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Abundance of introduced rhesus macaques (*Macaca mulatta*) in central Florida

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Abstract Introduced non-human primates threaten native ecosystems and have the potential to transmit diseases to humans and native wildlife, but primate population management is challenging and often controversial. Rhesus macaques (*Macaca mulatta*), native to much of Asia, were introduced to an island in the Silver River in central Florida (Marion County, U.S.A.) in the 1930s and 40s. An initial population of approximately twelve individuals has grown and spread throughout what is now Silver Springs State Park. In 2015, the park was home to at least 176 rhesus macaques despite the removal of approximately 1000 animals over the preceding 30 years. The Silver River flows east into the Ocklawaha River, where rhesus macaques were reported as early as the 1970s. Population management or further research on the effects of rhesus macaques in Florida requires estimates of abundance, home range, and distribution, yet prior to this study the abundance and spatial distribution of the Ocklawaha groups were unknown. In this study, we evaluated minimum population size, number of groups, and minimum winter home range size of Ocklawaha River groups, and compared these metrics with the previously-studied Silver River groups. We surveyed a 52 km section of the Ocklawaha River using baited camera traps and river surveys for ten weeks. We identified six Ocklawaha River macaque groups, each containing between fourteen and 39 individuals, for a minimum abundance of 134 individuals. Minimum winter home ranges were between 3.63 and 11.89 km, measured as the linear distance between the furthest points at which a group was observed. Overall, Ocklawaha groups were smaller and had larger winter home ranges than Silver River groups, a difference likely driven by provisioning from tourists along the heavily-visited Silver River. This information is crucial for management of the central Florida rhesus macaque population and for future research regarding population growth and ecology of this invasive species.

Keywords Abundance · Florida · Home range · Non-human primates · Rhesus macaque

Introduction

The introduction and establishment of non-human primates (hereafter: primates) pose unique challenges in invasive species management (Jones et al. 2018). At least ten species of primates have been introduced in the U.S., including one ape (Wilson and Elicker 1976), one gibbon (Rawlins and Kessler 1983), three lemurs (Mowry et al. 1997; Dierenfeld and McCann 1999; Hall et al. 2007), and six monkeys (Maples et al. 1976; Rawlins and Kessler 1983; Wolfe and

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Peters 1987; Taub and Mehlman 1989; Hyler 1995; Paterson 1996; Feild et al. 1997; Dierenfeld and McCann 1999; González-Martínez 2004; Engeman et al. 2010). Some of these introductions were unintentional or from unknown sources (Anderson et al. 2017b); those intentionally introduced have been for conservation of imperiled species (Dierenfeld and McCann 1999; Hall et al. 2007), increasing tourism (Wolfe and Peters 1987; Anderson et al. 2017b), and behavioral (Evans 1989) or biomedical research (Wilson and Elicker 1976; Rawlins and Kessler 1983; Klopchin et al. 2008). While some of these introductions were innocuous or short-lived (Wilson and Elicker 1976; Anderson et al. 2017b), others have led to invasive populations that have caused ecological degradation (Evans 1989; Kruer 1996; Feild et al. 1997), economic loss (Engeman et al. 2010), and threats to human health and safety (Wisely et al. 2018).

There have been at least nine separate introduced populations of primates in Florida, including rhesus macaques (*Macaca mulatta*), vervet monkeys (*Chlorocebus sabaeus*), and squirrel monkeys (*Saimiri sp.*; Anderson et al. 2017b). The oldest, largest, and demonstrably most problematic of these populations is a rhesus macaque population in Marion County, central Florida. Invasive rhesus macaque populations have been established in Florida and Puerto Rico, U.S.A., since the 1930s and 1960s, respectively. Introduced rhesus macaques in the U.S.A. have decreased bird populations via nest predation (Evans 1989), caused economic damage through crop raiding (Engeman et al. 2010), increased bacterial loads in water bodies (Klopchin et al. 2008), and destroyed mangroves leading to shoreline erosion (Kruer 1996). The ability of rhesus macaques to thrive in novel habitats is likely a product of this species' generalist habitat requirements. With populations ranging throughout central and southern Asia, this species has the largest native range of any primate other than humans (Southwick et al. 1996). Rhesus macaque populations occur across a wide variety of habitat types, including anthropogenically-modified habitats, and range in elevation from sea level to 4000 m (Fooden 2000). They are typically found within 1000 m of a water source (Lindburg 1977; Dong-Ming et al. 2012). Rhesus macaques are both arboreal and terrestrial, with a diet primarily consisting of fruits and insects, supplemented with other plant parts, eggs, honeycomb,

and small vertebrates and invertebrates (Kinzey 1997; Fooden 2000). They live in groups consisting of adult females and their offspring, a single adult alpha male, and subordinate adult males. Females remain with their natal group throughout their lifespan. Males emigrate upon reaching sexual maturity, after which they live individually or in bachelor groups before joining new groups (Maestripieri and Hoffman 2012).

