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Spatial Capture–Recapture Derived Turtle Capture Probabilities and Densities in the Chesapeake and Ohio Canal

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Abstract.—**More than half of turtle species worldwide are threatened because of habitat loss, invasive species, environmental pollution, disease, unsustainable use, and global climate change. However, some turtles are capable of existing in highly modified habitats, including structures designed to benefit human populations such as reservoirs and canal systems. Examining turtle distributions in large canal systems can inform conservation plans protecting turtle populations within a potential reservoir network and expand our understanding of underlying mechanisms regulating populations. We conducted spatial capture–recapture on turtles inhabiting sections of the Chesapeake and Ohio Canal. We developed a Bayesian spatial capture–recapture model to estimate densities, sex ratios, and associated capture probability parameters for *Chrysemys picta* (Painted Turtle), *Chelydra serpentina* (Common Snapping Turtle), *Sternotherus odoratus* (Eastern Musk Turtle), and *Pseudemys rubriventris* (Red-Bellied Turtle) captured at 12 sites along 28 km of the canal. We examined the impact of canal depth and forest cover on population densities and the variation in capture probability between sites and sampling days. We found population densities to vary between sites and the associated sex ratios to vary between species, as did the effect of depth and forest cover. Overall capture rates decreased each day, but there was trap-happy behavior from all species except *S. odoratus*. Our information can set a baseline for understanding turtle populations and inform management in the Chesapeake and Ohio Canal National Historical Park. It is also one of the first studies to establish methods for using new spatial capture–recapture to quantify densities and aquatic space use of turtles.**

In 2020, the International Union for Conservation of Nature (IUCN) listed more than half of turtle species evaluated worldwide as threatened (179 of 289 categorized as vulnerable, endangered, or critically endangered; IUCN, 2021). Threats to worldwide turtle populations include habitat loss and degradation, introduced invasive species, environmental pollution, disease, unsustainable collection, and global climate change (Gibbons et al., 2000; Ernst and Lovich, 2009; Lovich et al., 2018). Turtle populations are especially sensitive to threats impacting adult survival and reproduction because of a combination of long adult lifespans, low annual juvenile survivorship, and high annual adult survivorship (Ernst and Lovich, 2009). Yet, turtle species are often overlooked in management plans that are commonly aimed toward protecting bird and mammal species (Roll et al., 2017). Therefore, consideration of turtle species in conservation planning, including in already managed areas, is vital to maintaining global turtle populations.

Managed remnant canal systems are prevalent in the eastern United States and provide protected habitat for a large diversity of freshwater species, including numerous turtle species (National Park Service [NPS], 2017). In the northeastern United States specifically, the landscape is connected by a large network of canals created in the late 18th and early 19th Century (Rodrigue, 2020). Yet, while canals in the northeastern United States might provide a network of suitable habitat for various species, only a few studies have examined turtle behavior and populations within these canals (e.g., Conner et al., 2005; Peterman and Ryan, 2009; Ryan et al., 2014).

Running from Cumberland, Maryland to Washington, DC, The Chesapeake and Ohio Canal (C&O Canal) is inhabited by a variety of turtle species (NPS, 2017). The canal system is managed by the NPS as part of the Chesapeake and Ohio National Historical Park and now consists of varying-sized ephemeral and permanent pools within a 297-km linear system of intermittent connectivity (Thomas et al., 2014). Because of the park's narrow and linear structure, the canal's ecosystem and its inhabited species are especially vulnerable to surrounding land use and vegetation (Thomas et al., 2014). The 2014 National Resource Condition Assessment (Thomas et al., 2014) found impervious surface within and surrounding the park to be less than the 10% reference condition, and impervious surface coverage adjacent to the park was highest near both Cumberland, Maryland and Washington, DC. Estimating population dynamics of turtles inhabiting the C&O Canal, and their response to canal structure and surrounding land cover, is crucial for informing future management both in the C&O Canal and to augment our understanding of turtle dynamics within the larger canal network.

Understanding of turtle population dynamics in large canal systems can be informed by turtle demographics such as population size, density, sex ratios, recruitment rates, and death rates. Through spatial capture–recapture (SCR), we can attain reliable estimates of population densities and other demographics arising from individual space use and movement (Borchers and Efford, 2008; Royle et al., 2014). Over the past decade, SCR methodology and its derivatives have been conducted on a wide range of organisms from jaguars to salamanders and fish (Sollmann et al., 2011; Raabe et al., 2014; Muñoz et al., 2016). To our knowledge, researchers have yet to conduct SCR analysis on freshwater turtle populations.

