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INVASION NOTE

Predation of artificial nests by introduced rhesus macaques (*Macaca mulatta*) in Florida, USA

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Abstract Native throughout Asia, rhesus macaques are believed to have the widest native range of any non-human primate and are capable of adapting to an extensive diversity of habitats. Rhesus macaques have caused environmental degradation in introduced habitats, including decreasing bird populations through nest predation. In the 1930s, rhesus macaques were intentionally introduced into what is today Silver Springs State Park (SSSP), central Florida, in an effort to increase tourism. Our objective was to determine whether introduced rhesus macaques in SSSP would consume eggs presented in artificial nests. We used camera traps adjacent to 100 open-cupped artificial bird nests baited with quail eggs near the Silver River. Nests were placed in shrubs and left in the field site for 12 days, representative of the incubation period of native passerine species. Twenty-one nests were depredated by rhesus macaques, nine by nest predators other than macaques, and five nests by an unidentified predator. Nests were more likely to be depredated by macaques when located in areas of high macaque relative abundance. This study suggests introduced rhesus macaques may influence nest predation rates of native bird species in natural areas.

Keywords Invasive · *Macaca mulatta* · Nest predation · Rhesus macaque · Primate

Introduction

Florida has had the most non-native wildlife species introductions of any U.S. state (Hardin 2007). Prevention, management, and mitigation of invasive species in the state cost over $500 million annually (Beck et al. 2008). Florida is especially vulnerable to non-native species introductions due to its large numbers of tourists, several major ports of entry, thriving exotic pet trade, peninsular geography, and subtropical environment. Three species of non-human primates have established populations in Florida: the squirrel monkey (*Saimiri* sp.), the vervet monkey (*Chlorocebus sabaeus*), and the rhesus macaque (*Macaca mulatta*).

Among the non-human primates introduced in Florida, rhesus macaques may pose the greatest threat to native wildlife species and natural resources. Ranging from Afghanistan to the west, the Pacific coast of China to the east, and central India and Laos to the south, they are believed to have the widest native range of any non-human primate (Southwick et al. 1996).

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They have proven capable of adapting to an extensive diversity of habitats ranging in elevation from sea-level to 4000 m. They are both arboreal and terrestrial, and they are particularly adept at thriving in human settlements (Fooden 2000). They are primarily herbivorous, but supplement their diet with small vertebrates and invertebrates, honeycombs, and bird eggs (Fooden 2000). In introduced habitats rhesus macaques have increased bacteria loads in water bodies (Klopchin et al. 2008), destroyed mangrove trees leading to shoreline erosion (Kruer 1996), caused millions of dollars in crop destruction (USDA 2008), and threatened native wildlife populations (USFWS 2011).

When introduced into non-native habitats, macaque species (genus *Macaca*) have proven to be aggressive nest predators. Crab-eating macaques (*Macaca fascicularis*) were introduced on the island of Mauritius in the 1500s; nest predation by this population may have contributed to the extinction of the dodo (*Raphus cucullatus*; Hume and Walters 2012) and continues to be a substantial threat to breeding birds on the island (Safford 2011). Japanese macaques (*Macaca fuscata*) introduced in Texas were found to depredate artificial ground nests (Feild et al. 1997). Managers of St. Catherine's Island, Georgia, introduced lion-tailed macaques (*Macaca silenus*) in 1991 (Dierenfeld and Mccann 1999), and subsequently removed the animals after they proved to be aggressive towards humans and voracious predators of native bird eggs and hatchlings (R. Hayes, *pers. comm.*). Perhaps the most significant threat of introduced macaques to breeding birds in the U.S. is the introduced population of rhesus macaques in Desecheo Island National Wildlife Refuge, located off the western coast of Puerto Rico. The island historically provided home to tens of thousands of breeding seabirds. In the early 1900s, the introduction of non-native rodents began a decline of seabird nesting. Rhesus macaques were introduced in 1966, and nest predation by the macaques was severe enough to halt all seabird reproduction on the island within a few years. Managers have subsequently implemented an intense macaque removal program on the island (USFWS 2011).

