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POPULATION METRICS FOR THE PERCEIVED COMMON AND ABUNDANT PENINSULA COOTER AND FLORIDA RED-BELLIED COOTER IN A FLORIDA, USA, SPRING ECOSYSTEM

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Abstract.—**The Peninsula Cooter (*Pseudemys peninsularis*) and the Florida Red-bellied Cooter (*P. nelsoni*) are considered common throughout much of their respective ranges. Both species occur in numerous habitats in Florida, USA, including rivers, lakes, ponds, freshwater springs, and spring runs. We sampled Peninsula Cooter and Florida Red-bellied Cooter populations from 1999 through 2015 as a component of a long-term freshwater turtle assemblage monitoring study in a protected central Florida spring-run complex that experiences high levels of human recreation. For each species, we: (1) generated relative abundance and population estimates; (2) quantified survivorship and recruitment; and (3) calculated sex ratios, density, and biomass. Population estimates were similar for both species, and sex ratios were approximately 1:1 for both species, whereas density and biomass estimates were higher than previous studies. Recapture rates were moderate for each sex of both species. Apparent survivorship was higher in males than females for both species but lower than from comparable studies. Sensitivities for both species suggest adult female mortality followed by the percentage of females breeding had the greatest influence on population growth. Stable populations of common species are important in maintaining overall community integrity. Therefore, it is prudent to promote the conservation of common species to protect ecosystem structures and services.**

Key Words.—conservation; population; *Pseudemys peninsularis*; *Pseudemys nelsoni*; relative abundance; long-term mark-recapture studies

INTRODUCTION

Research and conservation efforts are typically directed towards rare, threatened, or endangered species. The rarer or more vulnerable a species is to extinction, the more conservation effort it will receive (Lindenmayer et al. 2011). Considering the high rate of biodiversity loss across all major taxa, it has become evident conservation efforts should also be provided for species considered common and relatively abundant (Lindenmayer et al. 2011). Species that are considered common, however, even those with little to no data to support the perception that they are common, receive much less attention than rare species (Gaston and Fuller 2007). The lack of attention is surprising as abundant species dominate ecosystem biomass and, therefore, contribute disproportionately to ecosystem function and services (Gaston and Fuller 2007). Common species shape our world and ecosystems (Winfree et al. 2015). Common species are often referred to as dominant and even foundational due to their overarching value toward their habitats. A few abundant species may account for most of individuals in an ecosystem assemblage.

Despite their importance in ecosystems, long-term population monitoring is lacking for many species deemed common, abundant, or both. Long-term population research and monitoring projects provide managers and researchers with critical insights into how wildlife populations interact and function within their ecosystems (Lindenmayer and Likens 2009; Clutton-Brock and Sheldon 2010). Numerous species remain understudied, and even fewer are represented by long-term studies (Lovich and Ennen 2013), even though turtles are known to perform important ecosystem services (Iverson 1982; Lovich et al. 2018).

Globally, turtle populations are struggling due to a litany of anthropogenic issues, including overharvest for meat and pet trades, habitat destruction and decline, and climate change (Gibbons et al. 2000; Lovich et al. 2018). Of the 356 recognized turtle species, an estimated 61% are protected by state, federal, or international law (Turtle Taxonomy Working Group [TTWG] 2017); however, many freshwater turtle and tortoise species are woefully understudied. A quantitative assessment of North American turtle species found that the genus *Pseudemys* ranked last in the number of citations amongst the 24 listed genera of turtles of the USA and Canada (Lovich and Ennen 2013). Of the 58 recognized turtle species within the USA and Canada, the six species within the genus *Pseudemys* ranked 30th to 55th in the number of citations (Lovich and Ennen 2013), all in the bottom half of the least studied with three in the bottom 20% (Lovich and Ennen 2013).

The Peninsula Cooter (*Pseudemys peninsularis*) and the Florida Red-bellied Cooter (*P. nelsoni*) are widespread and considered common species within their respective ranges (Jackson 2006; Thomas and Jansen 2006; Ernst and Lovich 2009; TTWG 2017). The Peninsula Cooter ranges throughout Peninsular Florida, USA (Thomas and Jansen 2006; Ernst and Lovich 2009; Kryskso et al. 2011). The Florida Red-bellied Cooter is one of three recognized Redbelly Cooter species in the U.S. (Ernst and Lovich 2009) and ranges across the Florida peninsula and into a few river drainages in the panhandle of the state (Krysko et al. 2011), as well as a few known populations in extreme southern Georgia (Ernst and Lovich 2009), and a small, introduced population in Texas, USA (Dixon 2013). In Florida, both species use various habitat types (Jackson 2006; Thomas and Jansen 2006), including freshwater springs and spring run systems (Kramer 1995; Hrychyshyn 2007; Munscher et al. 2015a,b; Riedle et al. 2016). Habitat preferences for both species are similar and can overlap. The Peninsula Cooter prefers habitats with slow-flowing water with abundant vegetation (Thomas and Jansen 2006). The Florida Red-bellied Cooter prefers habitats with slow-to-moderate water flow with abundant vegetation (Jackson 2006) but information is lacking about the two species occurring sympatrically (Hyrcyshyn 2007; Munscher et al. 2015b).

We sampled populations of the Peninsula Cooter and the Florida Red-bellied Cooter at Wekiwa Springs State Park (WSSP) in Florida for 15 y (May 1999 through July 2015) as part of a long-term multi-species monitoring study of the freshwater turtle assemblage (Munscher et al. 2013, 2015a,b, 2020; Walde et al. 2016). Given the nature and scope of our study, it afforded us a unique opportunity to examine specific aspects of the life histories of each species. For each species we: (1) provide morphometrics, generated relative abundance and population estimates; (2) quantified annual survivorship and recruitment; and (3) calculated sex ratios, density, and biomass estimates. Our primary goal was to better understand how protected populations of these two perceived common species may function over a long time.