The central Florida rhesus macaque population was introduced along the Silver River in the 1930s. Approximately six rhesus macaques were released in the initial intentional introduction, and approximately six additional individuals were released in the 1940s (Wolfe and Peters 1987) in an effort to increase tourism. Subsequent abundance estimates along the Silver River included 78 individuals in 1968 (Maples et al. 1976), at least 150 individuals in 1979, and nearly 400 individuals in the mid-1980s (Wolfe and Peters 1987; Wolfe 2002; Anderson et al. 2017b). At this population size, negative human-macaque interactions were reportedly high, as were concerns about potential environmental impacts of the rhesus macaque population (Montague et al. 1994). Consequently, approximately 1000 rhesus macaques were trapped and removed from the Silver River and adjacent Ocklawaha River between 1984 and 2012 (Wolfe 2002; Anderson et al. 2017b). Most of these animals were sold into the biomedical research industry, which caused extensive public protest and controversy (Wolfe and Peters 1987; Anderson et al. 2017b). Consequently, no population management has been implemented since 2012. A 2013 study estimated there were 118 rhesus macaques among four groups along the Silver River in the spring of that year (prior to the end of birthing season; Riley and Wade 2016), and a study found a minimum of 176 individuals among five groups in fall 2015 (Anderson et al. 2019).

Rhesus macaques were first documented along the Ocklawaha River in the 1970s (Montague et al. 1994). Because the Silver River flows into the Ocklawaha River, the animals along the Ocklawaha River are believed to be an extension of the animals originally introduced along the Silver River. Prior to this study, research on Marion County rhesus macaques was limited to Silver River groups, and no research had been conducted on the abundance or distribution of rhesus macaques on the Ocklawaha River. However, approximately 200 rhesus macaques were trapped and

removed along the Ocklawaha River from 2005 to 2012 (State of Florida 2013; Anderson et al. 2017b). A study conducted in March—June 2016 described a group of 22 macaques along the Ocklawaha River, approximately 14 km north of the confluence with the Silver River (Johnson 2017).

While Ocklawaha and Silver River macaques occupy similar habitats, the frequency and characterization of their interactions with humans is markedly different. The land along the Silver River—now Silver Springs State Park (SSSP)—has been a popular tourist destination since the 1870s, acquired by the state and named a state park in the 1980s. Glass-bottom boat tours of the spring-fed river, paddling opportunities, and the monkeys themselves draw over 400,000 visitors per year (Murray 2016). Macaque groups along the Silver River are provisioned with food by boaters (Riley and Wade 2016), and those groups near the headspring in the western section of the park have been provisioned for decades. Conversely, the land along the Ocklawaha River is not developed for tourism and boat traffic is substantially lower than that on the Silver River.

Rhesus macaque management is a growing concern in Florida. Individuals were reported in 22 counties between 2011 and 2019 (EDDMapS 2020). An adult male captured over 100 km from the Marion County population was found to have an identical haplotype to individuals in the population, indicating far-distance emigration is occurring (Anderson et al. 2016a). In recent studies, rhesus macaques along the Silver River have been found to potentially threaten native fauna (Anderson et al. 2016b), carry the zoonotic Herpes B Virus (Wisely et al. 2018), and be growing in population size at a rate of approximately 11% annually (Anderson et al. 2019). Along the Silver River, the growing rhesus macaque population is leading to an increase in human-macaque conflict; managers have repeatedly closed public areas of the park in response to aggressive macaque behavior (S. Lieb, *pers. comm*).

In this study, we conducted the first abundance estimate of rhesus macaques along the Ocklawaha River. Using baited camera traps and river surveys, we estimated the number of groups, minimum number of individuals per group, minimum winter home range size of each group, and distribution of rhesus macaque groups relative to the confluence with the Silver River. To evaluate whether human provisioning may be influencing rhesus macaque distribution and behavior in Florida, we compared our findings with those of the Silver River groups reported by Anderson et al. (2019). This information is critical to informing management decisions at the metapopulation level of the largest introduced primate population in the contiguous U.S.

Methods

Study area

Central Florida is characterized by a humid subtropical climate (Chen and Chen 2013). The area receives an average of approximately 129 cm of rain per year, with about 50% falling from June through September. Spring and fall are typically the driest seasons. In January the mean temperature is 14.5 °C (mean minimum = 7.1 °C, mean maximum = 21.8 °C) and average rainfall is 8 cm. July mean daily temperature is 27.9 °C (mean minimum = 21.9 °C, mean maximum = 34.0 °C) and average rainfall is 17.6 cm (SRCC 2018).