Rhesus macaques were introduced into what is today Silver Springs State Park (SSSP), central Florida, in the 1930s in an effort to increase tourism. The initial introduction included approximately six animals, and an additional six animals were released in 1948 (Wolfe and Peters 1987). A 1968 study estimated the population had grown to 78 individuals spread between two groups (Maples et al. 1976). By the 1980s the macaque population reached nearly 400 animals (Wolfe and Peters 1987). Several trapping efforts between 1984 and 2012 resulted in a removal of approximately 1000 rhesus macaques from SSSP (Wolfe and Peters 1987; Florida DEP Public Records 2013). This removal effort was halted after extensive public controversy. In Fall 2015 there were approximately 190 macaques in SSSP (C.J. Anderson, *pers. observation*), however there are no current management strategies or population control measures. The cessation of macaque removal has the potential to lead to significant population growth. It is not currently understood how this population growth could impact native species.

Wolfe and Peters (1987) reported the rhesus macaques in SSSP did not consume bird eggs when presented with them. This appeared to contradict evidence collected from other introduced rhesus macaque populations (USFWS 2011). In an effort to reconcile this apparent contradiction, we conducted a study to determine whether rhesus macaques in SSSP would consume bird eggs placed in artificial nests in the natural environment.

Methods

Study site

The area which is now SSSP became a tourist attraction in the 1870s (DEP 2015). The 4685 acre park was purchased by the state of Florida in 1985 (DEP 2014). It is an IUCN Category V Protected Landscape/Seascape (Hubbard and Judd 2013). The Silver River flows entirely within SSSP before flowing into the Ocklawaha River. During fiscal year 2012–2013 the park attracted approximately 243,080 visitors, contributed approximately $11 million in direct economic input, and provided 179 jobs to the area (DEP 2014). The park contains twenty-one unique natural communities and is home to eighteen endemic and ten endangered plant species (Hubbard and Judd 2013). This diversity of natural communities provides critical habitat for resident and migratory birds, including eight imperiled species (DEP 2014).

Study design

We conducted a study in areas of SSSP known to be occupied by the macaques from April through July 2014, which corresponded with the breeding period of passerine birds in the habitat. We conducted our study in four replicate study sites, one in the estimated range of each of four macaque groups (Fig. 1). While home ranges of each macaque group were unknown, we selected locations where each respective group had been observed at least two times (B. Gottschalk, *pers. comm.*). Groups were distinguished by location, group size, age/sex composition, and by individuals with unique physical characteristics. Within each study site we marked a 240 m transect every 10 m using flagging tape, for a total of 25 points per transect (100 total in the study). We placed one nest to the right or left of each marked point at a minimum distance of 5 m from the transect; this was done so the flagging tape would not become a visual cue for macaques to locate nests. Each nest was baited with two quail eggs and one clay egg; clay eggs were used because tooth marks left in the clay can assist with identifying nest predators. We used commercially produced, open-cupped artificial (wicker) nests, and placed them in shrubs or trees 0.5–2 m from the ground to represent typical nesting sites of several common shrub-nesting species in the study site [e.g., Northern Cardinal (*Cardinalis cardinalis*), Eastern Towhee (*Pipilo erythrophthalmus*), Northern Mockingbird (*Mimus polyglottos*), Brown Thrasher (*Toxostoma rufum*), White-Eyed Vireo (*Vireo griseus*), Prairie Warbler (*Setophaga discolor*), Red-Winged Blackbird (*Agelaius phoeniceus*); C. Anderson, *pers. observation*]. To minimize human scent, we handled the nests with nitrile or latex gloves, left them outdoors for a minimum of three days prior to placing them in the field (Sieving and Willson 1998), and lined the nests with natural materials from the field site to hide the wicker. Nests were left in the field for 12 days, the average incubation period of Northern Cardinals, with an adjacent camera trap set to record all motion. We checked the nests and cameras one time after 5–8 days to ensure the cameras were functioning with sufficient battery and memory capacity and to remove depredated nests. Nests were counted as depredated if eggs were removed, scratched, or had tooth marks.

We use a combination of the camera trap data and field signs to attempt to identify the predator of each depredated nest. Nests depredated by macaques typically had all three eggs removed and were removed from the vegetation, and typically the predation event was clear on the camera footage. No predation event was captured on video by a predator other than