MATERIALS AND METHODS

***Study site*.—**We captured turtles in the public swimming area (0.20 ha), main lagoon (off-limits to public swimmers (1.67 ha), and the adjacent 1.1 km spring run of WSSP (28°42’N, 81°27’W) Apopka, Florida (Orange and Seminole counties), USA (Fig. 1). As with many state parks in Florida, the history of WSSP is of notable merit. Purchased by Florida in 1969, WSSP expels approximately 164 million L of water a day (a second-class spring based on water flow). The spring has been used for recreational activities since 1941 (Philpott 2008; Stamm 2008). Amid an urban setting (greater metropolitan areas of Orlando), there is over 16,200 ha of protected habitat surrounding WSSP. To the north and east is Rock Springs Run State Preserve, purchased by Florida in 1983. To the east of WSSP, there is the Wekiva River Buffer Conservation Area (Philpott 2008). Wekiwa Springs represents a typical central Florida spring with bottomland hardwood wetlands surrounding the spring and associated water habitats. The surrounding terrestrial habitat consists of dry sandy hill uplands maintained by frequent prescribed fires (Philpott 2008; Stamm 2008). At WSSP, the area directly around the spring boil is modified with concrete walls and ladders to facilitate swimming and general recreational use. The swimming area empties into the large study lagoon where public swimming is prohibited, but other activities such as canoeing and fishing are permitted. At the outflow of the main lagoon, the water moves into the Wekiwa Springs Run. The study area consists of approximately 2.67 ha of protected aquatic habitat (Munscher et al. 2015a,b, 2020). The Wekiwa Springs Run joins Rock Springs Run to form the headwaters of the Wekiva River. The Florida Department of Environmental Protection Aquatics Preserve manages the entire aquatic system.

***Capture methods*.**—The study of the freshwater turtle community in WSSP began in May 1999 and continued semi-annually through July 2015 except for 1999 and 2001 (each containing only one sample) and 2005 (containing three samples). The study started as

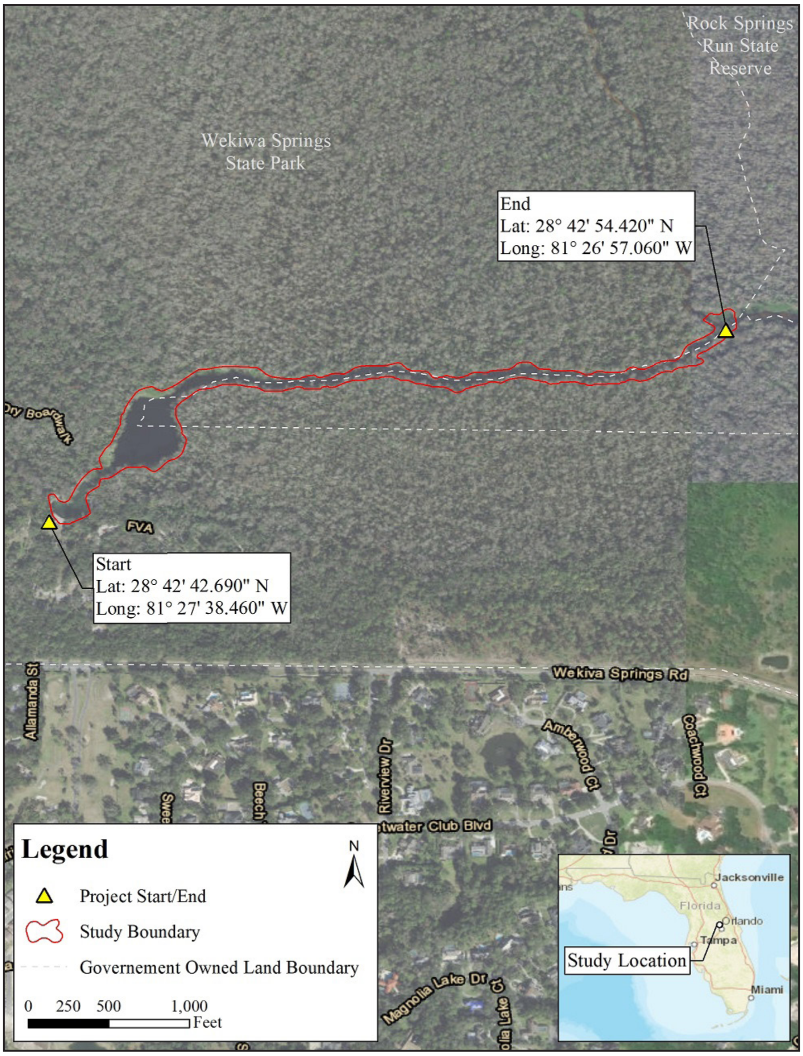

Figure 1. Aerial photograph of Wekiwa Springs State Park, Orange and Seminole counties, Florida, USA. The study site includes the public lagoon and main lagoon northeast of it, the connecting run between the lagoons, and 1.1 km of spring run habitat.

a field class, but changed over time into the long-term study described here, and levels of personnel effort were not always recorded, particularly during early sampling sessions. Sampling sessions were held somewhat regularly in March, May, July, and August of each year, with one exception being November 2005. For each sampling session, a variable number of snorkelers (typically between 15–20) captured turtles intermittently from approximately 0800 to 1600–1900, depending on the time of year and weather conditions. Each sampling session lasted for 3 d. We placed all captured turtles in canoes and brought them to a central location for data processing.

Data collection.—We recorded maximum straight-line measurements of carapace length (CL), plastron length (PL), carapace width (CW), and shell height (SH) to the nearest 1 mm. We determined the sex of turtles based on secondary sexual characteristics, notably tail length and girth, according to Ernst and Lovich (2009). We noted any unique features, physical anomalies such as damage, scars, or coloration for each turtle, which helped confirm individual identity. We weighed all turtles either using hanging Pesola spring scales (Pesola AG, Baar, Switzerland) or Ohaus top loading digital scales (Ohaus Corporation, Parsippany, New Jersey, USA) depending on turtle size and species. We then released turtles at their approximate capture location. We marked turtles using a variation of the technique described by Cagle (1939). In 2009, we also used passive integrated transponder (PIT) for turtles with CL > 70 mm as a secondary identification method. We injected PIT tags under the right bridge of the turtle into the inguinal cavity (Buhlman and Tuberville 1998; Runyan and Meylan 2005).