The study area spanned a 52 km portion of the Ocklawaha River in central Florida, ranging approximately 29 km north and 23 km south of the confluence with the 8 km Silver River (Fig. 1). Habitat along the Ocklawaha River is predominately floodplain swamp, with occasional patches of hydric and mesic hammock (FNAI 2021). Land within the study area primarily falls within the Marjorie Harris Carr Cross Florida Greenway (hereafter, Greenway), managed by the Florida Department of Environmental Protection (DEP). Habitat type adjacent to the floodplain swamp is highly variable and includes scrubby, mesic, hydric pine, and wet flatwoods, sand pine scrub, hydric hammock, improved pasture, and tree plantations (FNAI 2021). The southern portion of the survey included land within the Ocklawaha Prairie Restoration Area (St. Johns River Water Management District, SJRWMD), where habitat includes marsh, wet prairie, freshwater forested wetlands, and bare soil/clear cut. Tracts of Ocala National Forest and privately-owned land were interspersed within the study area, but all surveys were conducted on DEP and SJRWMD property (FNAI 2021). Water levels of the north-flowing Ocklawaha fluctuate significantly throughout the year in response to rainfall and
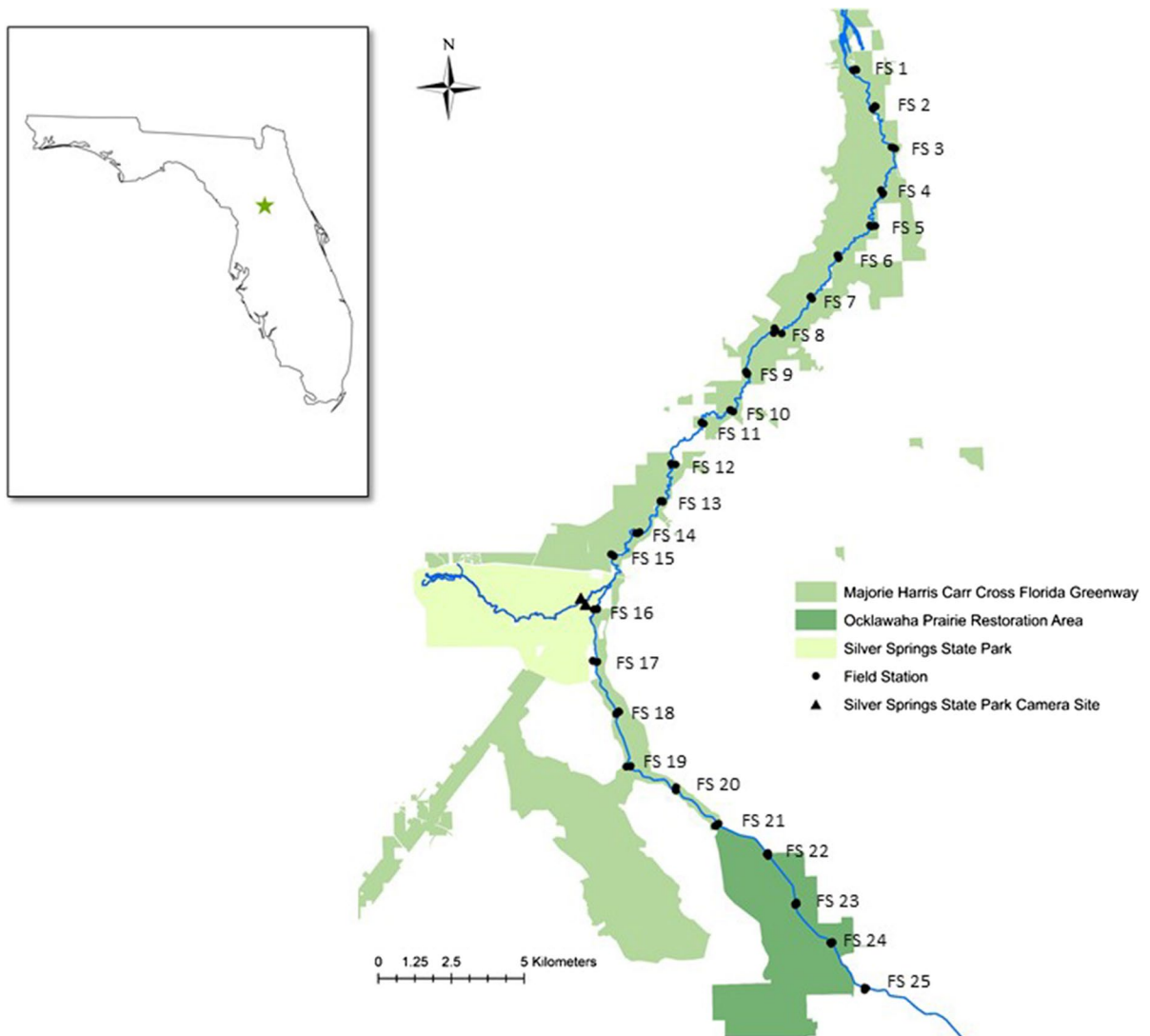
Fig. 1 Map of study area, covering approximately 52 km along the Ocklawaha River in Marion County, FL. Field stations were spaced approximately 2 km apart. The Silver River in Silver Springs State Park flows into the Ocklawaha River

