2018

Occupancy of Freshwater Turtles Across a Gradient of Altered Landscapes

Scott W. Buchanan
University of Rhode Island

Bill Buffum
University of Rhode Island

See next page for additional authors

Citation/Publisher Attribution
Buchanan, S. W., Buffum, B. , Puggioni, G. and Karraker, N. E. (2019), Occupancy of freshwater turtles across a gradient of altered landscapes. Jour. Wild. Mgmt., 83: 435-445. doi: 10.1002/jwmg.21596 Available at: https://doi.org/10.1002/jwmg.21596

Authors
Scott W. Buchanan, Bill Buffum, Gavino Puggioni, and Nancy E. Karraker

Published as:
Buchanan, S.B., B. Buffum, G. Puggioni, N.E. Karraker. 2019. Occupancy of freshwater turtles along a gradient of altered landscapes. Journal of Wildlife Management 83:435-445.

8 October 2018
Scott W. Buchanan
University of Rhode Island
1 Greenhouse Road
Kingston, RI 02881
(973) 951 3382
Scott_buchanan@uri.edu

Occupancy of Freshwater Turtles Across a Gradient of Altered Landscapes

SCOTT W. BUCHANAN,[1] *Department of Natural Resources Science, University of Rhode Island, 1 Greenhouse Road, Kingston, RI 02881, USA*

BILL BUFFUM, *Department of Natural Resources Science, University of Rhode Island, 1 Greenhouse Road, Kingston, RI 02881, USA*

GAVINO PUGGIONI, *Department of Computer Science and Statistics, University of Rhode Island, 9 Greenhouse Road, Kingston, RI 02881, USA*

NANCY E. KARRAKER, *Department of Natural Resources Science, University of Rhode Island, 1 Greenhouse Road, Kingston, RI 02881, USA*

ABSTRACT Turtles are one of the most threatened groups of vertebrates worldwide. In the northeastern United States, a legacy of centuries of dramatic landscape alteration has affected freshwater turtle populations, but the relationships between the current landscape and distributions and abundances of freshwater turtles remain poorly understood. We used a stratified random approach to select 88 small, isolated wetlands across a gradient of forest cover throughout Rhode Island, USA, and systematically sampled freshwater turtles in these wetlands. We report estimates of relative abundance and used a canonical correspondence analysis to investigate relationships between species relative abundance and environmental covariates. We

[1] *Current Email: scott.buchanan@dem.ri.gov*

also investigated which environmental covariates affect the occurrence and detection probabilities of each species. Eastern painted turtles (*Chrysemys picta picta*) and common snapping turtles (*Chelydra serpentina*) were widespread (occurring in 83% and 63% of wetlands, respectively) and relatively abundant. Spotted turtles (*Clemmys guttata*) were far less common, occurring in 8% of wetlands, and exhibited a positive association with shallow wetlands surrounded by forest. Non-native red-eared sliders (*Trachemys scripta elegans*) occurred in 10% of wetlands and exhibited a positive association with road density, likely reflecting a positive relationship between slider occurrence and human population density. Identifying landscape-scale habitat features that are associated with the occurrence of sensitive species can improve the ability of biologists to identify and protect turtle populations.

KEY WORDS *Chelydra serpentina*, *Chrysemys picta*, *Clemmys guttata*, endangered species, invasive species, occupancy analysis, pet trade, *Trachemys scripta elegans*.

Human-induced landscape alteration is often implicated as compromising vertebrate biodiversity, with habitat loss and degradation widely recognized as the leading causes of a loss of population stability across taxa (Gibbons et al. 2000, Brooks et al. 2002). New England, in the northeastern United States, has experienced substantial shifts in landscape composition since the time of European settlement. Deforestation associated with agriculture and logging peaked in the mid-nineteenth century when as much as 80% of the landscape had been cleared. Beginning around 1850 agriculture shifted to states farther west, ushering in a period of reforestation lasting approximately 100 years (Foster and Aber 2004). In Rhode Island, USA, this period was followed by another phase of deforestation for urban and suburban development. Total forested land area in Rhode Island has been decreasing since at least 1953, when an estimated 65% of the state was forested (Butler and Payton 2011). A recent estimate suggested that approximately

54% of the state is forested (Butler 2013). This extreme landscape alteration in a relatively short period of time has certainly led to changes in the distribution and abundance of wildlife, but the legacy of this change is poorly understood for many species, including freshwater turtles.

As a vertebrate group, turtles have an extremely high rate of extinction risk (Bohm et al. 2013). In the United States, freshwater turtles are of particular conservation concern largely because of a significant loss in wetland area beginning in the eighteenth century. An estimated 37% of the wetlands in Rhode Island were drained, filled, or otherwise lost between 1780 and 1980 (Dahl 1990). Additional factors putting freshwater turtle populations at risk include the loss of meta-population structure associated with terrestrial habitat loss and degradation (Dodd 1990, Gibbs 2000), collection for pet, food, and medicine trades (Shiping et al. 2006, Luiselli et al. 2016), and life-history characteristics that include delayed sexual maturity and low recruitment (Congdon et al. 1994, Heppell 1998). In Rhode Island, native freshwater turtles include the common snapping turtle (*Chelydra serpentina*), eastern painted turtle (*Chrysemys picta picta*), spotted turtle (*Clemmys guttata*), wood turtle (*Glyptemys insculpta*), and musk turtle (*Sternotherus odoratus*). An additional species, the red-eared slider (*Trachemys scripta elegans*), has been introduced to Rhode Island from the southern United States. The spotted turtle and wood turtle have been identified as endangered by the International Union for the Conservation of Nature (IUCN; van Dijk 2011, van Dijk and Harding 2011), and both are currently candidate species under review for listing under the United States Endangered Species Act (U.S. Fish and Wildlife Service 2015).

All freshwater turtle species use terrestrial habitats to some extent, using uplands to nest, move between wetlands, and estivate, but the proportion of time spent on land varies among species (Ernst and Lovich 2009). For example, spotted turtles move frequently between temporary and permanent wetlands and estivate terrestrially, spending as much as 30% of their time on land (Milam and Melvin 2001). The landscape adjacent to and between wetlands is directly linked to many ecological processes of freshwater turtles (Joyal et al. 2001). Landscape gradient analyses have been used for decades to investigate how changes in composition and configuration of the landscape affect wildlife (Gibbs 1998, Riem et al. 2012). Typically, data are collected based on some direct or indirect measure of varying anthropogenic intensity. For certain taxa, these studies have led to broad generalizations about the relationships between urbanization and patterns of distribution, abundance, and diversity (Marzluff 2001, McDonnell and Hahs 2008). Very few studies, however, have examined patterns in reptile distributions across urban gradients. A major review (McDonnell and Hahs 2008) of 201 studies investigating organismal distributions along urbanization gradients published between 1990 and 2007 included only 1 study of reptiles.

We conducted a 3-year investigation of the relationships between freshwater turtles and the landscape. Our intent was to describe the distribution and abundance of freshwater turtles across this landscape gradient to test the prediction that spotted turtles, as a result of human disturbance, are a forest-associated species and relatively rare in Rhode Island compared to native generalist species such as painted turtles and snapping turtles; determine what landscape- and wetland-scale features and conditions are associated with freshwater turtle occurrence; and improve our understanding of the conservation implications of landscape management for these species, especially spotted turtles.