Data analysis.—Due to variation of sampling efforts within years, we developed encounter histories for all individual turtles on an annual basis. We calculated adult population sizes, as well as juvenile population sizes when the available data set allowed, using the POPAN parameterization of Jolly-Seber models (Jolly 1965; Seber 1965) in Program MARK (White and Burnham 1999). We calculated density (turtles/ha) by taking the calculated population density estimate and dividing by the size of the sampling area (2.67 ha). We calculated apparent annual survival (Φ) and recaptured rates (p) using open population Cormack-Jolly-Seber models (CJS; Lebreton et al. 1992) in Program MARK (White and Burnham 1999). To test for differences in Φ and p between sexes in adults of both species separately, we generated CJS models to test whether Φ or p differed based on sex, time, or a sex-time interaction. We also generated Cormack-Jolly-Seber models to test whether Φ or p differed between the two species of *Pseudemys*, time, or a species-time interaction. We based model selection for all analyses on Akaike Information Criterion (AICc) values, with lower values denoting greater parsimony (Burnham and Anderson 2002).

We used our estimated demographic rates to develop deterministic population viability models in Program Vortex (Lacy and Pollack 2014). Default population-based scenarios were constructed using population and survivorship estimates and sex ratios were calculated from mark-recapture data collected as part of this project. We extracted reproductive and age-based data from summaries in Jackson (2006) and Thomas and Jansen (2006). For the Peninsula Cooter age at first reproduction in females was set at 6 y and males at 3 y, the maximum number of clutches annually was set at four, and the total number of eggs per year at 70. For the Florida Red-bellied Cooter, age at first reproduction in females was set at 7 y and males at 3 y, the maximum number of clutches annually was set at seven, and the total number of eggs per year at 60. We found little information on nest success, but as for most aquatic turtles, it is thought to be low, so egg mortality was arbitrarily set at 70% for the default scenario and later tested as part of the sensitivity tests. Environmental variation among these parameters is difficult to calculate, so we used the default setting in Vortex of 10%. We used 13 variables as scenario input for Vortex (Table 1).

Table 1. Population scenario input for population viability models in Program Vortex for Peninsula Cooter (*Pseudemys peninsularis*) and Florida Red-bellied Cooter (*P. nelsoni*) at Wekiwa Springs State Park, Florida, USA.

Scenario Entries	*P. peninsularis*	*P. nelsoni*
Number of iterations	100	100
Number of Years	100	100
Age at first reproduction of females	6	7
Age at first reproduction of males	3	3
Maximum Life Span	30	30
Maximum number Broods/Year	4	6
Maximum progeny/brood	15	30
Sex Ratio at Birth	1:1	1:1
Maximum age of Reproduction	30	30
Juvenile Female Mortality	0.70	0.86
Adult Female % Annual Mortality	0.15	0.13
Juvenile Male % Annual Mortality	0.70	0.86
Adult Male % Annual Mortality	0.20	0.21

We then ran a series of sensitivity tests for four parameters: (1) percentage of females breeding/year; (2) hatchling/egg mortality; (3) 1st-year mortality; and (4) adult female mortality. Values for each parameter range from 0–100% and increased by 5% with each iteration. Sensitivity tests within Vortex work by creating a series of scenarios in which each parameter can be varied. We set scenarios so that values for each parameter varied from 0–100%. For each scenario, we chose a value randomly for each of the three parameters from across the range specified. We graphed the mean value of the output variable, averaged across all combinations of values for the other tested variables.

Results

We captured and individually marked 1,016 Peninsula Cooters (3,017 total captures) and 705 Florida Red-bellied Cooters (2,062 total captures; Fig. 2). Of the 3,855 unique turtles (of nine species) we captured

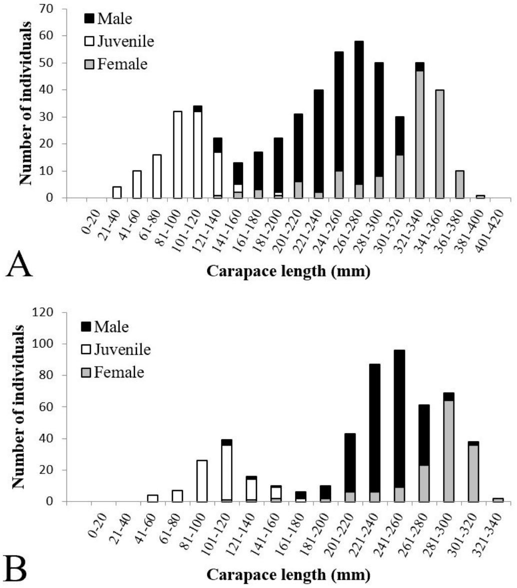

Figure 2. Histograms of *Pseudemys* captured at Wekiwa Springs State Park Florida, USA, by carapace length (mm) for (A) Peninsula Cooter (*P. peninsularis*) from 2000–2015 and (B) Florida Red-bellied Cooter (*P. nelsoni*) from 1999–2015.

Table 2. Population estimates (n) and 95% confidence intervals (in parentheses), mean density (number/ha), and mean biomass (kg/ha) for Peninsula Cooter (*Pseudemys peninsularis*) and Florida Red-bellied Cooter (*P. nelsoni*) at Wekiwa Springs State Park, Florida, USA. The biomass of *P. nelsoni* does not include five of the 326 males and eight of the 285 females that were not weighed due to lack of equipment on one day.