The SCR methodology is a relatively recent method derived from traditional capture–mark–recapture (Efford 2004). The use of SCR analysis improves demographic inference by incorporating a defined study area and spatial location per trap into modeling procedures (Wilson and Anderson, 1985; Royle and Young, 2008; Royle et al., 2014). More specifically, SCR models estimate the rate of decline in capture probability with distance from activity centers and define parameters such as densities

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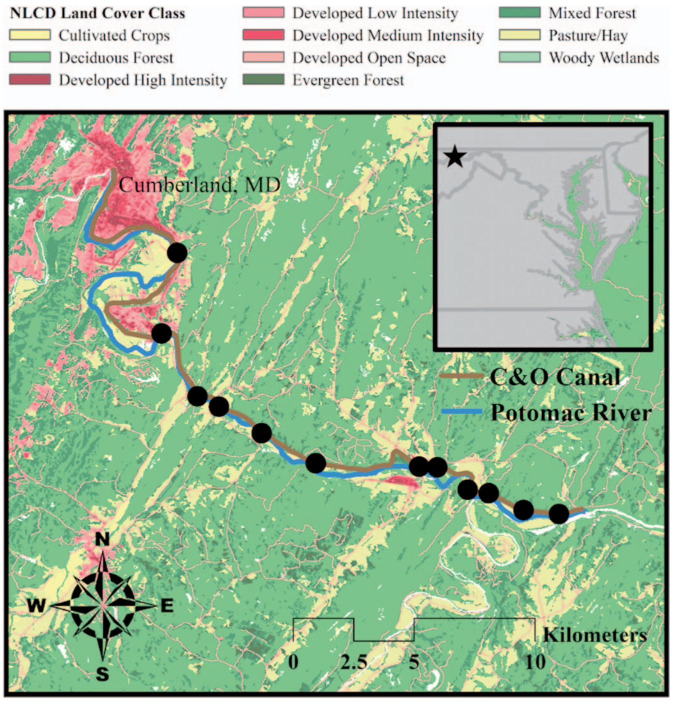

Fig. 1. Location of study sites along the Chesapeake and Ohio Canal and distribution of surrounding land cover (National Land Cover Database, 2016 products in Dewitz, 2019; ESRI, 2019).

and individual activity centers within a specified area (Royle et al., 2014; Muñoz et al., 2016; Sutherland et al., 2016).

Given the necessity for research on turtles inhabiting large canal systems, and the current accessibility of SCR field and modeling procedures, our study utilized SCR to elucidate population densities and the impact of environmental variables on turtles found in the western-most portion of the C&O Canal. We conducted SCR procedures on turtles inhabiting 12 sites along a 28-km stretch of the C&O Canal. We had two objectives for this study. First, we developed an SCR model to estimate turtle capture probabilities, densities, and trapping behavior. Second, we examined the impact of canal depth and percent forest cover adjacent to the canal on the model estimated densities.

Materials and Methods

Study Area.—We conducted field work along a 28-km stretch of the western portion of the C&O Canal, from Oldtown to Cumberland, Maryland, USA (Fig. 1). The portion of the C&O Canal included a hydrologically augmented section located in Oldtown, Maryland intermixing water diverted from the Potomac with water from connected streams and seepages. In 1945, volunteers rewatered and dammed a 7.4-km stretch from Oldtown, Maryland to Town Creek, Maryland (between locks 68 to 71) to serve as a fishing area. Because of the occurrence of rewatering, restorations, damming, and dredging, as well as natural degradation of the canal, depth along the canal varies drastically. The diverse topography provided turtles a gradient of available aquatic habitat with varying depths at different canal sections.

The sampled canal section contained a mosaic of open water stretches and stretches dominated by water lilies or other aquatic vegetation. Surrounding habitat included a bike trail along the northern edge of the canal that previously served as the barge towpath. Forest bracketed both sides of the canal, and forested areas and fields adjacent to the canal were occasionally broken up by small ephemeral wetlands. Pasture and crop land was interspersed between the canal and the Potomac River (Thomas et al., 2014). Additionally, human development such as roads and houses created a matrix of impervious surfaces alongside the canal (See Figure 1 for land use surrounding the C&O Canal; Thomas et al., 2014).

Study Species.—Turtle species documented in the Chesapeake and Ohio Canal National Historic Park and likely to be captured by aquatic traps included Snapping Turtles (*Chelydra serpentina*), Midland Painted Turtles (*Chrysemys picta marginata*), Eastern Painted Turtles (*Chrysemys picta picta*), Red-Eared Sliders (*Trachemys scripta elegans*), Northern Red-Bellied Cooters (*Pseudemys rubriventris*), and Eastern Musk Turtles (*Sternotherus odoratus*).