STUDY AREA

Our study was conducted throughout the state of Rhode Island (excluding Block Island) from 2013 to 2015. At approximately 2,700 km^2 (when excluding coastal waterways), Rhode Island is the smallest state geographically in the United States but ranks second highest in human population density. The highest levels of land development and human population densities occur along the south coast and around Narraganset Bay in the eastern part of the state. Mean elevation is approximately 60 m with a highest point of 247 m. The Wisconsin glaciation, which reached a maximum extent approximately 25,000 years ago and retreated completely from the area 10,000–12,000 years ago, is responsible for the dominant parent materials found in Rhode Island. These include glacial till, glacial outwash, and windblown silts (eolian mantle). Till soils are typically associated with higher elevation landforms, whereas outwash materials are located in valley landscape positions. A mantle of windblown silt can be found across various landscapes throughout the state (Rector 1981). Long-term (1981–2010) average annual temperature in Kingston, Rhode Island was 10.5 °C and long-term average annual precipitation was 134.3 cm. Long-term average monthly temperatures ranged from −1.4°C in January to 22.1°C in July (National Centers for Environmental Information [NCEI] 2016). Rhode Island consists of a matrix of different land use types and hosts a diverse assemblage of flora and fauna (RIDEM 2015).

METHODS

Site Selection

We used ArcGIS version 10.1 (Environmental Systems Research Institute, Redlands, CA, USA) to identify all freshwater wetlands ≤2 ha in size throughout the state. We then selected candidate wetland sites for sampling using a stratified random design to capture statewide variability in landscape composition. To minimize confounding factors among sites, we focused our sampling on relatively small (0.1–2.0 ha), isolated (i.e., discrete, non-riparian) wetlands. To further minimize potential confounding variables, we excluded wetlands that were within 500 m of the coastline, within 300 m of a federal or state highway, or within 10 m of a local road.

We grouped retained wetlands as small (0.1–0.4 ha) or large (>0.4–1.8 ha) using a 0.4 ha breakpoint, which was the approximate median of wetland size for all retained wetlands. We calculated percent forest cover within buffers of 300 m and 1 km from the wetland edge of all retained wetlands. We selected these distances to represent a core scale (Burke and Gibbons 1995, Semlitsch and Bodie 2003) and a more encompassing scale, respectively (Mitchell and Klemens 2000). We assigned wetlands into 1 of 8 hierarchically assembled forest cover classes, which we binned at the 300-m scale into increments of 10% (excluding 0–10% and 70–80%), and binned at the 1-km scale into 4, partially overlapping larger increments (0–40%, 20–60%, 40–80%, 80–100%) such that each value at the 300-m scale was encompassed within a value at the 1-km scale (Table 1). These cover classes created a near-continuous gradient of sites with different forest conditions that captured much of the variation in the landscape statewide. We identified 1,665 potential wetlands, assigned each wetland a random number, sorted them by random number in ascending order, and contacted property owners or land managers in that order until we received permission to sample the desired number of wetlands in each forest cover and size class. Our intent was to sample approximately 10–12 wetlands in each of the 10% forest cover classes and an equal number of wetlands in each size class.

Turtle Sampling and Data Collection

In 2013–2015 we sampled turtles from May–October, sampling approximately 30 wetlands per year. We sampled each wetland for only 1 year but surveyed each up to 4 times within that year, hydroperiod allowing. For each survey, we trapped turtles for an approximately 48-hour period, with trap checks every 24 hours, totaling 2 trapping sessions per survey. We sampled sites using small (30.5-cm-diameter collapsible minnow traps; Promar Nets, Gardena, CA, USA) and large (91.4-cm single throated hoop traps; Memphis Net and Twine, Memphis, TN, USA) traps baited with sardines placed inside perforated plastic containers. Alternating between small and large traps, we placed traps approximately 30 m apart around the perimeter of wetlands (within 10 m of the edge) such that the perimeter of each wetland determined the number of traps deployed. We opportunistically hand-captured a small number of turtles (<15) that were encountered when working with traps.

We collected data on all trapped turtles at each trapping session. We identified each new turtle to species; sexed, measured, and weighed them; and marked them along the marginal scutes with a unique code for each individual. We also recorded recaptured turtles, and released all turtles back into the wetland immediately after processing. At each wetland, we estimated percent cover of vegetation during the second or third survey after all vegetation had fully emerged. We estimated percent cover for each vegetation category while standing at the wetland edge (Table 2); the same individual made all estimates (S.B.). To assess water chemistry at each wetland, in spring 2015 we collected samples from 3 distinct points within each wetland and combined them to form 1 125-ml sample for subsequent laboratory analysis. We measured pH (model HI–902, Hanna Instruments, Woonsocket, RI, USA) and total dissolved solids (EcoTestr TDS Low, Oakton Instruments, Vernon Hills, IL, USA) on the same day as water sample collection. We measured concentrations of ammonia-nitrogen, nitrate-nitrogen, and dissolved phosphorous with a segmented flow nutrient autoanalyzer (Astoria Pacific, Clackamas, OR, USA). The limit of detection was 15 µg/L for ammonia and nitrate, and 4 µg/L for dissolved phosphorous.

We used aerial and digital imagery datasets available from Rhode Island Geographic Information System (RIGIS; RIGIS 2017) to quantify landscape features. We used the Forest Habitat dataset to determine percent cover of different landscape types and to quantify landscape metrics (Table 2). We examined historical aerial imagery taken at approximately 10-year increments and dating back to 1939 to determine the age (up to >77 years) of all sampled wetlands. By doing so, for the majority of wetlands, we were able to determine whether they were naturally occurring, constructed, or heavily modified by people.

Statistical Analysis

We estimated relative abundance for each species at each wetland by calculating the total number of unique individuals caught divided by the total number of trap nights. We used canonical correspondence analysis (CCA) to summarize relationships between species relative abundance and the environmental covariates measured at each wetland. We were primarily interested in using CCA as an exploratory technique to identify the major structure in the data and to identify the most important covariates associated with abundance (Everitt and Hothorn 2011). We built a correlation matrix consisting of all site-level covariates (Table 2; excluding geographic location and only considering landscape covariates at the 300-m scale) and the corresponding relative abundances for each species, at each site. We conducted the CCA using the vegan package in R (R Foundation for Statistical Computing, Vienna, Austria) using the scaling option, which standardized all data to a mean of zero and standard deviation of 1. We constructed a plot of the first 2 constraints with ellipses drawn around mean values for each species and representing 95% confidence ellipses based on the corresponding standard error. We used a permutation test with 999 permutations to assess the significance of constraints.

We modeled heterogeneous detection probabilities (*p*) using covariates that changed between surveys (i.e., survey-level; Table 2), including ordinal date (day 2 of survey), survey number, temperature, and precipitation. For each wetland, we downloaded temperature and precipitation data from the nearest of 7 available weather stations (NCEI 2016). For days 1 and 2 of each survey, we used mean maximum daily temperature for our temperature covariate and mean total daily precipitation for the precipitation covariate. To model heterogeneous occupancy probabilities (Ψ), we used covariates that changed from site to site (i.e., site-level). We used a single-species, single-season occupancy modeling framework (MacKenzie et al. 2002, 2006) using the occu function in the R package unmarked (Fiske and Chandler 2011). This function fits the standard occupancy model based on zero-inflated binomial models (MacKenzie et al. 2006) using maximum likelihood techniques to estimate model parameters, and uses a logit link function to scale covariates to a sampling history response of zeros (species non-detection) and ones (species detection). We used a simulated annealing optimization process for all models. We used the R package MuMIn to carry out model selection procedures and used the Bayesian Information Criterion (BIC) to select supported models from sets of candidate models (Burnham and Anderson 2002). We considered models with the lowest BIC score and fewest number of parameters within 2 BIC units of the lowest BIC score to be most supported. We treated all covariates as continuous data and standardized covariates to a mean of 0 and standard deviation of 1 prior to modeling (MacKenzie et al. 2006).

