R. C. Kyes, S. Akhtar, S. Begum, and M. M. Feeroz. 2013. Population variation in group size and composition distribution of rhesus macaques (*Macaca mulatta*) in Bangladesh: inter-population variation in group size and composition. Primate Conservation 26:125–132.

Hernández-Pacheco, R., D. L. Delgado, R. G. Rawlins, M. J. Kessler, A. V. Ruiz-Lambides, E. Maldonado, and A. M. Sabat. 2016. Managing the Cayo Santiago rhesus macaque population: the role of density. American Journal of Primatology 78:167–181.

Hernández-Pacheco, R., R. G. Rawlins, M. J. Kessler, L. E. Williams, T. M. Ruiz-Maldonado, J. González-Martínez, A. V. Ruiz-Lambides, and A. M. Sabat. 2013. Demographic variability and density-dependent dynamics of a free-ranging rhesus macaque population. American Journal of Primatology 75:1152–1164.

Hoffman, C. L., J. P. Higham, A. Mas-Rivera, J. E. Ayala, and D. Maestripieri. 2010. Terminal investment and senescence in rhesus macaques (*Macaca mulatta*) on Cayo Santiago. Behavioral Ecology 21:972–978.

Hubbard, J. R. 2008. Floristics and community analysis of Silver River State Park Marion county, Florida. Thesis, University of Florida, Gainesville, USA.

Hubbard, J. R., and W. S. Judd. 2013. Florisitics of Silver River State Park, Marion County, Floirda. Rhodora 115:250–280.

Huff, J., and P. Barry. 2003. B-virus (*Cercopithecine herpesvirus 1*) infection in humans and macaques: potential for zoonotic disease. Emerging Infectious Diseases 9:246–250.

Imam, E., and A. Ahmad. 2013. Population status of rhesus monkey (*Macaca mulatta*) and their menace: a threat for future conservation. International Journal of Environmental Sciences 3:1279–1289.

Jaman, M. F., and M. A. Huffman. 2013. The effect of urban and rural habitats and resource type on activity budgets of commensal rhesus macaques (*Macaca mulatta*) in Bangladesh. Primates 54:49–59.

Jiang, H., L. Jiangsheng, F. Min, W. Jun, and L. Yanhong. 1998. Studies on pouplation growth of *Macaca mulatta* at Nanwan, Hainan. Arcta Theriologica Sinica 18:100–106.

Johnson, R. L., J. Teas, N. Bishop, and C. H. Southwick. 1988. A decade of stability in a Nepalese macaque population. Journal of Mammalogy 69:178–180.

Jones-Engel, L., G. A. Engel, J. Heidrich, M. Chalise, N. Poudel, R. Viscidi, P. A. Barry, J. S. Allan, R. Grant, and R. Kyes. 2006. Temple monkeys and health implications of commensalism, Kathmandu, Nepal. Emerging Infectious Diseases 12:900–906.

Klopchin, J. L., J. R. Stewart, L. F. Webster, and P. A. Sandifer. 2008. Assessment of environmental impacts of a colony of free-ranging rhesus monkeys (*Macca mulatta*) on Morgan Island, South Carolina. Environmental Monitoring and Assessment 137:301–313.

Kruer, C. 1996. The inside story on the monkey islands of the Florida Keys. Florida Naturalist 68:10.

Li, C., C. Zhao, and P. F. Fan. 2015. White-cheeked macaque (*Macaca leucogenys*): a new macaque species from Medog, southeastern Tibet. American Journal of Primatology 77:753–766.

Long, J. 2003. Introduced mammals of the world. CABI Publishing, Cambridge, Massachusetts, USA.

López-Ortiz, R. 2016. Statistics about the removal of primates in southwest Puerto Rico from 2008 to January 28 2014. <http://drna.pr.gov/historico/oficinas/arn/recursosvivientes/negociado-de-pesca-y-vida-silvestre/division-de-recursos-terrestres-1/t-10-proyecto-control-de-primates-t-10-primates-control-project>. Accessed 13 Sep 2016.

Mackenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, B. Franklin, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84:2200–2207.

Maestripieri, D. 2010. Rhesus macaques. Pages 70–74 *in* M. D. Breed and J. Moore, editors. Encyclopedia of animal behavior, volume 3. Oxford Academic Press, Oxford, United Kingdom.

Maestripieri, D., and C. L. Hoffman. 2012. Behavior and social dynamics of rhesus macaques on Cayo Santiago. Pages 247–262 *in* Q. Wang, editor. Bones, genetics, and behavior of rhesus macaques. Cambridge University Press, Cambridge, United Kingdom.

Makwana, S. C. 1978. Field ecology and behaviour of the rhesus macaque (*Macaca mulatta*): group composition, home range, roosting sites, and foraging routes in the Asarori Forest. Primates 19:483–492.

Malik, I. 1989. Population growth and stabilizing age structure of the Tughlaqabad rhesus. Primates 30:117–120.

Malik, I., P. K. Seth, and C. H. Southwick. 1984. Population growth of free-ranging rhesus monkeys at Tughaqabad. American Journal of Physical Anthropology 7(4):311–312.

Maples, W. R., A. B. Brown, and P. M. Hutchens. 1976. Introduced monkey pouplations at Silver Springs, Florida. Florida Anthropologist 29:133–136.

Montague, C. L., S V Colwell, H. F. Percival, and J. F. Gottgens. 1994. Issues and options related to management of Silver Springs rhesus macaques: technical report #49. Florida Cooperative Fish and Wildlife Research Unit, Gainesville, USA.

Ocean Park Conservation Foundation [OPCF]. 2016. Wild macaques contraceptive programme. <http://www.opcf.org.hk/en/conservation-research/local-conservation-efforts/wild-macaques-contraceptive-programme>. Accessed 13 Sep 2016.

Pirta, R. S., M. Gadgil, and A. V. Kharshikar. 1997. Management of the rhesus monkey *Macaca mulatta* and Hanuman langur *Presbytis entellus* in Himachal Pradesh, India. Biological Conservation 79:97–106.

Radhakrishna, S., M. Huffman, and A. Sinha, editors. 2013. The macaque connection: cooperation and conflict between humans and macaques. Springer, New York, New York, USA.

Rawlins, R. G., and M. J. Kessler. 1986. The history of Cayo Santiago colony. Pages 13–46 *in* R. G. Rawlins, and M. J. Kessler, editors. The Cayo Santiago macaques: history, behavior, and biology. State University of New York Press, New York, USA.

Richard, A. F., S. J. Goldstein, and R. E. Dewar. 1989. Weed macaques: the evolutionary implications of macaque feeding ecology. International Journal of Primatology 10:569–594.

Riley, E. P., and T. W. Wade. 2016. Adapting to Florida's riverine woodlands: the population status and feeding ecology of the Silver River rhesus macaques and their interface with humans. Primates 57(2):195–210.

Rowcliffe, J. M., J. Field, S. T. Turvey, and C. Carbone. 2008. Estimating animal desnsity using camera traps without the need for individual recognition. Journal of Applied Ecology 45:1228–1236.

Saraswat, R., A. Sinha, and S. Radhakrishna. 2015. A god becomes a pest? Human-rhesus macaque interactions in Himachal Pradesh, northern India. European Journal of Wildlife Research 61:435–443.

Sarris, E. 1980. Aspects and implications of supplemental foraging among provisioned monkeys. Florida Scientist 43:164–168.

Sengupta, A., K. R. McConkey, and S. Radhakrishna. 2015. Primates, provisioning and plants: Impacts of human cultural behaviours on primate ecological functions. PLoS ONE 10:1–13.

Seth, P. K., and S. Seth. 1983. Brief report: population dynamics of free-ranging rhesus monkeys in different ecological conditions in India. American Journal of Primatology 5:61–67.