Age/Sex	n	Density	Biomass
P. peninsularis			
Male	576 (562, 594)	215.7	418.9
Female	489 (476, 506)	183.2	737.6
Juvenile	54 (50, 61)	20.22	3.28
Total		419.1	1,159.8
P. nelsoni			
Male	696 (646, 754)	260.7	482.8
Female	623 (576, 678)	230.7	705.7
Juvenile	92 (76, 115)	34.46	7.65
Total		525.9	1,196.2

and individually marked during this 15-y study period, these two species attributed relative abundance values of 0.26 and 0.18, respectively. Total population estimates (summation of estimates for males, females, and juveniles) were slightly higher for the Florida Red-bellied Cooter (1,411) than Peninsula Cooter (1,119; Table 2). Mean density estimates were 419.1 turtles/ha for the Peninsula Cooter and 525.9 turtles/ha for the Florida Red-bellied Cooter. Total biomass calculated for each species were 1,159.8 kg/ha for the Peninsula Cooter and 1,196.2 kg/ha for the Florida Red-bellied Cooter, respectively. For both species, all morphometric variables were significantly larger in females than in males (Table 3).

The most parsimonious model for apparent annual survival and recapture rates in both species was where survivorship varied by sex, and recapture rates varied between sampling periods (Tables 4 and 5). When comparing survivorship and recapture rates between species, the most parsimonious model was that survival varied by time, and recapture rates varied by group and time (Table 6). Apparent survivorship was higher in females for both species, although recapture rates were moderate for each sex (Table 7). While apparent survivorship was low for juveniles of both species, particularly the Florida Red-bellied Cooter, recapture rates were high (Table 7).

Table 3. Mean comparisons for morphometric variables for Peninsula Cooter (*Pseudemys peninsularis*) and Florida Red-bellied Cooter (*P. nelsoni*) from Wekiwa Springs State Park, Florida, USA. Values given ± one standard error. Asterisks (*) indicate the number of individuals available for the variable mass.

Variable	Male	Female	*t*	*P*
Pseudemys peninsularis				
Sample size	484	418		
Carapace length (mm)	248.0 ± 2.4 (95–354)	305.4 ± 2.6 (117–381)	16.13	< 0.001
Carapace width (mm)	170.3 ± 1.5 (78–228)	211.1 ± 1.6 (91–264)	18.98	< 0.001
Plastron length (mm)	215.3 ± 2.1 (87–307)	273.8 ± 2.3 (106–351)	18.83	< 0.001
Shell height (mm)	100.9 ± 1.0 (46–154)	133.5 ± 1.1 (52–175)	21.16	< 0.001
Mass (g)	1941.9 ± 60.7 (139–4875)	4027.0 ± 65.3 (250–7400)	23.4	< 0.001
Pseudemys nelsoni				
Sample size	326 (321*)	285 (277*)		
Carapace length (mm)	236.6 ± 2.3 (106–317)	269.6 ± 2.4 (97–327)	9.89	< 0.001
Carapace width (mm)	176.7 ± 1.4 (94–217)	193.6 ± 1.5 (83–235)	10.86	< 0.001
Plastron length (mm)	217.5 ± 2.1 (102–293)	253.1 ± 2.3 (88–307)	11.36	< 0.001
Shell height (mm)	98.4 ± 1.0 (47–137)	118.7 ± 1.1 (46–158)	13.43	< 0.001
Mass (g)	1852.1 ± 52.3 (262–4100)	3058.5 ± 56.3 (145–5000)	15.71	<0.001

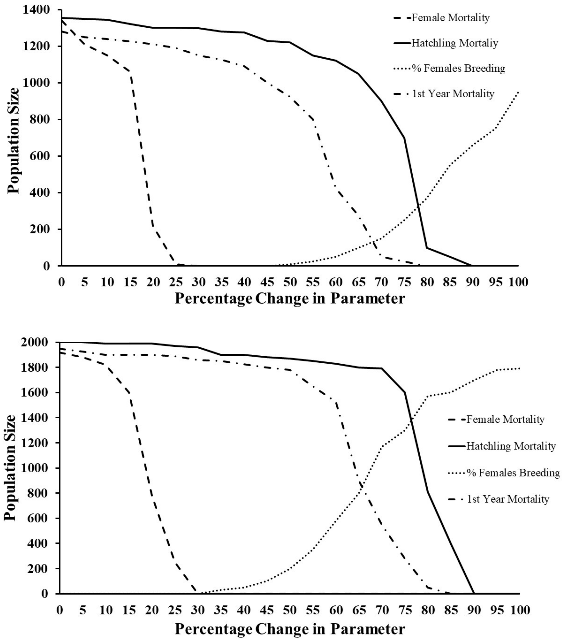

Figure 3. Sensitivity tests for (Top) Peninsula Cooter (*Pseudemys peninsularis*) and (Bottom) Florida Red-bellied Cooter (*P. nelsoni*) at Wekiwa Springs State Park, Florida, USA. Trends show shifts in population size related to variation in tested demographic traits.

Deterministic characteristics for *Pseudemys* at Wekiwa Springs based on the default scenario in Program Vortex suggests stable to slightly growing populations. Lambda values and net reproductive rate (R_0 or the average number of age class zero offspring produced by an average newborn organism during its lifetime) were higher than 1.0 (Table 8). Mean generation times for both species were similar (Table 8). Sensitivity tests for both species suggest adult female mortality followed by the percentage of females breeding had the greatest influence on population growth (Fig. 3). While egg/hatchling mortality were arbitrarily set at 70% due to a lack of data, this characteristic did not seem to have as strong an influence on population growth as adult mortality rates (Fig. 3).

Discussion

Most species of *Pseudemys* are considered common and relatively abundant across their ranges (Ernst and Lovich 2009), presumably because they are easily observable, large basking turtles. The statement is true considering the Peninsula Cooter and the Florida Red-bellied Cooter both appear to have large reproducing populations in Wekiwa Springs State Park. Throughout our 15-y study period, they comprised approximately 44% (Peninsula Cooter 26% and Florida Red-bellied Cooter 18%) of the total captures of the nine species observed in the assemblage. In contrast, studies using similar methods of capture including Huestis and Meylan (2004) who captured 2,552 turtles at Rainbow Run, in which the Coastal Plain Cooter (*P. concinna floridana*) attributed a relative abundance of 0.085 and *P. nelsoni* 0.012. Similarly, Johnston et al. (2011) estimated relative abundances of 0.029 and 0.025 for *P. peninsularis* and *P. nelsoni*, respectively. While at Volusia Blue Springs, Riedle et al. (2016) reported capturing 520 turtles during their study, of which the Peninsula Cooter attributed a relative abundance value of 0.41 and the Florida Red-bellied Cooter a value of 0.12.