anthropogenic manipulations via Moss Bluff Lock and Dam (SJRWMD) just south of the study area. Three months before our study began, Hurricane Irma raised the water level by nearly 2 m (USGS 2018).

Study design

We used camera traps (Moultrie A-30i, Bushnell Trophy Cam E3) baited with automated feed dispensers for ten weeks, 17 December 2017 through 12 March 2018, to estimate the abundance of rhesus macaques along the Ocklawaha River (University of Florida

IACUC Study #201709980; Florida Department of Environmental Protection Permit #09011713). We placed cameras within 50 m of the Ocklawaha River, as rhesus macaques along the Silver River have been found to select for floodplain swamp in close proximity to the river during winter months (Anderson et al. 2017a). Baited camera traps are an effective method for studying unhabituated or elusive terrestrial primate species (e.g., Kierulff et al. 2004; Gerber et al. 2014; Anderson et al. 2019). Twenty-five field stations were spaced approximately 2 km apart along the 52 km length of river (Fig. 1). Each field

station consisted of two camera traps on either side of the river (i.e., four cameras per field station), each directed at a separate automated feeder (Moultrie 6.5-gallon Pro Hunter Digital Hanging Feeder; Fig. 2) baited with deer corn; camera traps were divided on both sides of the river to maximize detectability because rhesus macaque groups can occur simultaneously on either side of rivers (Anderson et al. 2017a). At the southernmost field station (Field Station 25) all four cameras were on the western bank because land on the eastern shore was privately owned. To avoid double-counting individuals, cameras within each station were at least 20 m apart and time stamps