As of 2019, *C. serpentina*, *C. picta*, and *T. s. elegans* were common in the state of Maryland, precluding a conservation status, and all were species of least concern worldwide. *Trachemys s. elegans* was considered invasive in the state of Maryland (Maryland Invasive Species Council, 2019). *Pseudemys rubriventris* was considered stable throughout Maryland but, in 2015, the Maryland Department of Natural Resources listed *P. rubriventris* as a regional species of conservation need in the Northeast region (Maryland Department of Natural Resources, 2016). Along with being near threatened across their range, in 2015 *P. rubriventris* was listed as threatened in the state of Pennsylvania and is a species of greatest conservation concern (SGCN) in Delaware, Pennsylvania, West Virginia, and the District of Columbia (Delaware Division of Fish and Wildlife, 2015; Department of Energy and Environment, 2015; Pennsylvania Fish and Boat Commission, 2015; West Virginia Division of Natural Resources, 2015; IUCN, 2021).

Spatial Capture–Recapture Field Procedures.—We conducted SCR for four consecutive days at each of 12 sites along the Chesapeake and Ohio Canal from 7 June–19 August 2018 (Fig. 1). We sampled for 4 days per site in an effort to capture data during a period of population closure (no births, deaths, immigration, emigration) with the caveat that data collected during 4 days of sampling would likely not be fully representative of population dynamics during the full season or over multiple seasons (Dupont et al., 2019). Our sampling duration represented a short-term snapshot of individuals at each site. Furthermore, our short sampling periods also allowed us to sample numerous sites over a large section of the canal. We set 7–14 hoop net traps (large = diameter: 0.9 m, mesh: 2.5 cm; medium = diameter: 0.8 m, mesh: 4.0 cm) approximately 5 m from the canal bank 25 m apart within each straight trap line. Trap lines from the first to last trap ranged from 150–325 m based on the length of the section that was of consistent depth, width, and vegetative conditions and not interrupted by locks. We chose a 25-m increment resolution to ensure trapping histories would be representative of turtle movements (Anthonysamy, 2012).

We baited each trap with one perforated, lidded can of Kal Kan® Complete dry dog food. We chose dog food because researchers found it to be more efficient at attracting both *S. odoratus* and *T. s. elegans* (species we expected to capture) compared to canned sardines, the most common bait used to trap turtle species (Mali et al., 2014b). Each day we refilled cans with dog food to maintain bait effectiveness over each sampling period and reset the traps (Bluett et al., 2011). We submerged traps deep enough so water levels would cover trap funnels but would be unlikely to completely cover traps over the following

TABLE 1. Trap number and environmental data averaged per site. Mean and max depth represent average and max depth for all transects. Width represents the average average width for all transects. Forest cover represents the proportion of deciduous, evergreen, and mixed forest within a 300-m buffer around each site. We obtained land use data from the National Land Cover Database (Dewitz, 2019).

Site	Number of traps	Mean depth (m)	Max depth (m)	Width (m)	Forest cover (proportion)
1	7	0.84	1.95	17.03	0.19
2	8	0.79	1.25	20.92	0.30
3	10	0.47	0.85	14.72	0.66
4	10	0.77	1.33	14.26	0.60
5	10	0.32	0.55	10.97	0.72
6	8	0.43	0.75	13.03	0.70
7	14	1.06	2.00	23.19	0.40
8	10	0.50	0.83	16.79	0.34
9	7	0.82	1.70	16.59	0.50
10	12	0.69	1.45	20.57	0.54
11	10	1.22	2.40	46.33	0.53
12	10	1.30	2.95	25.33	0.59

24 h (e.g., because of precipitation). On each sampling day, we pulled traps from the canal and collected captured turtles for measuring and identification.

For each turtle, we measured midline carapace length, maximum carapace length, plastron length, maximum depth, and mass. We assessed each turtle's sex by examining secondary sex characteristics of Emydidae and Kinosternidae and by calculating the ratio of plastron posterior lobe to precloacal length of Chelydridae (Dustman, 2013). For all turtles caught, with the exception of large *C. serpentina*, we provided a unique code and used metal files to create square notches along the turtle's marginal scutes following a numerical coding system (Cagle, 1939). For larger *C. serpentina*, we drilled small holes near the edges of their marginal scutes following the same ID system restricted to the rear marginal scutes. After we obtained mark–recapture data, we released individual turtles back into the canal near their trapping location.

Environmental Data Collection.—We recorded trap locations at the edge of the canal bank using a Garmin global positioning system (GPS) device (Garmin GPSMAP® 76CXs; see Supplementary Data, Table 1 for trap coordinates). We measured the canal wetted width from the bank next to each trap to the opposite bank using a laser rangefinder (Bushnell Yardage Pro Sport 450). We additionally measured depth transects across the canal at first, middle, and end trap locations. We measured depth along each transect at five points, equally dividing the canal's width with the first and fifth measurements occurring about 15 cm from the water edge. After lowering a polyvinyl chloride (PVC) pipe marked in 5-cm increments into the water, we recorded how far the pipe fell before hitting debris on the canal floor.