Table 4. Comparison of Cormack-Jolly-Seber models for apparent annual survival (Φ) and recapture rates (p) for Peninsula Cooter (*Pseudemys peninsularis*) at Wekiwa Springs State Park, Florida, USA. Models differ in whether Φ and p are assumed to be constant (.), fully time-dependent (t), or differ between sexes (g), and whether there are interactions (*) among these factors.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Number of Parameters	Deviance
Φ(g) p(t)	6249.912	0	0.98733	1	18	2092.058
Φ(g*t) p(t)	6258.628	8.7166	0.01264	0.0128	58	2017.907
Φ(g) p(g*t)	6270.56	20.6481	0.00003	0	47	2052.933
Φ(g*t) (g*t)	6274.639	24.7268	0	0	77	1993.467
Φ(t) p(g*t)	6282.504	32.5919	0	0	58	2041.783
Φ(.) p(g*t)	6287.28	37.3678	0	0	45	2073.826
Φ(t) p(t)	6291.787	41.875	0	0	29	2111.447
Φ(g) p(g)	6294.794	44.882	0	0	6	2161.213
Φ(g) p(.)	6295.534	45.6219	0	0	4	2165.973
Φ(.) p(t)	6297.091	47.1795	0	0	16	2143.301
Φ(g*t) p(.)	6301.136	51.2241	0	0	45	2087.682
Φ(g*t) p(g)	6301.245	51.3334	0	0	47	2083.618
Φ(t) p(g)	6316.426	66.5137	0	0	18	2158.571
Φ(.) p(g)	6326.721	76.8088	0	0	4	2197.16
Φ(t) p(.)	6331.21	81.2979	0	0	16	2177.42
Φ(.) p(.)	6340.453	90.5411	0	0	2	2214.905

Table 5. Comparison of Cormack-Jolly-Seber models for apparent annual survival (Φ) and recapture rates (p) for Florida Red-bellied Cooter (*P. nelsoni*) at Wekiwa Springs State Park, Florida, USA. Models differ in whether Φ and p are assumed to be constant (.), fully time-dependent (t), or differ between sexes (g), and whether there are interactions (*) among these factors.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Number of Parameters	Deviance
Φ(g) p(t)	3987.563	0	0.99999	1	19	1572.129
Φ(g) p(g*t)	4011.606	24.0428	0.00001	0	47	1537.448
Φ(g*t) p(t)	4021.43	33.8666	0	0	59	1521.37
Φ(.) p(g*t)	4031.845	44.2816	0	0	45	1561.96
Φ(g*t) p(g*t)	4035.161	47.5979	0	0	77	1495.388
Φ(.) p(t)	4041.028	53.4643	0	0	17	1629.699
Φ(t) p(g*t)	4042.147	54.5842	0	0	59	1542.088
Φ(g) p(g)	4046.947	59.3838	0	0	6	1657.993
Φ(t) p(t)	4048.172	60.6092	0	0	31	1607.859
Φ(g) p(.)	4051.017	63.4542	0	0	4	1666.094
Φ(g*t) p(g)	4055.179	67.6156	0	0	47	1581.021
Φ(g*t) p(.)	4060.193	72.6302	0	0	45	1590.309
Φ(t) p(g)	4060.849	73.2859	0	0	19	1645.415
Φ(.) p(g)	4077.633	90.0701	0	0	4	1692.71
Φ(t) p(.)	4086.748	99.1843	0	0	17	1675.419
Φ(.) p(.)	4103.028	115.4649	0	0	2	1722.124

Our study and that of Riedle et al. (2016) found high relative abundances for both species compared to other species captured, including Florida Softshell Turtles (*Apalone ferox*) and Snapping Turtles (*Chelydra serpentina*). An examination of the current literature (Appendix A) revealed a trend of low relative abundance and capture success for each species. Their herbivorous nature as adults likely makes *Pseudemys* species extremely difficult to capture with traditional trapping methods (Lindeman 2007; Mali et al. 2018). No effective lures or baits are known at this time. Most studies that successfully capture these species in large numbers have done so via hand capture while snorkeling (Marchand 1942; Huestis and Meylan 2004; Munscher et al. 2015b; Riedle et al. 2016).

Population demography studies for either species are rare. Few studies have calculated population metrics, including population, density, biomass, and survivorship estimates with which we can compare our results. Our results lie on the high end of the few reported values for

Table 6. Comparison of Cormack-Jolly-Seber models for apparent annual survival (Φ) and recapture rates (p) between Peninsula Cooter (*Pseudemys peninsularis*) and Florida Red-bellied Cooter (*P. nelsoni*) at Wekiwa Springs State Park, Florida, USA. Models differ in whether Φ and p are assumed to be constant (.), fully time-dependent (t), or differ between sexes (g), and whether there are interactions (*) among these factors.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Number of Parameters	Deviance
Φ(t) p(g*t)	10318.05	0	0.99984	1	46	2840.021
Φ(.) p(g*t)	10336.58	18.5266	0.00009	0.0001	32	2887.165
Φ(g) p(g*t)	10338.06	20.0084	0.00005	0.0001	33	2886.61
Φ(g*t) p(g*t)	10339.79	21.7362	0.00002	0	60	2832.915
Φ(t) p(t)	10359.48	41.432	0	0	31	2912.106
Φ(g*t) p(t)	10368.87	50.815	0	0	46	2890.836
Φ(.) p(t)	10377.48	59.4264	0	0	17	2958.481
Φ(g) p(t)	10379.5	61.4463	0	0	18	2958.481
Φ(t) p(.)	10406.68	88.6284	0	0	17	2987.683
Φ(t) p(g)	10407.06	89.0063	0	0	18	2986.041
Φ(g*t) p(g)	10417.9	99.8464	0	0	33	2966.448
Φ(g*t) p(.)	10418.11	100.0566	0	0	32	2968.695
Φ(.) p(g)	10441.89	123.8412	0	0	3	3051.058
Φ(.) p(.)	10442.85	124.7939	0	0	2	3054.014
Φ(g) p(g)	10443.48	125.4266	0	0	4	3050.639
Φ(g) p(.)	10444.85	126.7972	0	0	3	3054.014

Table 7. Apparent survivorship (Φ), recapture probability (*p*), and 95% confidence interval (in paretheses) for Peninsula Cooter (*Pseudemys peninsularis*) and Florida Red-bellied Cooter (*P. nelsoni*) at Wekiwa Springs State Park, Florida, USA.