were carefully synchronized (Anderson et al. 2019). Because non-provisioned rhesus macaque groups can contain dozens of individuals (mean = 32; Fooden 2000) and subordinate macaques are not always permitted to feed with alphas (Belzung and Anderson 1986), multiple feeders and cameras enabled subordinates and alphas to feed simultaneously and maximize the proportion of the group detectable by cameras at a given time. We placed an additional two field stations in the eastern portion of Silver Springs State Park to differentiate between groups that range exclusively along the banks of the Ocklawaha River and any groups with ranges spanning both rivers.
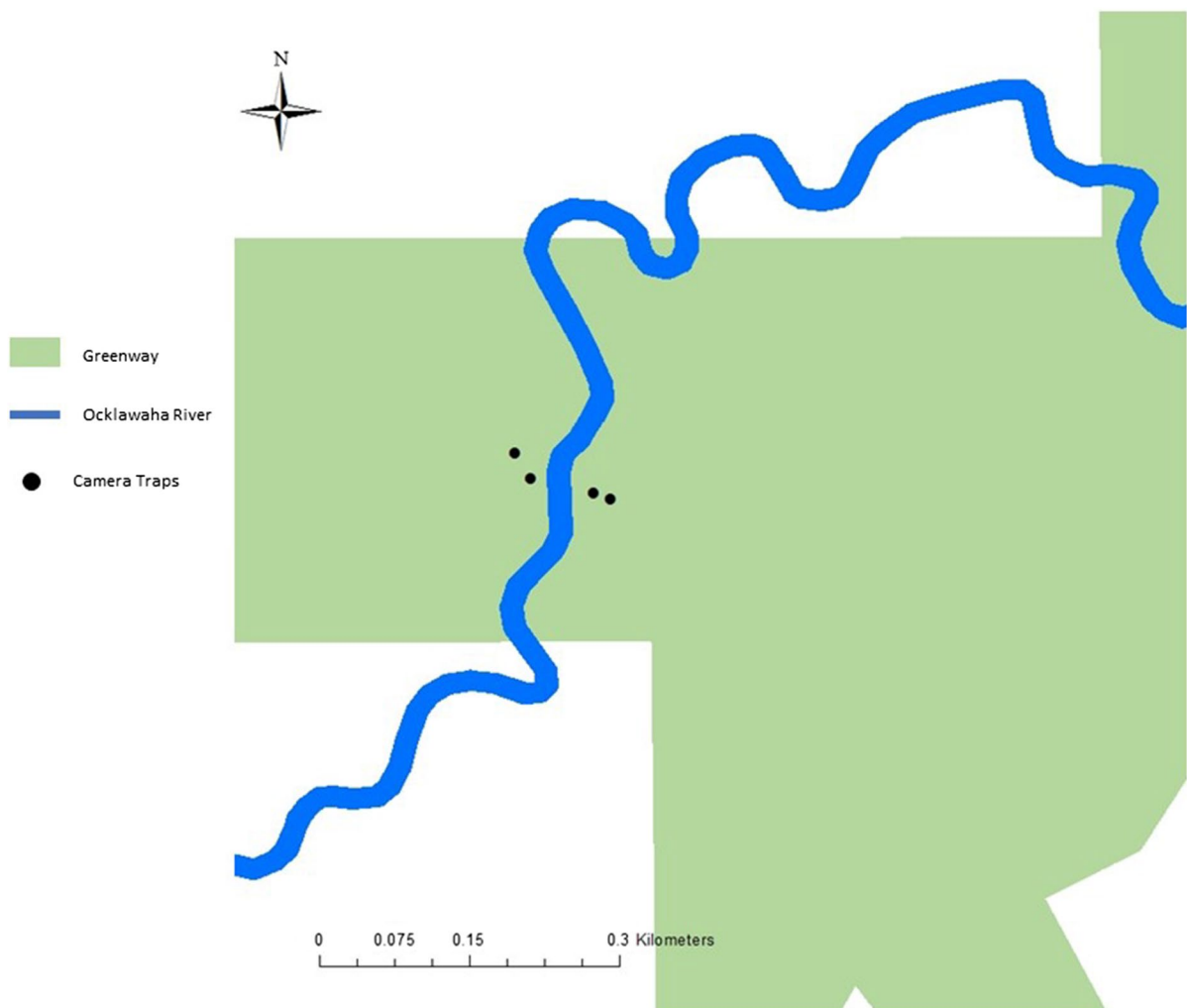
Fig. 2 Sample field station. Each field station contained two cameras on either side of the river, since macaque groups can forage on both sides of the river simultaneously. Each camera was aimed at a separate feeder filled with corn. Cameras were separated by at least 20 m to prevent double-counting individuals

Feeders were programmed to dispense one pound of corn per day for ten weeks. We conducted four surveys per week via motorized boat from 17 December 2017 through 12 March 2018. Surveys included monitoring the riverbanks for rhesus macaque groups as well as visiting field stations to refill feeders and monitor cameras. Each survey covered approximately one-fourth of the study area, so that each field station was monitored once per week. When macaque groups were observed during surveys, we recorded coordinates, time of day, and number of individuals observed, and used a DSLR camera to take high quality photographs to aid in identifying specific individuals and differentiating groups; these photos were used to compare with data from the Silver River and ensure groups weren't double-counted from data collected by Anderson et al. (2019). Due to elevated water levels as a result of Hurricane Irma, we installed platforms made of tarps, paracord, and pool noodles under feeders in some flooded areas to ensure macaques would be able to locate the corn (Fig. 3).

Data analysis

Using the camera trap data supplemented by boat survey observations, we identified individual groups using spatial and temporal separation from other groups, age and sex composition, and individuals with unique physical attributes (Anderson et al. 2019); traits such as injuries, scars, and distinct facial features can reliably identify individuals (Hasan et al. 2013). After confirming the number of groups, we estimated the minimum number of individuals in each group by counting individuals from the camera trap data within four age and sex classifications: adult males, adult females, subadults, and infants. Adult males and females are easily distinguishable by external sex organs. Additionally, males have elongated faces and prominent canines which are absent in females, and adult females that have had infants have extended nipples. Adults were further identified by body size and reddening of the facial and anogenital skin (Fooden 2000) not yet developed in subadults. Infants are individuals under one year of age and were identified by size. Sex could not be determined among subadults or infants. The minimum number of animals in each group was determined by calculating the sum of the largest number of simultaneously observed individuals in each age and sex class (Anderson et al. 2019). To estimate minimum abundance of rhesus macaques along the Ocklawaha River, we combined estimates from each group.