We conducted the following modeling procedure for each species. We first modeled the probability of detection by keeping the occupancy parameter constant and allowing detection to vary as a function of the survey-level covariates. For each covariate, we considered both a linear and quadratic functional form when building models. For model selection, we considered all subsets and used BIC to identify the most supported model. We retained the most supported model to serve as the detection parameter for all subsequent models for that species.

Next, to model the probability of occupancy, we built an initial additive global model consisting of the retained detection parameter and linear terms for each site-level covariate (for landscape covariates these included only the 300-m scale). We considered all subsets and identified the most supported models using BIC. When assessing subsets, we limited the number of occupancy parameters (excluding the intercept) in any model to 5 to limit the ratio of parameters to sample size (MacCallum et al. 2001). We retained all site-level covariates included in any model within 2 BIC units of the top model and used these to build a secondary global model. To determine which functional form to include in the secondary global model, for the appropriate covariates, we then built separate, single-covariate linear and quadratic models and compared them using BIC. We retained the term from the most supported model. If the covariate was a landscape covariate, we compared both functional forms at both spatial scales (i.e., linear 300 m, quadratic 300 m, linear 1 km, and quadratic 1 km) and retained the term from the most supported model. If 2 remaining covariates were highly correlated (≥0.9 Pearson correlation coefficient), we compared single covariate models containing each term using BIC and retained the term from the more supported model. With these retained terms, we then built the secondary global model, evaluated all subsets, and considered the most supported model as our top model. To assess fit of each top model, we used a MacKenzie-Bailey goodness-of-fit test with parametric bootstrapping employing 1,000 simulations to approximate the distribution of the test statistic (MacKenzie and Bailey 2004). We used ArcGIS 10.1 to visualize spatial data.

The Institutional Animal Care and Use Committee of the University of Rhode Island approved our methods (protocol #12–11–005). All work was carried out under scientific collecting permits (numbers 2013–12, 2014–25, and 2015–5) of the Rhode Island Department of Environmental Management.

RESULTS

We sampled 88 wetlands over 3 years (Fig. 1, Tables S1 and S2, available online in Supporting Information). Traps were deployed for a total of 5,824 trap nights yielding 1,661 unique individuals consisting of 5 species (Table 1). We conducted 4 surveys at 79.5% (70/88) of wetlands and <4 at the remaining wetlands. The average number of days between surveys was 38.9 ± 0.77 (SE; n = 228). Painted turtles were the most abundant species and were detected in 84.1% of wetlands (1,369 individuals; 74/88 wetlands). We detected snapping turtles in 62.5% of wetlands (207 individuals; 55/88 wetlands), red-eared sliders in 10.2% of wetlands (21 individuals; 9/88 wetlands), spotted turtles in 7.9% of wetlands (52 individuals; 7/88 wetlands), and musk turtles in 4.5% of wetlands (12 individuals; 4/88 wetlands). We did not capture any wood turtles because we did not sample riparian wetlands. We did not detect turtles in 10.2% of wetlands (9/88 wetlands).

Relative abundance of painted turtles was highest at the lowest forest cover class and generally decreased with increasing forest cover. Relative abundance of spotted turtles was substantially higher in the highest forest cover class and we detected only 1 individual below the 60–70% forest cover class. Relative abundance of snapping turtles exhibited minor variation across most of the gradient of forest cover (Fig. S1). Non-native red-eared sliders did not occur in cover classes >50–60% forest cover.

For the first CCA axis, pH, woody vegetation, and forest cover accounted for the most variation in relative abundance of freshwater turtles (Table S3). This axis accounted for 43.3% of the total variation in the data. Total dissolved solids, wetland age, and road density accounted for the most variation in the second axis, but this axis accounted for only 4.9% of the total variation in the data. Ellipses for painted turtles and snapping turtles were both positioned towards the center of the plot (Fig. 2). The spotted turtle ellipse was positioned towards the negative end of the first axis (more forest cover and woody vegetation). The red-eared slider ellipse was positioned farthest towards the positive end of the first axis (more development and higher pH) and the negative end of the second axis (higher road density and total dissolved solids). The CCA was marginally significant based on the permutation test *P*-value of 0.078.

We modeled occupancy for 4 species of freshwater turtles (Table 3, Table S5). We did not consider musk turtle occupancy because detection probability fell below 5% (MacKenzie et al. 2006). In occupancy models, we did not include 1 wetland, which yielded no turtle detections, because of incomplete covariate data. There was evidence for lack of fit ($P < 0.05$) and overdispersion ($\hat{c} > 1$) in the top model for painted turtles, but all top models for other species exhibited evidence of model fit ($P > 0.05$). For snapping turtles, the estimate of detection probability was 0.399 ± 0.041 and the estimate of occupancy probability was 0.776 ± 0.070 in the null model with no survey-level or site-level covariates. This was also the top model for snapping turtles. For painted turtles the estimates of detection and occupancy were 0.805 ± 0.025 and 0.867 ± 0.039, respectively, in the null model. The top model for painted turtles included a negative logistic relationship with ordinal date for the detection parameter, and a positive logistic relationship with wetland size and a negative logistic relationship with woody vegetation for the occupancy parameter. For spotted turtles, the estimate of detection was 0.554 ± 0.121 and the estimate of occupancy was 0.086 ± 0.032 in the null model. The top model for spotted turtles included a positive logistic relationship with temperature for the detection parameter, and for the occupancy parameter included a positive logistic relationship with forest cover at the 1-km scale, and a negative logistic relationship with wetland depth. For red-eared sliders, the estimate of detection was 0.407 ± 0.098 and the estimate of occupancy was 0.125 ± 0.042 in the null model. The detection parameter of the top model included a positive logistic relationship with air temperature, and a positive logistic relationship with road density at the 1-km scale for the occupancy parameter (Fig. 3; Fig. S2).

DISCUSSION

Spotted turtles and red-eared sliders were encountered far less frequently than painted turtles and snapping turtles. The fact that the introduced red-eared slider was found in a greater number of wetlands than the native spotted turtle is concerning from a conservation standpoint. However, CCA ellipses for these 2 species exhibited the greatest divergence, suggesting a strong difference in the land cover types where they are found, which would suggest a limited possibility for direct interactions in the near future. The relatively low statewide occupancy rate of spotted turtles is consistent with the idea that populations of this species are rare and that they are disproportionately affected by human disturbance (Enneson and Litzgus 2008, Anthonysamy et al. 2014). Spotted turtles were once considered an abundant species in southern New England (Storer 1840, Babcock 1919), including Rhode Island (Drowne 1905), but habitat loss and fragmentation, road mortality, and collection have led to strong declines in the region (Ernst and Lovich 2009, van Dijk 2011).