We obtained C&O Canal topography data from the NPS (National Capital Region, 2018). Using the editing toolbox in ArcGIS software (Environmental Systems Research Institute [ESRI], 2019), we traced both canal edges at each site (resolution = 1:150 m). We buffered each site edge 300 m perpendicular to the canal edge (terrestrial buffer) to encompass the majority of area potentially used for nesting behavior by a population of turtles at a given site (Semlitsch and Bodie, 2003; Steen et al., 2012). We obtained forest cover data from the National Landcover Database (Dewitz, 2019). To measure percent forest cover surrounding each site (perpendicular to canal), we used the tabulate area tool in ArcGIS to calculate area containing forest cover within 300 m perpendicular from both canal edges (combining deciduous, evergreen, and mixed; Environmental Systems Research Institute, 2019). Refer to Table 1 for number of traps, mean depth, maximum depth, mean width, and mean proportion forest cover for each site.

Spatial Capture–Recapture Model Development.—To estimate short-term turtle densities along the C&O Canal, we built a spatial capture–recapture model using JAGS (Just Another Gibbs Sampler; Plummer, 2003; JAGS version 4.3.0) implemented with the jagsUI package (Kellner, 2018; jagsUI version 1.5.0) in R (R Development Core Team, 2019; R version 4.0.0). We created a model to estimate density and individual activity centers within a unidimensional state–space for each sampled site assuming independence of population size (N) between sites (Royle et al., 2014). The state–space contained the trap line as well as a buffer both upstream and downstream from the trap line. The state–space formed a straight line (adjacent terrestrial habitat was not included). We created a 1,000-m buffer upstream and downstream from our trapping transects to contain all activity centers of individuals with nonnegligible probabilities of being caught in a trap within a site, thus accounting for individuals with activity centers outside the traplines that still used the site (Royle and Young, 2008; Royle et al., 2014). This 1000-m distance was greater than both maximum daily distances and home range estimates of trapped species. We assumed that turtles with activity centers (home range centers) more than 1,000 m downstream or upstream from the site would have negligible probabilities of capture over each 4-day sampling session. The full model included a state–space model with linear distance between traps and latent activity centers influencing a probability distribution function for individual detection (see Raabe et al., 2014; Royle et al., 2014, 2018). All model inputs and parameters and their associated indices can be found in Table 2.

Capture histories (y) per individual caught were arranged in a 4-dimensional array, indicating whether an individual (i) was caught at a specific trap (j), on a specific sampling day (k), and at a specific site (g). The model calculated whether an individual (i) at site (g) was encountered at trap (j) on day (k). Each potential encounter was mutually independent, and individuals were unique between sites with captures following a Bernoulli distribution,

$$y_{i,j,k,g} \sim Bernoulli(P_{i,j,k,g})$$

with capture probability ($P_{i,j,k,g}$).

The individual capture probability (P_i) was modeled as a function of site, sampling day, and trap and declined with Euclidean straight-line distance from activity center (d) to account for a linear trap array (instead of the more common 2-dimensional array). Number of individuals caught tended to

TABLE 2. All model input objects and output parameters with associated symbols and indices (Site, Individual [Ind], Trap, Sampling day). All parameters were estimated for each species.

Parameters	Symbol or identifier	Site (g)	Ind (i)	Trap (j)	Day (k)
Model input (data)					
Buffered upstream site distance	xlim1	×			
Buffered downstream site distance	xlim2	×			
Trap location	trap location	×		×	
Canal width	width	×			
Canal depth	depth	×			
Proportion forest cover	forest	×			
Encounter matrix	y	×	×	×	×
Sex (0/1)	t	×	×		×
Matrix indicating whether an individual was caught previously	C	×	×		×
Estimated parameters (estimated for both captures and augments)					
Activity center	s	×	×		
Distance between activity centers and traps	d	×	×	×	
Probability of individual being part of sampled population	ψ	×			
Probability of female being part of sampled population	ψ_{sex}				
Occurrence in population (Y/N)	z	×	×		
Baseline capture probability	p0	×	×	×	×
Baseline capture probability intercept	α_0	×			×
Capture probability	P	×	×	×	×
Decay rate in capture probability over distance	α_1				
Standard deviation of capture probability decay rate over distance	σ				
Impact of trap behavior on capture probability	α_2				
Derived parameters					
Capture probability per sampling day	P_{day}				×
Number of individuals in state space	N	×			
Linear density	density	×			
Density per hectare	density_ha	×			
Linear home range (50% of posterior distribution)	home_50				
Linear home range (95% of posterior distribution)	home_95				
Regression parameters					
Density intercept	β_0				
Forest cover covariate	β_1				
Depth covariate	β_2				

decrease over time in sampling sessions, thus we augmented the model to estimate a separate detection probability per day (days 1, 2, 3, and 4). During sampling sessions, we observed that captured turtles tended to avoid recapture, so we allowed for behavioral trap responses (i.e., "trap-shy" or "trap-happy" behavior). The conditional capture probability (conditional on an individual being in the population, $z_{i,g}$) was estimated per site (g), individual (i), sampling day (k), and trap (j).