We calculated the minimum spatial area occupied by each group by measuring the linear distance between the northern and southernmost field stations at which the respective group was observed. This area was likely smaller than the respective home range of each group, as macaque home ranges can vary seasonally (Lindburg 1977; Fooden 2000); further, provisional feeding typically reduces rhesus macaque home range size (Sengupta et al. 2015; Fooden 2000), and therefore by incorporating baiting our study may have artificially decreased range size. Thus, we refer to this metric as "minimum winter home range." Overall distribution of rhesus macaques along the Silver River was estimated by the northern and southernmost coordinates at which rhesus macaque groups were observed.

We compared minimum observed group size of Ocklawaha River macaque groups to Silver River groups as reported by Anderson et al. (2019). We calculated minimum observed winter home range sizes of Silver River macaque groups as the distance between the furthest observed points of four of the Silver River groups using findings reported by Anderson et al. (2019); the fifth Silver River group was omitted, as it was only observed at one location. We compared both metrics, minimum group size and minimum winter home ranges, with Mann–Whitney U tests (R version 3.6.0).

Results

We observed rhesus macaque groups on camera traps at each station north to Field Station 5 and south to Field Station 21 (Fig. 4). This 31 km stretch of the Ocklawaha River spans from approximately 20 km north to 11 km south of the confluence with the Silver River. Solitary males or small bachelor groups (one to four individuals per group) were observed at Field Stations 1, 5–19, 22, 23, and 25, which included the northern and southern limits of the study area. Although we did not identify or quantify peripheral adult males, one distinct individual was identified within SSSP and at each station south to Field Station 20, a range of at least 9 km, moving between stations throughout the study period. We encountered

Fig. 3 Top: A group of rhesus macaques eats corn dispensed from a feeder on a temporary platform in floodplain swamp along the Ocklawaha River. Bottom: An adult female rhesus macaque balances on cypress knees to reach corn that landed in the water

monkeys during boat surveys on 28 occasions, from Field Station 7 to Field Station 17. Water level fluctuated throughout the study period; macaques regularly ate corn from the platforms we installed, but also frequently found and ate bait that fell in standing water (Fig. 3).
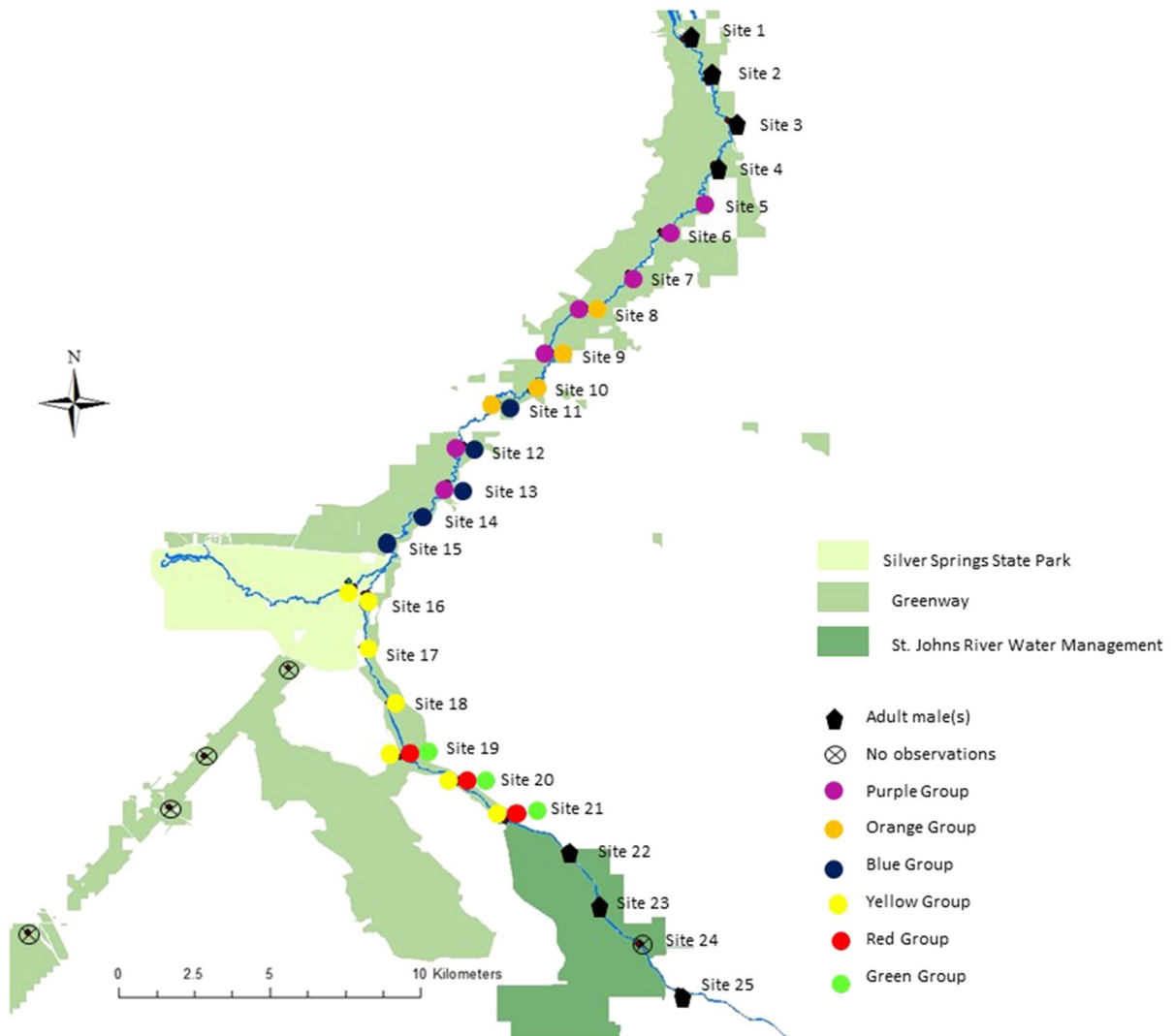
Fig. 4 Summary of rhesus macaque detections. Rhesus macaque groups were detected at Field Station 5 through Field Station 21. Largest minimum winter home range was 11.89 km, defined as the linear distance between the furthest feeders at which a group was observed. Solitary adult males or bachelor groups visited every site except 24. Groups were concentrated near the confluence with the Silver River, but individual males were detected at the limits of the study area