There was strong evidence of an association between spotted turtles and forest cover. Spotted turtles were absent, except for a single individual, from wetlands surrounded by <60% forest cover, and relative abundance increased in wetlands with 90–100% forest cover. Similarly, the top spotted turtle occupancy model indicated a positive relationship with forest cover at the 1-km scale. Forest cover at the 1-km scale was negatively correlated with road density (Pearson *r*

= −0.889) and development (Pearson r = −0.901; Table S4), indicating that human disturbances are generally reduced in areas of higher forest cover. Although wetland age was not a significant covariate in the occupancy models, all wetlands in which spotted turtles were detected belonged to the oldest age class (pre-1939). These are wetlands that are less likely to have been created or significantly altered by people. Occupancy models also indicated that spotted turtles prefer shallow wetlands with abundant woody vegetation, results that are consistent with other studies of spotted turtle habitat selection (Milam and Melvin 2001, Ernst and Lovich 2009, Rasmussen and Litzgus 2010). In the northeastern United States, the creation and maintenance of early successional vegetation communities is often a management priority for the management of rare species and because the land cover type can be locally rare (Buffum et al. 2014). The techniques most often employed include timber harvest, mowing, and fire, and have potential to negatively affect populations of spotted turtles. We recommend sampling for spotted turtles at sites slated to undergo the creation of early successional vegetation communities and urge extreme caution when initiating these practices if spotted turtles are present (Buchanan et al. 2017).

Probability of red-eared slider occupancy increased with higher road density which serves as a strong proxy for human population density. Red-eared sliders have been introduced via the pet trade in many urban and suburban areas outside of their natural range (Winchell and Gibbs 2016) and the individuals we caught are almost certainly former pets or the offspring of former pets. Whether the detected individuals constitute breeding populations remains unknown, but it is clear that the species is extant and widespread in the state. Red-eared sliders have been considered one of the world’s 100 most detrimental invasive species (Lowe et al. 2000) and future work should investigate if they are breeding in the region and the extent to which they are competing with native turtle species.

Painted turtles and snapping turtles exhibited relatively high occurrence and abundance in our study area with CCA ellipses positioned towards the center of the ordination plot. These results support the idea that both species are habitat generalists with wide niche breadths (Ernst and Lovich 2009, Anthonysamy et al. 2014). Painted turtle abundance was highest in the lowest forest cover class, where sites were heavily modified by either urban development or agriculture. In New Hampshire, forest cover surrounding wetlands did not emerge as an important covariate for painted turtle abundance, but open nesting areas (measured in the field as suitable soils and open canopies) within 30 m of wetlands was positively correlated with abundance (Marchand and Litvaitis 2004). Freshwater turtles prefer open areas for nesting (Janzen 1994, Kolbe and Janzen 2002) and it is likely that nesting habitat becomes more limited with increasing forest cover (Baldwin et al. 2004). Other studies have suggested that painted turtle abundance is not influenced by landscape fragmentation (Rizkalla and Swihart 2006).

Our top occupancy model for painted turtles suggests that they are associated with larger wetlands with little woody vegetation. However, for this model the observed chi-square test statistic is large relative to the bootstrapped distribution, suggesting lack of fit. Therefore, this and other competing models for this species should be interpreted with caution, especially with respect to the precision of the estimates. Given that the MacKenzie-Bailey goodness-of-fit test has no power to assess heterogeneity in occupancy, the lack of fit probably stems from unmodeled detection heterogeneity (MacKenzie and Bailey 2004, MacKenzie et al. 2006). One can use the model overdispersion parameter ($\hat{c}$) to inflate parameter standard errors, thereby adapting their biological inference (MacKenzie and Bailey 2004). We think it is likely that larger, often more permanent, wetlands contain higher densities of painted turtles, which could be influencing detection (and occupancy) probability from site to site. An alternative explanation is simply that painted turtles are cosmopolitan in the study area and that none of the covariates we measured adequately captured variation in occupancy or detection. Painted turtles are the most widespread North American turtle and populations appear to be resilient to intense alteration of habitats, perhaps owing to their ability to disperse and readily colonize modified and created wetlands (Cosentino et al. 2010). Heavily modified land cover types (i.e., urban, suburban, golf courses, and agriculture) may be beneficial to painted turtles by providing enhanced nesting habitat, basking habitat, and increased aquatic plant production resulting from nutrient runoff (Marchand and Litvaitis 2004, Failey et al. 2007, Foley et al. 2012, Price et al. 2013, Winchell and Gibbs 2016).

Snapping turtle abundance exhibited relatively little variation across the forest cover gradient but was lowest in the lowest forest cover class. Snapping turtles are also widespread and considered capable of occupying almost every kind of freshwater habitat (Ernst and Lovich 2009), but are large compared to most species of freshwater turtles and may be more vulnerable to road mortality and collection in areas of high population density (Gibbs and Shriver 2002). Though widespread and still abundant in many areas, snapping turtles are being harvested in the United States at unprecedented rates to meet demands from Asian markets (Luiselli et al. 2016, Colteaux and Johnson 2017). Exports of live snapping turtles have increased 3 orders of magnitude since 1999, exceeding 1.3 million individuals in 2014, and approximately 16% of these were wild caught (Colteaux and Johnson 2017). Small wetlands that occur in developed landscapes are likely to play an increasingly important role in maintaining snapping turtle meta-population structure if this demand persists.

Precise estimates of abundances of freshwater turtles are considered very difficult to obtain, without longer-term mark-recapture studies, because of inherent variation in catchability and observability (Dorland et al. 2014). Although we marked individuals, recapture rates for most species (except for painted turtles) were too low to yield estimates of abundance via mark-recapture modeling, particularly because we sampled each wetland for only 1 season. Nonetheless, we report relative abundance estimates for descriptive purposes and to compare to other studies. Occupancy modeling is more robust to these issues and can be interpreted in the context of presence or absence and habitat selection. Although the utility of occupancy modeling is limited in that it does not permit estimation of important population parameters such as density, survival, or recruitment, the technique contributes to knowledge of geographic distribution and allows for the identification of habitat features associated with a particular species, especially when multiple species are compared (Nielsen et al. 2010).

Our sampling was limited to small, hydrologically isolated wetlands and may not be representative of the interplay between the landscape and different wetland types (e.g., lacustrine and riparian wetlands). Moreover, it is possible that we violated the assumption of closure when modeling occupancy, but because we sampled each wetland for only 1 year that concern is minimized.

As human populations grow and development continues apace, conservation biologists will be tasked with identifying the lands most critical for maintaining native species and those most likely to be colonized by non-native species. Illuminating these relationships can improve the ability of biologists to predict where sensitive species occur within a region and inform management decisions for those species.

MANAGEMENT IMPLICATIONS

Results from this study indicate that human development has influenced the distribution of spotted turtles and red-eared sliders in Rhode Island, albeit in different ways. Identifying habitat features at the landscape scale that are associated with species occurrence has long been an objective in conservation biology. For spotted turtles, future work should aim to identify viable populations in the region using these occupancy models as a way to narrow search effort. This work also serves as a baseline for the current state of the invasion of red-eared sliders in Rhode Island. With future sampling, wildlife managers may be able to assess whether existing regulations intended to slow the invasion are proving effective.