$$P_{i,j,k,g} = z_{i,g} \times P_{0i_{j,k,g}} e^{-\alpha_1 (d_{i,j,g})^2}$$

Conditional capture probability was informed by the baseline capture probability (p_0) per site (g), individual (i), sampling day (k), and trap (j),

$$\text{logit}(P_{0_{i,j,k,g}}) = \alpha_{0_{k,g}} + \alpha_2 C_{i,k,g}$$

with trap behavior ($C_{i,k,g}$).

Whether an individual was estimated to be part (1) or not part (0) of the population ($z_{i,g}$) followed a Bernoulli distribution informed by the model-estimated probability of an individual being part of the population at that site (ψ_g),

$$z_{ig} \sim Bernoulli(\psi_g)$$

with ψ_g having a uniform prior between zero and one. We separated $z_{i,g}$ to represent males and females, resulting in an estimate of proportion females per species (ψ_{sex}). Occurrence data drove the estimation of both ψ_g and ψ_{sex}, which was reflected in the model estimates for uncaptured individuals. Given enough capture and recapture data, it is possible to associate ψ_{sex} with both detection probability and space use, resulting in separate estimates of both metrics per sex.

$$\text{Sex}_i \sim Bernoulli(\psi_{sex})$$

From the above model, we estimated capture probabilities per species as well as overall density per site (per species), converting density per 100 m (linear density) to density per hectare (accounting for canal width per site). We converted to density per hectare to allow for easier comparison of our density estimates to estimates from previous studies. We first estimated capture probability for each sex, but later simplified the model to estimate a single joint capture probability after viewing nonconvergence of Markov Chain Monte Carlo (MCMC) chains. To examine whether behavioral characteristics impacted turtle densities, we quantified potential trap behavior for each species. To additionally examine whether site characteristics impacted turtle densities, we ran a linear regression model examining the relationship between site depth, surrounding forest cover, and density using the resulting densities estimated from the SCR model at each iteration of the MCMC. We related depth and forest cover explicitly to density, separate from individual space use or capture probability. See Table 2 for a list of model parameters and associated indices. Refer to Supplementary Appendix 2 for details of the model including equations, distributional assumptions, and priors.

For Bayesian inference from the MCMC, we ran eight MCMC chains, each with 5,000 burn-ins and 55,000 further iterations (thinned by 10), resulting in 40,000 total iterations for the posterior. We examined chain convergence and mixing by observing traceplots for each parameter and checking that all $\hat{R}$ values were <1.1 (Brooks and Gelman, 1998). In addition, we calculated effective sampling size, examined size of CRI, and compared prior and posterior distributions per parameter to assess the MCMC mixing and convergence.

Results

Summary of Field Data.—During spatial capture–recapture procedures we made 1,074 captures of 936 individual turtles among all 12 sites. The mean proportion of recaptures to total captures was 0.12 for all sites and species, ranging from 0.05 to 0.25 of captured turtles recaptured per site. We caught 683 *C. picta* (73% of all captures) across 12 sites with a mean of 56.9 captures per site and a mean recapture rate of 0.16. We caught 62 *C. serpentina* (6.6% of all captures) across 12 sites with a mean of 5.2 captures per site and a recapture rate of 0.18. We caught 77 *S. odoratus* (8.2% of all captures) across 10 sites with a mean of 6.4 captures per site and an average recapture rate of 0.07. We caught 111 *P. rubriventris* (11.8% of all captures) across seven sites with a mean of 9.25 captures per site and a recapture rate of 0.13. We caught two Wood Turtles (Glyptemys insculpta) across two sites and one *T. s. elegans* at one site with zero recaptures. Given the low number captured, we did not include *G. insculpta* or *T. s. elegans* in the SCR model analyses. See Supplementary Data (Table 2) for number caught, number of recaptures, and morphometric measurements of *C. picta*, *C. serpentina*, *S. odoratus*, and *P. rubriventris*.

Capture Probabilities.—We observed a decline in the number of captures over most 4-day sampling sessions, with a much higher number of turtles caught on first sampling days compared to all subsequent sampling days. Model results corroborated this observation for all four species, with the mean initial-day capture probabilities (0.1, 0.1, 0.1, and 0.0 for *C. picta*, *C. serpentina*, *S. odoratus*, and *P. rubriventris*, respectively) estimated to be higher than the mean capture probabilities for the second, third, or fourth sampling days (Fig. 2).