Age/Sex	Φ	*P*
P. peninsularis		
Male	0.80 (0.78, 0.83)	0.37 (0.34, 0.40)
Female	0.85 (0.83, 0.87)	0.37 (0.34, 0.40)
Juvenile	0.30 (0.18, 0.45)	0.78 (0.31, 0.96)
P. nelsoni		
Male	0.79 (0.77, 0.82)	0.37 (0.34, 0.41)
Female	0.87 (0.85, 0.89)	0.31 (0.28, 0.35)
Juvenile	0.14 (0.07, 0.27)	0.99 (0.98, 1.00)

all measured variables except survivability (Appendix A). Our population estimates are much larger than any previous study (Appendix A). Despite being a common and abundant species, only three previous studies report calculated population sizes of the Peninsula Cooter at > 200 individuals (Giovanetto 1992; Huestis and Meylan 2004; Riedle et al. 2016; Appendix A), and only one project did so for the Florida Red-bellied Cooter (Kramer 1995). In comparison, our estimates for the Peninsula Cooter and the Florida Red-bellied Cooter were 1,119 and 1,411, respectively. We attribute the lower population values of other studies to the aforementioned capture difficulties.

Historically, some turtle species were known to achieve extremely high population density values, comparable to prolific schools of fish (Iverson 1982; Lovich et al. 2018). Wildlife managers often rely on population density estimates to make recommendations for species management, yet accurately estimating this parameter remains difficult (Gibbons 1997) due to the limited number of long-term studies available for analysis. In the early 1900s, the Coastal Plain Cooter was reported as the most abundant species in the Okefenokee Swamp (Wright and Funkhoser 1915; Thomas and Jansen 2006). The species was estimated to represent approximately 62% of all turtles collected at Homosassa Springs, Florida (Giovanetto 1992). At Rock Springs Run State Preserve, a connected preserved area to WSSP, Kramer (1995) estimated population densities of 24.1 turtles/ha for adult Peninsula Cooters (reported as Coastal Plain Cooters before classification change) and 78.6 turtles/ha for adult the Florida Red-bellied Cooter, far less than those estimated in our study, which found 419 Peninsula Cooters/ha and 526 Florida Red-bellied Cooters/ha. Wekiwa Springs State Park is an extensive open system that ultimately connects to the Wekiva River and Rock Springs Run. Movement of both cooter species within the WSSP ecosystem has been examined, and both travel far greater ranges and possess far larger home ranges than previously documented (Hootman 2019). Florida Red-bellied Cooters prefers habitats with more water flow and aquatic vegetation (Kramer 1995; Jackson 2006). There could have been an influx of this species into WSSP because it was the preferred habitat with an abundance of food enhanced by the presence and dominance of Hydrilla (*Hydrilla verticillata*), a prolific invasive species (Bjorndal et al. 1997; Munscher et al. 2015b). Both species have been documented to use Hydrilla, as it is a high-energy dense food source (Bjorndal et al. 1997; Munscher et al. 2015b).

Further density comparisons can be made with studies at Rainbow Run. Marchand (1942) found three species of cooter including: River Cooter, Coastal Plain Cooter, and Florida Red-bellied Cooters. The most abundant of the three was *P. concinna* (Iverson 1982), and *P. nelsoni* was consistently less abundant than either of its congeners (Marchand 1942). A more recent study at Rainbow Run, nearly 50 y after Marchand (1942), found that Coastal Plain Cooter had a density of 3.8–6.5 turtles/ha, whereas the Florida Red-bellied Cooter was captured too infrequently to estimate density (Meylan et al. 1992; Huestis and Meylan, 2004). In their report, Huestis and Meylan (2004) acknowledged that Marchand documented collecting large numbers of *Pseudemys*. Nearly 70% of the captures that Marchand (1942) reported were *Pseudemys*, while only 7% of Meylan et al. (1992) sample were *Pseudemys*. Overharvesting of the large *Pseudemys* species from Rainbow Run during the 50 y between the two studies likely resulted in an extreme decrease in densities (Meylan et al. 1992).

Biomass is an important metric in wildlife population ecology as it reflects the available and stored energy within the food web in a given ecosystem (Iverson 1982; Congdon et al. 1986; Lovich et al. 2018). Typically, the higher biomass a species or group of species attains, the more integral functions they provide for their ecosystem (Gaston and Fuller 2008; Lindenmeyer et al. 2011; Lovich et al. 2018). To our knowledge, our results constitute the highest documented biomass value for either species (Appendix A). Surprisingly, few studies have attempted to calculate biomass of *Pseudemys* populations, despite their status as common and

Table 8. Deterministic characteristics of Peninsula Cooter (*Pseudemys peninsularis*) and Florida Red-belled Cooter (*P. nelsoni*) populations at Wekiwa Springs State Park, Florida. Symbols are represented by population growth rate (λ), net replacement rate (R_0), and mean generation time (T). Values derived from baseline model in Vortex.