Southwick, C. H., T. Richie, H. Taylor, H. J. Teas, and M. F. Siddiqi. 1980. Rhesus monkey popualations in India and Nepal: patterns of growth, decline, and natural regulation. Pages 151–170 *in* M. N. Cohen, R. S. Malpass, and H. G. Klein, editors. Biosocial mechanims of population control. Yale University Press, London, United Kingdom.

Southwick, C. H., and M. F. Siddiqi. 1977. Population dynamics of rhesus monkeys in northern India. Pages 339–362 *in* H. S. H. Rainier III, and G. H. Bourne, editors. Primate Conservation. Academic Press, New York, New York, USA.

Southwick, C. H., R. A. M. I. Termeier, J. G. Robinson, and R. A. Tenaza. 1986. Report of the American Society of Primatologists Subcommittee on the Status of Primates in the Wild. American Journal of Primatology 10:371–378.

Southwick, C. H., Z. Yongzu, J. Haisheng, Z. Liu, and Q. Wenyuan. 1996. Population ecology of rhesus macaques in tropical and temperate habitats in China. Pages 95–105 *in* J. E. Fa, and D. G. Lindburg, editors. Evolution and ecology of macaque societies. Cambridge University Press, Cambridge, United Kingdom.

Stubben, C., and B. Milligan. 2007. Estimating and analyzing demographic models using the popbio package in R. Joual of Statistical Software 22(11):1–23.

Tian, J. D., Z. L. Wang, J. Q. Lu, B. S. Wang, and J. R. Chen. 2013. Reproductive parameters of female *Macaca mulatta tcheliensis* in the temperate forest of Mount Taihangshan, Jiyuan, China. American Journal of Primatology 75:605–612.

van de Kerk, M. 2009. Matrix models as a tool for conservation management of Carnivora: possibilities and limitations. Thesis, Radboud University Nijmegen, Nijmegen, Netherlands.

Verbrugge, L. N. H., R. J. G. Van Den Born, and H. J. R. Lenders. 2013. Exploring public perception of non-native species from a visions of nature perspective. Environmental Management 52:1562–1573.

Wang, S., and G. Quan. 1986. Primate status and conservation in China. Pages 213–220 *in* K. Benirschke, editor. Primates: the road to self-sustaining populations. Springer-Verlag, New York, New York, USA.

Wellem, C. W. W. 2014. A review of the management measures of feral macaques in Hong Kong. Thesis, The Chinese University of Hong Kong, Hong Kong, China.

Wells, K., P. Cassey, R. G. Sinclair, G. J. Mutze, D. E. Peacock, R. C. Lacy, B. D. Cooke, R. B. O'Hara, B. W. Brook, and D. A. Fordham. 2016. Targeting season and age for optimizing control of invasive rabbits. Journal of Wildlife Management 80:990–999.

Wisely, S. E., K. A. Sayler, C. J. Anderson, C. L. Boyce, A. R. Klegarth, and S. A. Johnson. 2018. Macacacine herpesvirus 1 antibody prevalence and DNA shedding among invasive rhesus macaques, Silver Springs State Park, Florida, USA. Emerging Infectious Diseases 24(2):345–351.

Wolfe, L. D. 2002. Rhesus macaques: a comparative study of two sites, Jaipur, India, and Silver Springs, Florida. Pages 310–330 *in* A. Fuentes and L. D. Wolfe, editors. Primates face to face: the conservation implications of human-nonhuman primate interconnections. Cambridge University Press, Cambridge, United Kingdom.

Wolfe, L. D., and E. H. Peters. 1987. History of the freeranging rhesus monkeys (*Macaca mulatta*) of Silver Springs. Florida Scientist 4:234–245.

Wong, C. L., and G. Chow. 2004. Preliminary results of trial contraceptive treatment with SpayVac. Hong Kong Biodiversity 6:13–16.

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