Amassing herpetological occurrence records, through herpetological atlases or natural heritage programs, is a priority among state biologists in the northeastern United States and these occupancy models may be used by biologists for targeting areas for sampling or prioritizing areas for conservation. Moreover, with a better understanding of the conditions under which each species is most likely to be detected, there is strong potential to improve sampling methodology. Few studies of freshwater turtle populations consider variation in detection when estimating important demographic parameters (e.g., abundance and sex ratio).

ACKNOWLEDGMENTS

We thank J. R. Atutubo, K. R. Belleville, S. J. Davis, K. A. Dyer, M. P. Long, R. J. Marchinkoski, D. J. Moore, J. Peltier, and V. Tiburcio for their assistance in the field. R. P. Cook, A. E. Devan-Song, C. J. Raithel and M. A. Walden provided helpful comments throughout the research process. The work was supported by a McIntire-Stennis grant (RI00–MS–978–INT) of the National Institute of Food and Agriculture of the United States Department of Agriculture.

LITERATURE CITED

Anthonysamy, W. J. B., M. J. Dreslik, D. Mauger, and C. A. Phillips. 2014. A preliminary assessment of habitat partitioning in a freshwater turtle community at an isolated preserve. Copeia 2014:269–278.

Babcock, H. L. 1919. The turtles of New England. Boston Society of Natural History, Boston, Massachusetts, USA.

Baldwin, E. A., M. N. Marchand, and J. A. Litvaitis. 2004. Terrestrial habitat use by nesting painted turtles in landscapes with different levels of fragmentation. Northeastern Naturalist 11:41–48.

Bohm, M., et al. 2013. The conservation status of the world's reptiles. Biological Conservation 157:372–385.

Brooks, T. M., R. A. Mittermeier, C. G. Mittermeier, G. A. B. DaFonseca, A. B. Rylands, W. R. Konstant, P. Flick, J. Pilgrim, S. Oldfield, G. Magin, and C. Hilton-Taylor. 2002. Habitat loss and extinction in the hotspots of biodiversity. Conservation Biology 16:909–923.

Buchanan, S. W., B. Buffum, and N. E. Karraker. 2017. Responses of a spotted turtle (*Clemmys Guttata*) population to creation of early successional habitat. Herpetological Conservation and Biology 12:688–700.

Buffum, B., C. Modisette, and S. R. McWilliams. 2014. Encouraging family forest owners to create early successional wildlife habitat in southern New England. PLoS ONE 9(2):e89972.

Burke, V. J., and J. W. Gibbons. 1995. Terrestrial buffer zones and wetland conservation: a case study of freshwater turtles in a Carolina bay. Conservation Biology 9:1365–1369.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information–theoretic approach. Springer Science and Business Media, Berlin, Germany.

Butler, B. J. 2013. Rhode Island’s forest resources, 2012. U.S. Forest Service, Northern Research Station, Newton Square, Pennsylvania, USA.

Butler, B. J., and B. Payton. 2011. Rhode Island's forest resources, 2009. U.S. Forest Service, Northern Research Station, Newton Square, Pennsylvania, USA.

Colteaux, B. C., and D. M. Johnson. 2017. Commercial harvest and export of snapping turtles (*Chelydra serpentina*) in the United States: trends and the efficacy of size limits at reducing harvest. Journal for Nature Conservation 35:13–19.

Congdon, J. D., A. E. Dunham, and R. C. van Loben Sels. 1994. Demographics of common snapping turtles (*Chelydra serpentina*): implications for conservation and management of long–lived organisms. American Zoologist 34:397–408.

Cosentino, B. J., R. L. Schooley, and C. A. Phillips. 2010. Wetland hydrology, area, and isolation influence occupancy and spatial turnover of the painted turtle, *Chrysemys picta*. Landscape Ecology 25:1589–1600.

Dahl, T. E. 1990. Wetlands losses in the United States, 1780's to 1980's. U.S. Fish and Wildlife Service, Washington, D.C., USA.

Dodd, K. C. 1990. Effects of habitat fragmentation on a stream–dwelling species, the flattened musk turtle *Sternotherus depressus*. Biological Conservation 54:33–45.

Dorland, A., T. Rytwinski, and L. Fahrig. 2014. Do roads reduce painted turtle (*Chrysemys picta*) populations? PLoS ONE 9(5):e98414.

Drowne, F. P. 1905. The reptiles and batrachians of Rhode Island. Roger Williams Park Museum Monograph Number 15. C. Abbott Davis, Providence, Rhode Island, USA.

Enneson, J. J., and J. D. Litzgus. 2008. Using long-term data and a stage-classified matrix to assess conservation strategies for an endangered turtle (*Clemmys guttata*). Biological Conservation 141:1560–1568.

Ernst, C. H., and J. E. Lovich. 2009. Turtles of the United States and Canada. Second edition. John Hopkins University Press, Baltimore, Maryland, USA.

Everitt, B., and T. Hothorn. 2011. An introduction to applied multivariate analysis with R. Springer Science and Business Media, Berlin, Germany.

Failey, E. L., J. C. McCoy, S. J. Price, and M. E. Dorcas. 2007. Ecology of turtles inhabiting golf course and farm ponds in the western Piedmont of North Carolina. Journal of North Carolina Academy of Science 123:221–232.

Fiske, I., and R. Chandler. 2011. unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43:1–23.

Foley, S. M., S. J. Price, and M. E. Dorcas. 2012. Nest-site selection and nest depredation of semi-aquatic turtles on golf courses. Urban Ecosystems 15:489–497.

Foster, D. R., and J. D. Aber. 2004. Forests in time: the environmental consequences of 1,000 years of change in New England. Yale University Press, New Haven, Connecticut, USA.

Gibbons, J. W., D. E. Scott, T. J. Ryan, K. A. Buhlmann, T. D. Tuberville, B. S. Metts, J. L. Greene, T. Mills, Y. Leiden, S. Poppy, and C. T. Winne. 2000. The global decline of reptiles, déjà vu amphibians. BioScience 50:653–666.

Gibbs, J. P. 1998. Distribution of woodland amphibians along a forest fragmentation gradient. Landscape Ecology 13:263–268.

Gibbs, J. P. 2000. Wetland loss and biodiversity conservation. Conservation Biology 14:314–317.

Gibbs, J. P., and W. G. Shriver. 2002. Estimating the effects of road mortality on turtle populations. Conservation Biology 16:1647–1652.

Heppell, S. S. 1998. Application of life–history theory and population model analysis to turtle conservation. Copeia 1998:367–375.

Janzen, F. J. 1994. Vegetational cover predicts the sex ratio of hatchling turtles in natural nests. Ecology 75:1593–1599.

Joyal, L. A., M. McCollough, and M. L. Hunter Jr. 2001. Landscape ecology approaches to wetland species conservation: a case study of two turtle species in southern Maine. Conservation Biology 15:1755–1762.

Kolbe, J. J., and F. J. Janzen. 2002. Impact of nest-site selection on nest success and nest temperature in natural and disturbed habitats. Ecology 83:269–281.

Lowe, S., M. Browne, S. Boudjelas, and M. De Poorter. 2000. 100 of the world's worst invasive alien species: a selection from the global invasive species database. The Invasive Species Specialist Group, Species Survival Commission, International Union for the Conservation of Nature (IUCN) 12:1–12.