Species	λ	R_0	Female T	Male T	Mean T	Extinction Risk
P. peninsularis	1.01	1.17	11.32	6.68	9.09	0.00
P. nelsoni	1.02	1.43	13	6.5	9.75	0.00

conspicuous species within their ecosystems. Marchand (1942) reported a biomass of 384.2 kg/ha for Peninsula Cooters and 311.1 kg/ha for Florida Red-bellied Cooters. At Volusia Blue Springs a neighboring spring on the St. Johns River, Florida, Riedle et al. (2016) reported biomass per species of 779 kg/ha for Peninsula Cooters and 173 kg/ha for Florida Red-bellied Cooters. The high biomass recorded for each species at WSSP could indicate the high-quality habitat that WSSP offers. The ecosystem is protected and has seemingly abundant resources (Munscher et al. 2015b). Additionally, the constant temperature of the spring allows for year-round activity and growth (Munscher et al. 2015b; Walde et al. 2016); however, the system has environmental issues, including invasive species and increasing nitrate levels (Toth and Fortich 2002; Munscher et al. 2015b). The effect of these issues on the turtle populations at WSSP should be further investigated.

Annual apparent survival probabilities are different from true survival probabilities in that mortality and emigration are confounded, and therefore likely to be biased low (White and Burnham 1999). Our survivorship results are lower than those reported in habitats outside of WSSP. In comparison, the highest value presented (Appendix A) calculated apparent annual survival with sexes pooled of 0.97 ± 0.01 (standard error) for Peninsula Cooters and 0.98 ± 0.01 for Florida Red-bellied Cooters in Volusia Blue Springs (Riedle et a. 2016). Our survivorship estimates are contrary to what would be expected from a protected habitat and from species that obtain large adult sizes. The differences here could be an artifact of the differences in population sizes and the ecosystems themselves. Volusia Blue Springs is a small system that the authors noted as having a small resident population of Red-bellied Cooters, while individual Peninsula Cooters acted more like transients within the spring/river system (Riedle et al. 2016). Our study only sampled a very small portion of a large open system in which these species have been documented as having made extensive movements in and out of regularly (Hootman 2019). Males were documented as moving more often and traveling greater overall distances than female for both species (Hootman, 2019). These long-distance movements, particularly by males, may account for the lower apparent survival estimates reported in this study.

Our estimated overall/adult/operational sex ratios were not significantly sexually biased for either species. Male-biased sex ratios seem common for these species (Bancroft et al. 1983; Huestis and Meylan 2004; Riedle et al. 2016; Appendix A). Sex ratios can help determine effective population sizes, reproductive output for populations, and ultimately the long-term success of a population (Gibbons 1990; Hrycyshyn 2007). Many turtle populations throughout the USA have become increasingly male-biased over the past century (Gibbs and Steen 2005; Thompson et al. 2018), a trend that could continue with rising global temperatures and increasingly fragmented landscapes (Schwanz and Janzen 2008; Thompson et al. 2018).

The Population Viability Analyses calculated here suggest that female mortality and percentage of breeding females had the most influence on population growth. While the results of the sensitivity tests suggest similar life-history characteristics for both species, there is some variation in reproduction between the two species that may contribute to maintenance of stable populations. Based on available literature (Jackson 2006; Thomas and Jansen 2006) and data collected for this study, female Florida Red-bellied Cooters mature a year later than Peninsula Cooters and exhibited higher juvenile mortality. In turn though, Florida Red-bellied Cooters tend to produce more clutches/year and more eggs/year than Peninsula Cooters. Despite these differences in age at maturity, populations of both species are reliant on the number of females surviving and reproducing in a given year.

Various environmental factors can differently affect male and female survival. Female turtles may experience high mortality during the nesting season, as they are in greater danger of predation and road mortality (Steen and Gibbs 2004; Aresco 2005; Tucker et al. 1999). Over the past 15 y, we have found six large, marked females of both species walking over a 1 km away from the study site. Large turtle species like *Pseudemys* have few predators once they reach adulthood. The three major threats facing these species and others within this genus are: (1) overharvesting for human consumption (Heinrich et al. 2010); (2) high mortality from boat collisions (Jackson 2006; Heinrich et al. 2012); and (3) habitat degradation, including insufficient basking sites (Jackson 2006; Heinrich et al. 2012).

The conservation of Wekiwa Springs State Park has resulted in a large and diverse turtle community (Munscher et al. 2015a,b, 2020; Walde et al. 2016); however, eutrophication of the aquatic system is a major threat. Over the past few decades, this iconic state park ecosystem has seen decreases in both water quality and quantity due to loss of recharge area, primarily due to more impervious surfaces (pavement/concrete) from the greater metropolitan Orlando area, and high nitrate levels due to in-ground, old septic tanks (Saint Johns River Water Management District 2006; Hrysychyn 2007; Tucker et al. 2014). The water coming out of the spring during this study has spent roughly 20 y underground, accumulating nitrates from the use of fertilizers and septic tanks in place before the 1980s (Toth and Fortich 2002; Kennedy et al. 2009). These high nitrate levels could explain the dominance and increased abundance of invasive plant species (Kennedy et al. 2009). We first observed Hydrilla in small quantities in 2001, and within a year, it had overtaken native vegetation and choked off a significant part of the study site lagoon and into the spring run (Hrysychyn 2007). Staff of the Wekiwa Springs State Park and the Florida Department of Environmental Protection Aquatics Preserve attempted several removal/management strategies to combat this invasive species over the subsequent 15 y (Virginia Oros, pers comm.). One strategy employed was to use an aquatic barrier that effectively bisected the main lagoon, with one side having the spring flow cut off in which treatment could be applied through the use of a photosynthetic inhibitor. They also attempted manual removal in areas of the spring and lagoon. In 2015, the removal efforts seemed to be successful, with Hydrilla effectively removed from the system.

The presence of Hydrilla made the capture of *Pseudemys* difficult in certain areas of the study site during years when the plant was abundant, which may have influenced apparent survivorship calculations for the species. Hydrilla, however, does act as an abundant and primary food source for the turtles and provides cover from predators such as American Alligators (*Alligator mississippiensis*; Munscher et al. 2015b; Alder et al. 2018). Over the following years, researchers noticed an accumulation of dead plant matter and detritus associated with the dead Hydrilla and stormwater runoff. Wekiwa Springs is a second-class spring that does not seem to have the necessary flow rate to push suspended organic materials downstream. As of late 2015, there was a noticeable, approximately 1-m deep detritus/muck layer at the bottom of the study site lagoon (Wetland Solutions 2007; Munscher et al. 2015b, 2020). This muck layer will need monitoring for the impact it may have on aquatic vegetation within the system and the species that rely on it for various aspects of their life history.