We identified six distinct groups along the Ocklawaha (identified as Groups Purple, Orange, Blue, Yellow, Green, and Red in Fig. 4). While all groups were observed at multiple Field Stations, all were either north or south of the confluence with the Silver River. One additional group appeared on a few occasions at Field Stations 15 and SSSP near the confluence with the Silver River, but using photographs collected during our boat surveys we confirmed this group had been included in the previous estimate of the Silver River macaque abundance estimate (Anderson et al. 2019) and we therefore excluded the group from the Ocklawaha abundance estimate. The three groups north of the Silver River were each detected via camera trap on at least 21 days (n = 21–61) during the study period, but groups Green and Red in the southern portion of our study area were only observed on 3 and 6 days, respectively.

We estimated there were a minimum of 134 rhesus macaques among the six groups along the Ocklawaha River prior to the 2018 birthing season: 14 adult males, 46 adult females, 45 subadults, and 29

infants (Table 1). Minimum estimated group size ranged from 14 to 39 individuals (mean = 22.3). Group adult male to adult female ratios ranged from 1:2 to 1:5. While the minimum group size was smaller than those reported by Anderson et al. (2019) on the Silver River (mean = 27.6), the difference was not significant (p value = 0.36; Wilcoxon rank sum test with continuity correction).

Minimum winter home range size per group ranged from 3.63 to 11.89 km (mean = 6.19). Observed home ranges overlapped spatially (Fig. 4) but rarely temporally; for example, home ranges of the Orange and Purple Groups overlapped and on at least one occasion the Orange Group was observed leaving Field Station 8 when Purple arrived. No interactions between the groups were observed during that event. The Blue Group ranged from Field Station 11 to Field Station 15, over 5 km apart, and Orange moved within the 4 km between Station 8 and Station 11. Purple Group was usually detected between Field Station 5 and Field Station 9 but was seen as far south as Station 13 early in the study. Yellow Group ranged south to Field Station 21 in December, but for the majority of surveys only visited feeders within or near the eastern portion of Silver Springs State Park. The observed minimum winter home range sizes on the Silver River ranged from 0.67 to 2.56 km (mean = 1.68 km; Anderson et al. 2019) and were significantly smaller than those of the Ocklawaha River (p value = 0.01; Wilcoxon rank sum test with continuity correction).

Table 1 Minimum group size and number of individuals per age class of rhesus macaque groups along the Ocklawaha River

Group	Adult Males	Adult Females	Subadults	Infants	Total
Purple	3	5	6	4	18
Orange	2	4	5	3	14
Blue	2	9	10	4	25
Yellow	2	8	7	7	24
Green	3	15	12	9	39
Red	2	5	5	2	14
Total	14	46	45	29	134

Discussion

Rhesus macaque groups along the Ocklawaha River were centered near the confluence with the Silver River and did not reach the northern or southernmost Field Stations. This provides strong evidence that we identified all rhesus macaque groups currently living along the Ocklawaha River. It also supports the idea that Ocklawaha River groups are an extension of the Silver River population; future research could confirm this by genetic analysis. We detected adult male macaques at the limits of the study area, suggesting these individuals are dispersing beyond the portion of the river we surveyed.