Trap Behavior.—Our model estimated positive mean behavior coefficients for *C. picta*, *C. serpentina*, and *P. rubriventris*. Estimated mean behavior coefficients (α_2) were 0.5 (95% credible interval [CRI] = 0.2–0.8; 99.9% of estimates >0), 0.7 (95% CRI = −0.6–1.9; 87.2% of estimates >0), and 0.4 (95% CRI = −0.4–1.2; 85.5% of estimates >0) respectively. The mean behavior coefficient for *S. odoratus* was negative (−0.6; 95% CRI = −2.0–0.6; 82.6% of estimates <0).

Model Estimated Densities.—Mean *C. picta* density per site ranged from 40 ± 6 to 97 ± 10 (±standard deviation [SD]) individuals per hectare. The mean proportion of *C. picta* females estimated in the population for all sites (ψ_{sex}) was 0.3, with a 95% CRI ranging from 0.3 to 0.3. Mean *C. serpentina* density per site ranged from 8 ± 6 to 25 ± 10 (±SD) individuals per hectare. The mean proportion of *C. serpentina* females estimated in the population for all sites was 0.5, with a 95% CRI ranging from 0.4 to 0.6. Mean *S. odoratus* density per site ranged from 3 ± 3 to 31 ± 12.5 (±SD) individuals per hectare. The mean proportion of *S. odoratus* females estimated in the population for all sites was 0.6, with a 95% CRI ranging from 0.5 to 0.7. Mean *P. rubriventris* density per site ranged from 4 ± 5.0 to 35 ± 11.7 (±SD) individuals per hectare. The mean proportion of *P. rubriventris* females estimated in the population for all sites was 0.3, with a 95% CRI ranging from 0.3 to 0.4. See Supplementary Data (Figs. 2, 3, 4, 5) to visualize variation in densities between sites per species.

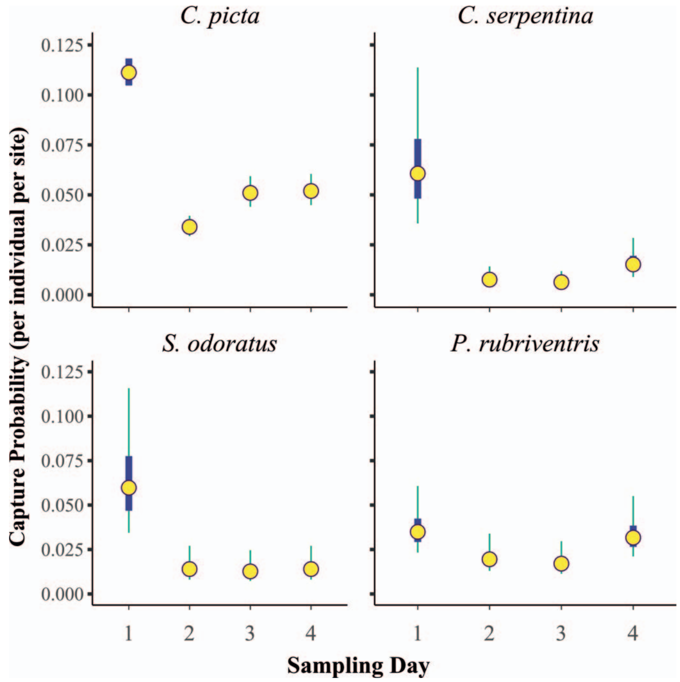

FIG. 2. Distribution of *C. picta*, *C. serpentina*, *S. odoratus*, and *P. rubriventris* capture probability estimates for each of four subsequent sampling days, averaged for all individuals, sexes, and sites. Each capture probability per distribution represents the capture probability that one individual is caught in any trap per site on one sampling day, averaged across sites. Yellow center points indicate median values. Dark blue boxes represent values within the 50% CRI and teal lines represent values within the 90% CRI.

Model Estimated Habitat Associations.—For *C. picta*, the mean parameter values associated with forest cover and depth were −19.4 (95% CRI = −27.4 to −11.6; 100% of estimates <0) and −6.6 (95% CRI = −12.8 to −0.3; 97.9% of estimates <0). For *C. serpentina*, the mean parameter values associated with forest cover and depth were −4.8 (95% CRI = −12.7 to 1.2; 94.1% of estimates <0) and 0.1 (95% CRI = −5.4 to 6.6; 51.8% of estimates >0). For *S. odoratus*, the mean parameter values associated with forest cover and depth were −8.9 (95% CRI = −17.4 to −2.4; 99.9% of estimates <0) and 0.3 (95% CRI = −3.4 to 4.8; 55.0% of estimates >0). For *P. rubriventris*, the mean parameter values associated with forest cover and depth were −6.8 (95% CRI = −15.7 to 0.9; 96.2% of estimates <0) and 6.9 (95% CRI = −0.3 to 14.2; 96.7% of estimates >0). See Supplementary Data (Tables 3–6) for mean, SD, median, CRI, $\hat{R}$, and effective sample size values for all saved parameters for *C. picta*, *C. serpentina*, *S. odoratus*, and *P. rubriventris*.