The perception in much of the literature and anecdotally regarding these two species of turtles is that they are common or abundant (Jackson 2006; Thomas and Jansen 2006). Though seemingly abundant in some studies (Riedle et al. 2016; this study), they are far less so in others (Huestis and Meylan 2004; Johnston et al. 2011). While *Pseudemys* species appear abundant and widespread, perhaps their size and variation in environmental and anthropogenic threats result in site-specific variation in abundance.

Wekiwa Springs State Park is an iconic and protected natural area surrounded by other natural reserve areas encompassing over 16,200 ha of state park and preserve land amid metropolitan Orlando. The site boasts a diverse and thriving turtle assemblage (Munscher et al. 2015a,b, 2019, 2020; Walde et al. 2016; Hootman 2019). We found both *Pseudemys* species had robust and stable populations. Our study serves as a reference and illustrates the need for demographic studies of lesser-studied and apparently abundant species. Continued monitoring of this community could help document how various changing environmental factors such as nutrient load, decreased water flow, and climate change affect turtle species. Future changes in population demography from this baseline might also indicate changes in water and habitat quality, and therefore act as a critical signal that remediation or management is required.

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Andrew S. Weber is currently an Ecologist with the U.S. National Park Service at Upper Delaware Scenic and Recreational River in Beach Lake, Pennsylvania, USA, where he mainly focuses on aquatic systems. He obtained his A.S. and B.S. from Pennsylvania State University, State College, USA, and his M.S. from Tennessee Technological University, Cookeville, USA. Andy is an Associate Researcher for the Turtle Survival Alliance - North American Freshwater Turtle Research Group (TSA-NAFTRG) and has been helping with various projects since 2003. Andy also serves as the Director of Field Programs for theTurtleRoom and helps facilitate collaborative efforts with TSA-NAFTRG and other groups. (Photographed by Jess Weber).

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Brian P. Butterfield earned a B.S. from Harding University, Searcy, Arkansas, USA, an M.S. from Arkansas State University, Jonesboro, USA, and a Ph.D. from Auburn University, Auburn, Alabama, USA. He is currently a Professor and Chair of the Department of Biological, Physical and Human Sciences at Freed-Hardeman University in Henderson, Tennessee, USA. His current research focuses on freshwater turtle ecology and conservation, and the biology of invasive amphibians and reptiles. Brian frequently publishes with undergraduate students and is committed to providing his undergraduate students with quality research experiences. (Photographed by Bret Jones).

J. Brian Hauge is Professor of Biology at Peninsula College in Port Angeles, Washington, USA, and Adjunct Professor for Huxley College of the Environment, Western Washington University, Bellingham, USA. He earned B.S. and M.S. degrees from South Dakota State University, Brookings, USA, and a Ph.D. from Auburn University, Auburn, Alabama, USA. Brian is a co-founder of the Turtle Survival Alliance - North American Freshwater Turtle Research Group. Brian has studied turtle populations, invasive amphibians, and reptiles (especially in Florida), and tropical herpetology in Costa Rica and Belize. (Photographed by Renae Gilles).

Appendix A. Population metrics including population, density, biomass, and survival estimates as well as sex ratios for Peninsula Cooter (*Pseudemys peninsularis*) and Florida Red-belled Cooter (*P. nelsoni*) from the literature.

Source	Location	Captured #	Population Estimates	Density Estimates (turtles/ha)	Biomass Estimates (kg/ha)	Survival Estimates	Sex Ratios (M:F)
Pseudemys peninsualris							
Reidle et al. 2016	Volusia Blue Springs	214	240 ± 6	—	779	0.97 ± 0.01	1.99:1
Huestis and Meylan 2004	Rainbow Run	218	250–750	—	—	—	1.57:1
Meylan et al. 1992	Rainbow Run	15	—	3.8–6.5	—	—	—
Bancroft et al. 1983	Lake Conway	465	—	—	—	—	2.27:1
Kramer 1995	Rock Springs Run	39	71	24.1	—	—	1.42:1
Marchand 1942	Rainbow Run	439	—	—	384.2	—	1:1.15
Giovanetoo 1992	Homosassa Springs	239	233–436	48.4	—	—	1.24:1
Johnston et al. 2011	Santa Fe River	8	—	—	5.7	—	—
Johnston et al. 2016	Sana Fe River / Springs	29	—	—	—	—	—
Congdon and Gibbons 1989	Ellenton Bay	77	—	7	7.8	—	—
Current Study	Wekiwa Springs State Park	1016	1119	419.1	1159.8	0.825	1.16:1
Pseudemys nelsoni							
Reidle et al. 2016	Volusia Blue Springs	63	62 ± 2	—	173	0.98 ± 0.01	1.23:1
Bancroft et al. 1983	Lake Conway	83	—	—	—	—	Female bias
Kramer 1995	Rock Springs Run	126	231	78.6	153.8	—	1.16:1
Huestis and Meylan 2004	Rainbow Run	26	—	—	—	—	Male dominated
Meylan et al. 1992	Rainbow Run	1	—	—	—	—	—
Marchand 1942	Rainbow Run	29	—	—	311.1	—	1:1.41
Giovanetoo 1992	Homosassa River	125	98–233	22.2	—	—	0.54:1
Johnston et al. 2011	Santa Fe River	7	—	—	5.7	—	—
Johnston et al. 2016	Santa Fe River / Springs	35	—	—	—	—	—
Chapin and Meylan 2010	Ichetucknee Springs	3	—	—	—	—	—
Current Study	Wekiwa Springs State Park	705	1411	525.9	1196.2	0.83	1.14:1