Our minimum abundance estimate of 134 individuals along the Ocklawaha River does not account for detection probability and is therefore a conservative estimate of population size (Mackenzie et al. 2002). Anderson et al. (2019) estimated detection probability for this camera trap method with the Silver River groups by conducting censuses of habituated rhesus macaque groups and comparing those results to estimates from camera traps. Detection probability of camera traps for the Silver River groups was estimated to be 83% for adult males and adult females, 54% for subadults, and 100% for infants (Anderson et al. 2019). Rhesus macaques along the Ocklawaha River are not as habituated to humans as the Silver River subpopulation and tend to scatter when approached, which precluded the possibility of conducting a census of groups in the study area to determine detection probability for this study. However, if detection rates are similar between the Silver and Ocklawaha River groups, the population of rhesus macaques along the Ocklawaha may be closer to approximately 185 individuals. This estimate excludes solitary males and new young of the year, as our counts were completed prior to the beginning of the birthing season.

Among Ocklawaha groups, there were noticeable differences in frequency of detection and the spatial range of field stations where groups were detected. Groups north of the Silver River (Purple, Orange, and Blue) regularly visited feeders, and the Purple and Blue groups appeared on camera almost daily. Groups Red and Green in the southern portion of the study area visited feeders infrequently, indicating their ranges include habitat away from the Ocklawaha River. Rhesus macaque home ranges can vary seasonally (Lindburg 1977; Fooden 2000. Although

we did not evaluate covariates that could explain seasonal variation in group location, it appears rhesus macaque group home ranges may vary throughout the year in central Florida. Both the Purple and Yellow groups were observed along a longer portion of the river early in the study, moving less as the study progressed; this may have represented a natural shift in the home range or may have been a response to baiting conducted in this study.

Overall, macaque groups along the Ocklawaha River were smaller and had larger minimum winter home ranges than their Silver Springs counterparts. While minimum group size means were not significantly different, only one Ocklawaha River group was estimated to include over 25 individuals; four of the five Silver River groups included at least 25 individuals. The minimum winter home ranges on the Ocklawaha River were markedly larger than those of the Silver River, as well as those of rhesus macaque groups in their native range (Fooden 2000). Provisional feeding from humans provides food that is abundant and calorically rich, and generally leads to larger group sizes, smaller home ranges, and increased density among rhesus macaques (Sengupta et al. 2015; Fooden 2000). Average group size of provisioned rhesus macaque groups is over twice as large (n = 76.9) as non-provisioned groups (n = 32.3), and average home ranges are twice as large (0.65 km^2 and 1.69 km^2, respectively; Fooden 2000). Similarly, densities of provisioned macaque populations are five times larger (201.1/km^2) in human-dominated environments compared to forested environments (37.2/km^2: Fooden 2000). Differences in group size and winter home range between the Silver River and Ocklawaha River macaque groups may therefore stem from higher numbers of tourists and supplemental feeding available within SSSP (Riley and Wade 2016). Because anthropogenic feeding of macaques tends to reduce home range size, it is possible that the bait provided during this study temporarily affected the home ranges of Ocklawaha River macaque groups (Sengupta et al. 2015; Fooden 2000); thus, while we observed unusually high winter home range sizes, our observations may be underestimations.

As the rhesus macaque population in central Florida grows and spreads, the related potential for environmental, human health, and economic impacts are exacerbated. Rhesus macaques are generalists that thrive in anthropogenically-modified habitats, so habitat is unlikely to limit their spread in Florida. Management intervention is critical to reduce the potential for macaque-human conflict and threats to native species. However, rhesus macaque management is a contentious issue in Florida. Euthanasia of a charismatic species is likely to generate opposition (e.g., Sharp et al. 2011; Verbrugge et al. 2013), and sterilization efforts present significant logistical challenges (Anderson et al. 2019; e.g., cost, trap shyness, pathogen exposure). In addition to concerns from animal rights activists, rhesus macaques may increase tourism and therefore contribute to the local economy. However, increasing media coverage of human-macaque conflict, including a widely-circulated video documenting an encounter with an aggressive group of macaques within Silver Springs in summer 2017, may have affected public support for controlling the population. Confirmation that rhesus macaques in Silver Springs carry the Herpes B virus (Wisely et al. 2018) highlighted management as a public health and safety issue. As public perception has influenced management in the past, research is warranted to evaluate stakeholder attitudes regarding management options. By providing inference to the size of the rhesus macaque population, age and sex composition, and extent of their current range, our study provides critical understanding to inform management decisions.

Data availability statement The dataset generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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