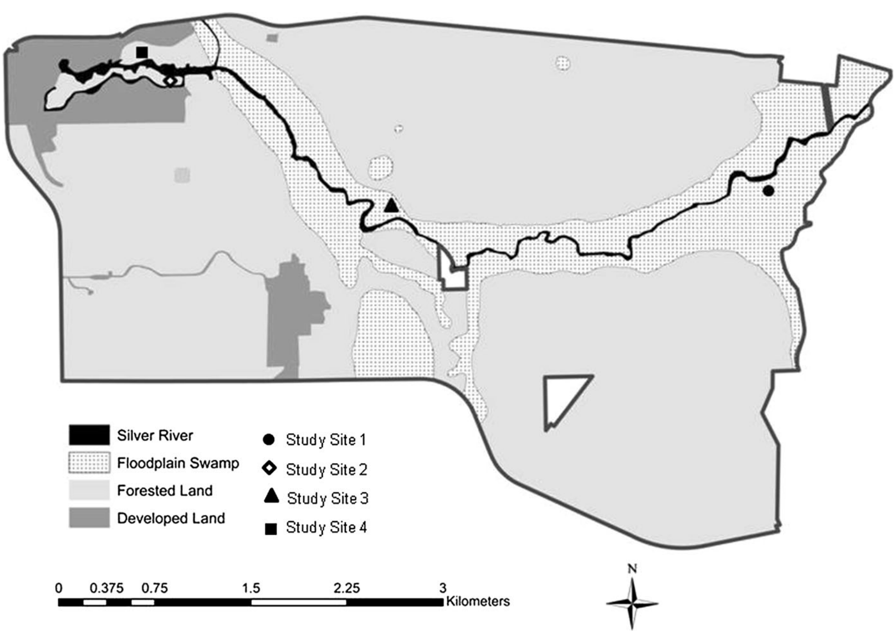

Fig. 1 Locations of the four study sites in SSSP

macaques, but nests consumed by non-macaque predators were identified through field signs not indicative of macaques; for example, only one egg would be removed or tooth/scratch marks on the eggs were too small to have been attributed to a macaque. Nests were characterized as an unknown predator if the field signs were potentially indicative of a macaque, but the camera was not activated by the predation event.

Analyses

We used the camera trap data to determine the day each nest was depredated by a macaque. We used the Mayfield estimator in Program MARK (Dinsmore and Dinsmore 2007) to estimate the day of nest depredation for those consumed by non-macaque predators and to calculate Daily Survival Rate (DSR) for all nests. We compared DSR between nests depredated by macaques and other predators.

To determine the relative abundance of macaques between sites, we used the timestamps recorded by the camera traps to determine the minimum number of days the macaques were present in each study site during the respective study period. We conducted a logistic regression to determine if the proportion of nests depredated by macaques in each of the four sites was correlated with the number of days macaques were present in the respective site ($\alpha = 0.05$; Agresti 2002) using R (version 3.0).

Results

Of the one-hundred nests, two were lost to inclement weather and excluded from the study. Of the remaining ninety-eight, twenty-one nests were depredated by macaques (Fig. 2), nine nests by other predators, and five nests were consumed but the predator could not be identified with certainty (Table 1). Nest consumed by macaques had a higher DSR (0.97) than those consumed by other predators (0.68; Table 2), indicating nests depredated by predators other than macaques were destroyed earlier in the study than those destroyed by macaques. We determined the proportion of nests depredated by macaques was positively correlated to macaque relative abundance ($P < 0.001$), indicating nest mortality rate by macaques increased with macaque relative abundance (Table 3). The odds ratio was 1.75 (95 % CI 1.40–2.19), which suggested for each day macaques were present in a site, the likelihood of a nest being depredated by macaques nearly doubled. Post-hoc observations indicated a single macaque group may have visited two of the research sites, indicating we may have sampled three macaque groups rather than four; however, because no group-specific analyses were conducted (e.g., impacts of macaque group age ratio on nest predation rates), this did not impact our results.

Discussion

Artificial nests lack the parental care and protection of natural nests, they cannot fully mimic native passerine nests in size, smell, or placement, and predation rates may be influenced by researcher presence (Major and Kendal 1996). Therefore, the results of this study do not suggest rhesus macaques in SSSP are consuming 21 % of native shrub-nesting bird nests, nor does it confirm they are capable of locating native passerine nests. However, it does confirm rhesus macaques in SSSP will consume eggs when they locate them in the natural habitat. We believe this merits concern regarding the potential impact of this introduced population to native breeding birds.