Discussion

The western portion of the C&O Canal supports large populations of four species of turtle, *C. picta*, *C. serpentina*, *S. odoratus*, and *P. rubriventris*. The majority of captured individuals (n = 683) were *C. picta*, a species often found at high densities in sites containing slow-moving water and numerous basking objects (Ernst and Lovich, 2009). *Chrysemys picta* are often the most abundant species throughout its range from the Atlantic to the Pacific coast, and many studies have surveyed large numbers of individuals (Anderson et al., 2002; Ernst and Lovich, 2009).

We found that individuals of all species modeled were less likely to be captured after the first day of sampling, regardless of whether they had been previously captured or not (Fig. 2). Some studies have suggested trap shyness in freshwater turtles, as evidenced by low recapture rates, but the evidence is weak (Mali et al., 2012, 2014a). Our model estimated trap-happy behavior for *C. picta*, *C. serpentina*, and *P. rubriventris*, indicating turtles captured on subsequent days were more likely to be recaptures than expected at random. Our data provided evidence that the temporal decrease in capture probability was not a result of trap-shy behavior. Rather, all individuals seemed to increase their avoidance of traps after the first sampling day, yet captured individuals avoided traps less than noncaptured individuals, potentially because of partitioning of behavioral tendencies (e.g., boldness, exploratory behavior).

In contrast, our model estimated a mean negative behavior covariate for *S. odoratus*, potentially indicating trap avoidance after capture. *Sternotherus odoratus* individuals displaying trap-shy behavior could account for their low recapture rate, which was the lowest amongst the four species analyzed. A handful of studies have found low recapture rates in *S. odoratus*, even when sampling seemingly robust populations (Munscher et al., 2019, 2020). Long-range movements, both within or outside the study area, are unlikely to influence the rate of recapture in *S. odoratus*, as they are known to move short daily distances (25 to 131 m/day) and display high site fidelity (Smar and Chambers, 2005; Belleau, 2008; Committee on the Status of Endangered Wildlife in Canada [COSEWIC], 2012).

Model Estimated Densities.—Our model estimated the mean density to range (between sites) from 40 to 97 *C. picta*, 8 to 25 *C. serpentina*, 3 to 31 *S. odoratus*, and 4 to 35 *P. rubriventris* per hectare. The highest density estimates of *C. picta* we obtained were similar to, if a bit lower than, estimates from a cluster of previous studies (Sexton, 1959; Bowne et al., 2006; Eskew et al., 2010). Several studies have estimated substantially higher densities of *C. picta*, with some finding higher densities during dry sampling seasons compared to wet sampling seasons (Sexton, 1959; Frazer et al., 1991; Bowne et al., 2006). Densities of *C. serpentina* (8–25) were similar or slightly higher compared to estimates from previous studies (Flaherty et al., 2008; Johnston et al., 2012; Munscher et al., 2019). Studies conducted in warmer, more productive waters have tended to discover even higher densities of *C. serpentina* (Froese and Burghardt, 1975; Major, 1975; Ernst and Lovich, 2009). Densities of *S. odoratus* (3–31) in our study were generally lower, yet within the range of densities estimated in previous studies. Previous estimates of *S. odoratus* densities are highly variable, ranging from 7.5 per ha to 1,690 per ha (Congdon et al., 1986; Dodd, 1989; Elain, 2007; Munscher et al., 2020). Ernst and Lovich (2009) suggest high variance in *S. odoratus* density is largely driven by the carrying capacity of the aquatic habitat. Densities of *P. rubriventris* (4–35) in our study were higher than those in another study conducted in a maritime forest in North Carolina (Hanscom et al., 2020). There are too few other studies estimating *P. rubriventris* densities for further comparisons because of difficulty sampling in riverine systems as well as the presence of few populations (Ernst and Lovich, 2009).