Luiselli, L., A. Starita, G. M. Carpaneto, G. H. Segniagbeto, and G. Amori. 2016. A short review of the international trade of wild tortoises and freshwater turtles across the world and throughout two decades. Chelonian Conservation and Biology 15:167–172.

MacCallum, R. C., K. F. Widaman, K. J. Preacher, and S. Hong. 2001. Sample size in factor analysis: the role of model error. Multivariate Behavioral Research 36:611–637.

MacKenzie, D. I., and L. L. Bailey. 2004. Assessing the fit of site-occupancy models. Journal of Agricultural, Biological, and Environmental Statistics 9:300–318.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, A. J. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, Cambridge, Massachusetts, USA.

Marchand, M. N., and J. A. Litvaitis. 2004. Effects of habitat features and landscape composition on the population structure of a common aquatic turtle in a region undergoing rapid development. Conservation Biology 18:758–767.

Marzluff, J. M. 2001. Worldwide urbanization and its effects on birds. Pages 19–47 *in* J. M. Marzluff, R. Bowman, and R. Donnelly, editors. Avian ecology and conservation in an urbanizing world. Springer, New York, New York, USA.

McDonnell, M. J., and A. K. Hahs. 2008. The use of gradient analysis studies in advancing our understanding of the ecology of urbanizing landscapes: current status and future directions. Landscape Ecology 23:1143–1155.

Milam, J. C., and S. M. Melvin. 2001. Density, habitat use, movements, and conservation of spotted turtles (*Clemmys guttata*) in Massachusetts. Journal of Herpetology 35:418–427.

Mitchell, J. C., and M. W. Klemens. 2000. Primary and secondary effects of habitat alteration. Pages 5–32 *in* M. W. Klemens, editor. Turtle conservation. The Smithsonian Institution, Washington, D.C., USA.

National Centers for Environmental Information [NCEI]. 2016. Climate, temperature, and precipiation data for Rhode Island. <https://www.ncei.noaa.gov>. Accessed 15 Mar 2016.

Nielsen, S. E., G. McDermid, G. B. Stenhouse, and M. S. Boyce. 2010. Dynamic wildlife habitat models: seasonal foods and mortality risk predict occupancy-abundance and habitat selection in grizzly bears. Biological Conservation 143:1623–1634.

Price, S. J., J. Guzy, L. Witczak, and M. E. Dorcas. 2013. Do ponds on golf courses provide suitable habitat for wetland-dependent animals in suburban areas? An assessment of turtle abundances. Journal of Herpetology 47:243–250.

Rasmussen, M. L., and J. D. Litzgus. 2010. Habitat selection and movement patterns of spotted turtles (*Clemmys guttata*): effects of spatial and temporal scales of analyses. Copeia 2010:86–96.

Rector, D. D. 1981. Soil survey of Rhode Island. U.S. Department of Agriculture, Soil Conservation Service, Washington, D.C., USA.

Rhode Island Department of Environmental Management [RIDEM]. 2015. Rhode Island Wildlife Action Plan. < http://www.dem.ri.gov/programs/fish-wildlife>. Accessed 30 Sep 2018.

Rhode Island Geographic Information System [RIGIS]. University of Rhode Island Environmental Data Center. <http://www.rigis.org>. Accessed 15 Mar 2013.

Riem, J. G., R. B. Blair, D. N. Pennington, and N. G. Solomon. 2012. Estimating mammalian species diversity across an urban gradient. American Midland Naturalist 168:315–332.

Rizkalla, C. E., and R. K. Swihart. 2006. Community structure and differential responses of aquatic turtles to agriculturally induced habitat fragmentation. Landscape Ecology 21:1361–1375.

Semlitsch, R. D., and J. R. Bodie. 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conservation Biology 17:1219–1228.

Shiping, G., W. Jichao, S. Haitao, S. Riheng, and X. Rumei. 2006. Illegal trade and conservation requirements of freshwater turtles in Nanmao, Hainan Provence, China. Oryx 40:331–336.

Storer, D. H. 1840. Reptiles of Massachusetts. Dutton and Wentworth, Boston, Massachusetts, USA.

U.S. Fish and Wildlife Service. 2015. Petition to list spotted turtle in Connecticut, Delaware, Florida, Georgia, Illinois, Maine, Maryland, Massachusetts, Michigan, Pennsylvania, New Hampshire, New York, North Carolina, Ohio, South Carolina, Vermont, Virginia, and West Virginia under the Endangered Species Act of 1973, as amended. Federal Register Docket ID FWS–R5–ES–2015–0064.

van Dijk, P. P. 2011. *Clemmys guttata*. The IUCN red list of threatened species. International Union for the Conservation of Nature, Gland, Switzerland. <http://www.iucnredlist.org/details/4965/0>. Accessed 15 Mar 2017.

van Dijk, P. P., and J. Harding. 2011. *Glyptemys insculpta*. IUCN red list of threatened species. International Union for the Conservation of Nature, Gland, Switzerland. <http://www.iucnredlist.org/details/4968/0>. Accessed 15 Mar 2017.

Winchell, K. M., and J. P. Gibbs. 2016. Golf courses as habitat for aquatic turtles in urbanized landscapes. Landscape and Urban Planning 147:59–70.

Associate Editor: Cynthia Paszkowski.

Figure Captions

Figure 1. Locations of wetlands sampled for freshwater turtles in Rhode Island, USA, 2013–2015. An additional 7 sites are not pictured where we detected spotted turtles.

Figure 2. Canonical correspondence analysis ordination biplot for wetlands in Rhode Island, USA, based on the relative abundance of 4 freshwater turtle species in 2013–2015 and relativized values for 17 environmental covariates. Vectors indicate the direction and magnitude of covariate scores. Ellipses are centered on the mean values for each species and represent 95% confidence ellipses based on the corresponding standard error. Site-level ovariates included wetland age (Wetland.age), surface area of wetland (Hectares), maximum depth of wetlands (Max.depth), pH (pH), total dissolved solids (TDS), dissolved nitrate (Nitrate), dissolved phosphorous (Phos), percent of wetland surface containing graminoid vegetation (Graminoid), percent of wetland surface containing herbaceous vegetation (Herbaceous), percent of unvegetated wetland surface (Open.water), percent of wetland surface containing algae or Lemnaceae (Surficial), percent of wetland surface containing woody shrubs and trees (Woody), percent of forest within 300 m of wetland (Forest.300), percent of wetland area within 300 m of wetland (Wetland.300), percent of developed area within 300 m of wetland (Develop.300), percent of early successional vegetation within 300 m of wetland (ESH.300), road density within 300m of wetland (Road.dens.300).

Figure 3. Predicted red-eared slider occupancy in Rhode Island, USA, developed from the top model at a 100-m cell size and based on detections from 2013–2015. Inset map shows human population density for comparison.

Table 1. Occurrence and abundance of freshwater turtle species by forest cover class, Rhode Island, USA, 2013–2015.