Rhesus macaques are believed to be opportunistic rather than intentional or specialized nest predators, which aligns with our observation that they were less efficient at locating nests than other nest predators in SSSP. As generalist omnivores with broad diets and opportunistic diet choices (Fooden 2000), macaques are very likely to encounter and depredate natural bird nests at rates correlated with macaque density or relative abundance. This suggests that in areas where macaque populations achieve higher abundance, bird nests will be at proportionately greater risk of macaque predation. However, the net indirect effects of macaques on nest predation rates via interactions with other nest predators (e.g., squirrels, raccoons, etc.) in SSSP is unknown. Macaque effects on nest loss could (a) be additive (if abundance of other predators are unaffected by macaques), (b) be compensatory (if macaques replace other predators in determining nest losses), or (c) result in decreased overall nest mortality (if macaques reduce other predator abundance and eliminate their portion of nest loss). Given that the non-macaque nest predators attacked nests more quickly

Fig. 2 Image captured by a camera trap of a rhesus macaque consuming a quail egg from an artificial nest

Table 1 Nest mortality by study site

	Total # nests used	# Nests depredated by macaques	# Nests depredated by other predators	# Nests depredated by unknown predator	# Days macaques present in study site
Study site 1	25	2	0	1	2
Study site 2	25	3	1	1	1
Study site 3	25	1	3	1	2
Study site 4	23[a]	15	5	2	7
Total	98	21	9	5	

[a] Twenty-five nests were placed on the transect, however 2 were lost to inclement weather

Table 2 Daily survival rate of depredated nests by predator

	DSR	Standard error	Lower confidence interval	Upper confidence interval
Nests depredated by macaques	0.973	0.006	0.959	0.982
Nests depredated by other predators	0.682	0.105	0.452	0.848
Nested depredated by unknown predators	0.802	0.085	0.586	0.921

than macaques (Table 2), and that Site 4 had the highest macaque relative abundance and the highest nest mortality, we suggest that additive predation by macaques may be more likely than compensatory predation effects on bird nest success. Without knowing the effect of macaques on native nest predators, we hypothesize that areas with high macaque abundance could experience relatively high nest mortality rates because of their generalist foraging and likelihood that their predation pressure on native nests could be additive. Replicating this and similar studies both in and outside of macaque ranges would provide additional valuable information for determining the direct and indirect effects of macaques on native species, which would be useful for managers.

We provide the first confirmation that introduced rhesus macaques are potential nest predators in the continental U.S. Compared to island bird species (e.g., those in Desecheo Island National Wildlife Refuge) that do suffer from introduced macaque nest predation,

Table 3 Logistic regression predicting proportion of nests depredated by macaques by macaque abundance

	Coefficient	Standard error	*P* value
Intercept	−3.3478	0.5732	<0.001
Macaque abundance	0.5596	0.1141	<0.001

it is unlikely the common breeding birds in SSSP are experiencing negative population responses to nest mortality at the current rhesus macaque population size and density. Many continental bird communities evolved sympatrically with very diverse nest predators, and in turn they exhibit generalized nest defense strategies (e.g., nest guarding, inconspicuous nest placement, multiple nestings per season); similar nest defense strategies are often lacking in island birds that evolved naïve of native nest predators (Humphrey et al. 1987), making them vulnerable to introduced predators. However, our results clearly show that bird eggs are on the macaque menu in SSSP and that macaque nest depredation may well add to native rates of nest loss. For natural areas with sensitive bird species nesting sympatrically with introduced macaques, especially in areas that are frequented by macaques, the inclusion of nest contents in macaque diets should be of concern to managers. Specific to SSSP, our findings are concerning because the population of rhesus macaques in the park is below carrying capacity and likely rebounding from its current estimated 190 animals upwards, in the direction of the previous high of nearly 400 animals (Wolfe and Peters 1987). It is possible the current population size of rhesus macaques in SSSP is causing minimal environmental impacts, however if allowed to grow uncontrolled, the predatory effects of this population on native birds could become problematic.

Primates pose a unique challenge in invasive species ecology. At least nine macaque species have successfully established populations outside of their native range (Wolfe and Peters 1987; Feild et al. 1997; Dierenfeld and McCann 1999; Lowe et al. 2000; Long 2003). Crab-eating macaques are among the IUCN's "100 of the World's Worst Alien Invasive Species" (Lowe et al. 2000). Macaques introduced throughout the world pose various environmental, economic, and human health threats. However, macaques hold cultural and religious significance in many cultures (Radhakrishna et al. 2013) and even in introduced ranges can increase tourism and subsequent revenue for natural areas (Wolfe and Peters 1987). Managers of macaque-introduced habitats must carefully balance ecological considerations with public perceptions of these charismatic, yet potentially destructive animals.

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