Model Estimated Habitat Associations.—Our model estimated densities of all four species to display a negative trend with increasing forest cover within a surrounding 300 m buffer (*C. picta* $= -19.36$, *C. serpentina* $= -4.84$, *S. odoratus* $= -8.85$, *P. rubriventris* $= -6.79$). Our estimates provide further evidence that freshwater turtles prefer open or potentially warmer microhabitats with more emergent aquatic vegetation, which has been previously suggested for *C. picta* (e.g., Cosentino et al., 2010). In contrast, the association between canal depth and densities varied amongst our studied species. Our model estimated *C. picta* densities to be negatively correlated with canal depth, *C. serpentina* and *S. odoratus* densities to be minimally impacted by canal depth, and *P. rubriventris* densities to be positively correlated with canal depth (mean depth covariate for *C. picta* $= -6.63$, *C. serpentina* $= 0.05$, *S. odoratus* $= 0.34$, *P. rubriventris* $= 6.18$). Given that water levels in 8 of our 12 study sites were above 60 cm (range = 32–130 cm), and all study sites were part of a highly connected canal waterway, we expect turtles in our study were less restricted by landscape-scale habitat structure or connectivity (compared to other studies in smaller, less connected systems) and more affected by local-scale characteristics (such as forest cover, emergent vegetation, and basking site abundance).

As we observed shallower sites in our study to contain more locations for aerial basking (e.g., unsubmerged logs, fallen trees, or debris), we hypothesize that the variable effect size of depth between species was partially in response to differences in basking tendencies. *Chrysemys picta* and *P. rubriventris* will frequently bask aerially and studies have found depth and the number of basking locations to be the important variables influencing abundances of both *Chrysemys* and various *Pseudemys* species (Kornilev et al., 2010; Hill and Vodopich, 2013). While *P. rubriventris* are known to show aerial basking, Ernst and Lovich (2009) document *P. rubriventris* to prefer deep aquatic habitats, which is consistent with our observations. *Pseudemys rubriventris* might therefore prioritize habitat selection by water depth over habitat with numerous basking sites. Yet, given the few published studies on *P. rubriventris* habitat preferences, much more research is needed to characterize their preferred micro- and macrohabitats. In contrast, both *C. serpentina* and *S. odoratus* do not commonly aerial bask (Ernst and Lovich, 2009). Thus, the amount of basking sites likely does not play a role in site selection for both species and could possibly explain why we did not find depth to significantly impact the density of either species.

Implications.—Our study demonstrates the feasibility of conducting SCR procedures to estimate demographic parameters for freshwater turtles and their responses to habitat variables in a linear stretch of high-quality habitat. Numbers of individual *C. picta*, *P. rubriventris*, *S. odoratus*, and *C. serpentina* captured indicate that large populations and estimated densities additionally indicate relatively dense populations under the hydrological and landscape conditions present in the 2018 sampling season. Our results highlight the adaptability of our study species to anthropogenic structures and reveal the C&O Canal to be a system currently highly suited for native turtle inhabitation. Habitat suitability throughout the canal is likely to fluctuate with constant canal maintenance practices. Canal alterations could support freshwater turtle populations by minimizing the production of low suitability habitat and maximizing potentially suitable habitat (e.g., maximizing area of open canal stretches or maintaining water depth suitable for target species in the C&O Canal). Given that turtle species likely play a large role in canal ecosystem dynamics, by maintaining current population densities in the western C&O Canal as well in other large canal systems we can maintain ecosystem stability within individual canals and safeguard a system of potential reservoirs (Lovich et al., 2018). With more than 50% of turtle species currently threatened, managing reservoirs of potentially highly diverse turtle populations can help to stabilize both threatened and nonthreatened species.

Our SCR model can be used as a foundation for future models examining turtle densities and movements in the C&O Canal and in other canal systems with their own unique turtle communities and habitat associations. Future studies could test whether the correlation between turtle densities and forest cover holds as negative for a larger range of species in canal systems and examine the mechanisms behind such correlations. Additionally, patterns and mechanisms associated with species variability in depth preferences, especially for *P. rubriventris*, should be further investigated. We acknowledge that our 4-day sampling session is short and estimates from our model likely provide only a snapshot of turtle population dynamics. To provide a measure of uncertainty for all model estimates, we present all posterior distributions with CRIs and effective sample sizes (See Supplementary Data, Tables 3–6). We parameterized the model to use the same capture probability decay with distance (σ) and trap behavior coefficient values (Table 2) across all sites, and the posterior estimates therefore reflect the uncertainty across space. Our statistical technique allows estimation of densities at sites with low recapture rates, assuming values were approximately constant across sites during this one summer. Future studies with higher recapture rates could relax these assumptions to have site-specific estimates pulled from a common distribution.

To calculate density estimates that are potentially more representative of long-term population dynamics, future studies implementing SCR methods for aquatic turtles should involve higher-density trapping and might benefit by having single-day trap sessions a few days apart. Relatively high-density trapping over relatively long periods of time might allow for increased capture and recapture that potentially reduce the daily decline in capture rates. Spatial capture–recapture models rely on numerous recaptures of individuals in multiple traps to estimate sigma; therefore, this should be of primary consideration when conducting SCR on turtles with low recapture rates.

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Supplementary Data

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