	Forest cover 1 km									
	0–40%		20–60%		40–80%		80–100%			
	Forest cover 300 m									
	10–20%	20–30%	30–40%	40–50%	50–60%	60–70%	80–90%	90–100%	Total number of wetlands (% of total)	Total number of individuals
Number of wetlands	8	12	11	12	12	11	10	12	88	
Snapping turtle										
Number of wetlands where species detected	2	10	8	9	9	4	8	5	55 (62.5)	
Number of individuals detected	7	53	42	24	21	8	21	31		207
Eastern painted turtle										
Number of wetlands where species detected	8	11	10	10	10	9	9	6	73 (82.9)	
Number of individuals detected	209	206	204	204	196	129	103	118		1,369
Spotted turtle										
Number of wetlands where species detected	0	1	0	0	0	1	2	3	7 (7.9)	
Number of individuals detected	0	1	0	0	0	3	4	44		52
Musk turtle										
Number of wetlands where species detected	1	0	1	1	0	0	1	0	4 (4.5)	
Number of individuals detected	1	0	1	6	0	0	4	0		12
Red-eared slider										
Number of wetlands where species detected	1	5	1	1	1	0	0	0	9 (10.2)	
Number of individuals detected	2	11	3	4	1	0	0	0		21
Total										1,661

Table 2. Detection and occupancy covariates considered for freshwater turtle occupancy models, Rhode Island, USA, 2013–2015.

Covariate	Description
Survey-level (*p*)	
Ordinal[a]	Ordinal date (1–365) of day 2 of each survey
Temp[a]	Mean of maximum daily temperature (from nearest weather station) for days 1 and 2 of each survey
Precip[a]	Mean of total daily precipitation (from nearest weather station) for days 1 and 2 of each survey
Time[a]	Survey number (1, 2, 3, or 4)
Site-level (Ψ)	
Wetland covariates	
Wetland.age	Age of wetland as determined using historical imagery (continuous variable 1–77)
Hectares	Surface area (ha) of wetland as measured via geographic information system
Max.depth	Maximum detected (m) depth measured using a weighted measuring tape
pH[a]	pH
TDS[a]	Total dissolved solids
Nitrate[a]	Dissolved nitrate (ppb) as measured from the water column
Phos[a]	Dissolved phosphorous (ppb) as measured in the water column
Graminoid[a]	Percent of wetland surface containing emergent graminoid vegetation
Herbaceous[a]	Percent of wetland surface containing emergent forbs and other non-woody vegetation (including Nymphaea)
Open.water[a]	Percent of unvegetated wetland surface
Surficial[a]	Percent of wetland surface containing floating algae or Lemnaceae
Woody[a]	Percent of wetland surface containing woody shrubs and trees (including dead wood and swamp loosestrife [*Decadon verticillatus*])
Landscape covariates	
Easting[a]	Longitude expressed in Universal Transverse Mercator units (Zone 19N)
Northing[a]	Latitude expressed in Universal Transverse Mercator units (Zone 19N)
Forest (300, 1000)[a]	Percent of forest within buffers of 300 m and 1 km
Wetland (300, 1000)[a]	Percent of wetland within buffers of 300 m and 1 km
ESH (300, 1000)[a]	Percent of early successional vegetation (agriculture, grassland, upland shrubland) within buffers of 300 m and 1 km
Develop (300, 1000)[a]	Percent of human development within buffers of 300 m and 1 km

Road.dens (300, 1000)[a]	Road density (m/ha) within buffers of 300 m and 1 km

[a]Indicates that we considered both a linear and quadratic relationship.

Table 3. Occupancy models (from secondary global model subset) within 2 Bayesian Information Criterion (BIC) units of top models, which show the strongest relationship between species presence and measured covariates in Rhode Island, USA, 2013–2015; *p* is detection parameter; Ψ is occupancy parameter; *K* is number of parameters in the model; MacKenzie-Bailey goodness-of-fit parameters are included for the top model of each species and include χ^2, *P*-value, and $\hat{c}$ as the overdispersion parameter.

Species	Model	K	BIC	ΔBIC	weight	χ^2	P-value	$\hat{c}$
Snapping turtle	$p(.) + p(\text{Ordinal}) + p(\text{Ordinal})^2 + \Psi(.)$	4	346.15	0.00	0.716	27	0.59	0.84
	$p(.) + p(\text{Ordinal}) + p(\text{Ordinal})^2 + \Psi(.) + \Psi(\text{Nitrate})$	5	347.65	1.50	0.284			
Eastern painted turtle	$p(.) + p(\text{Ordinal}) + \Psi(.) + \Psi(\text{Hectares}) + \Psi(\text{Woody})$	5	316.64	0.00	0.552	64.19	0.027	2.06
	$p(.) + p(\text{Ordinal}) + \Psi(.) + \Psi(\text{Hectares}) + \Psi(\text{Woody}) + \Psi(\text{Wetland.300})$	6	318.25	1.61	0.229			
	$p(.) + p(\text{Ordinal}) + \Psi(.) + \Psi(\text{Hectares}) + \Psi(\text{Woody}) + \Psi(\text{Phos})$	6	318.51	1.87	0.219			
Spotted turtle	$p(.) + p(\text{Temp}) + \Psi(.) + \Psi(\text{Forest.1000}) + \Psi(\text{Max.depth})$	5	74.36	0.00	0.398	16.82	0.814	0.64
	$p(.) + p(\text{Temp}) + \Psi(.) + \Psi(\text{Forest.1000}) + \Psi(\text{Woody})$	5	75.09	0.73	0.217			
	$p(.) + p(\text{Temp}) + \Psi(.) + \Psi(\text{Forest.1000}) + \Psi(\text{Max.depth}) + \Psi(\text{Woody})$	6	76.13	1.77	0.212			
	$p(.) + p(\text{Temp}) + \Psi(.) + \Psi(\text{Forest.1000}) + \Psi(\text{Max.depth}) + \Psi(\text{Wetland.age}) + \Psi(\text{Woody})$	7	76.17	1.83	0.173			
Red-eared slider	$p(.) + p(\text{Temp}) + \Psi(.) + \Psi(\text{Road.dens.1000})$	4	101.06	0.00	0.608	16.87	0.742	0.52
	$p(.) + p(\text{Temp}) + \Psi(.) + \Psi(\text{Road.dens.1000}) + \Psi(\text{pH})$	5	101.98	0.92	0.392			

Survey-level covariates in top models included ordinal date (Ordinal) and air temperature (Temp). Site-level covariates in top models included wetland age (Wetland.age), surface area of wetland (Hectares), maximum depth of wetlands (Max.depth), pH (pH), dissolved nitrate (Nitrate), dissolved phosphorous (Phos), percent of wetland surface containing woody shrubs and trees (Woody), percent of forest within 1 km of wetland (Forest.1000), and road density within 1 km of wetland (Road.dens.1000).

Figures

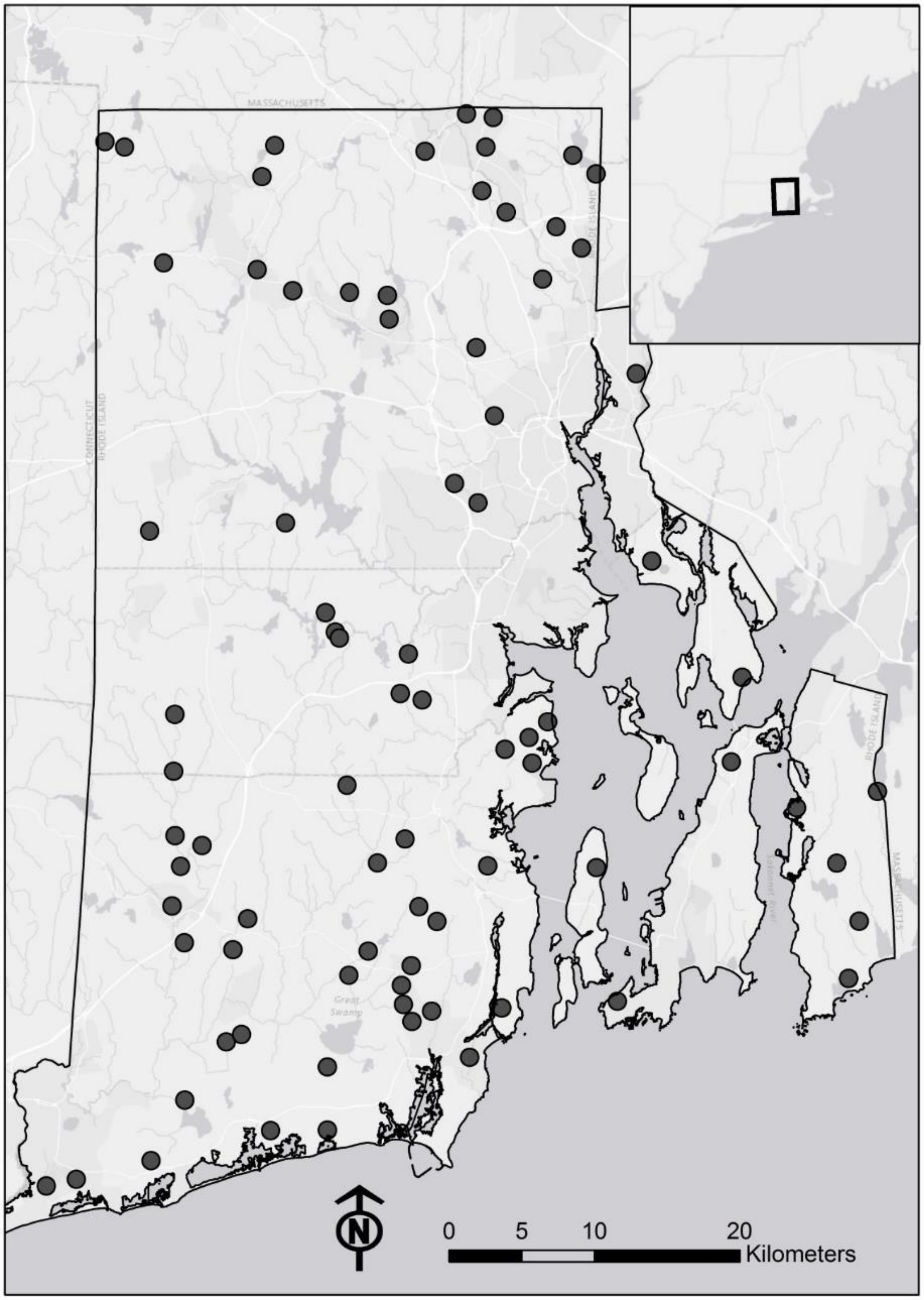
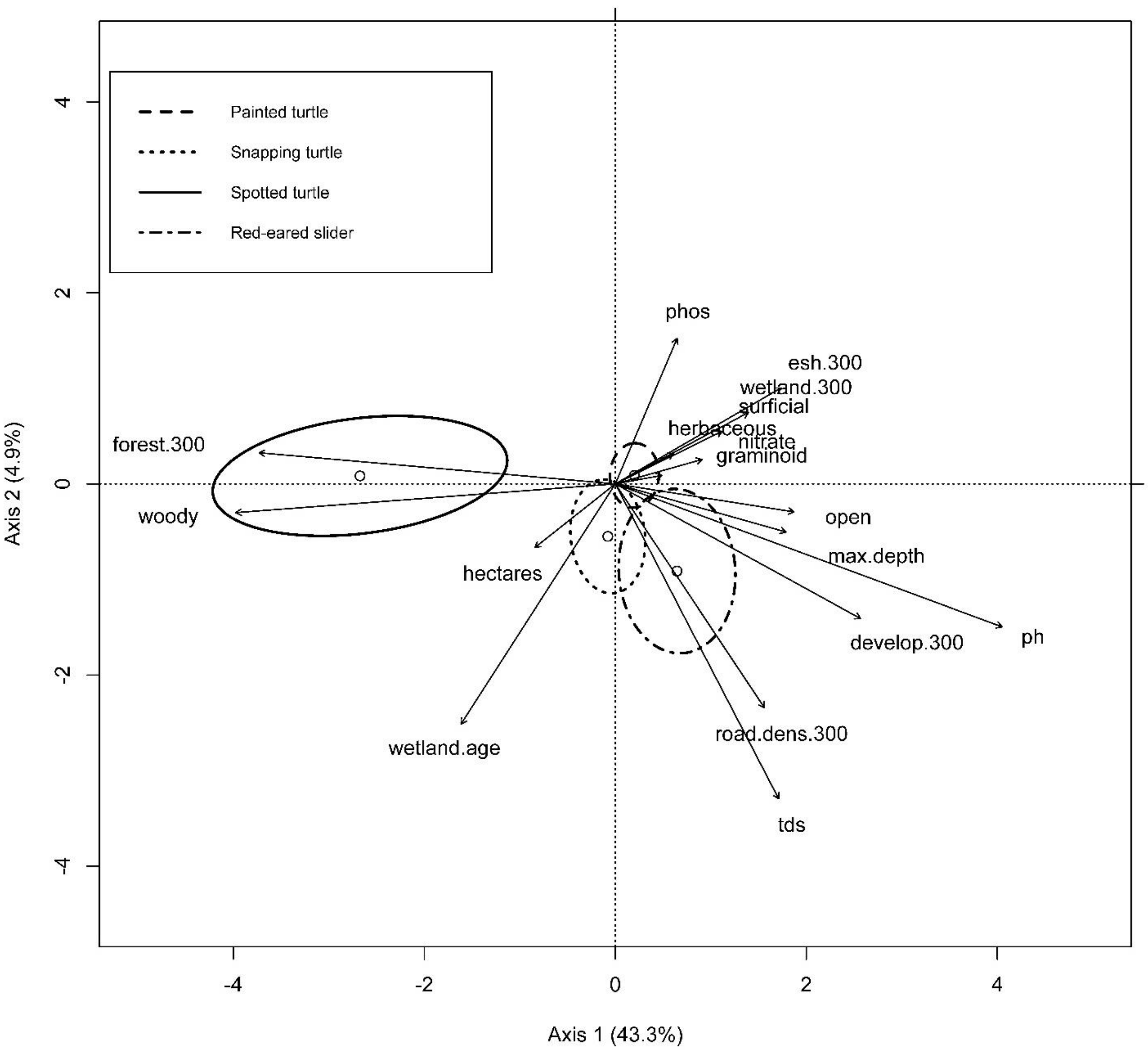


Figure 1. Locations of wetlands sampled for freshwater turtles in Rhode Island, USA, 2013–2015. An additional 7 sites are not pictured where we detected spotted turtles.



Painted turtle
Snapping turtle
Spotted turtle
Red-eared slider
phos
esh.300
wetland.300
surficial
herbaceous
nitrate
graminoid
forest.300
woody
open
hectares
max.depth
develop.300
ph
wetland.age
road.dens.300
tds
4
2
0
-2
-4
Axis 2 (4.9%)
Axis 1 (43.3%)

Figure 2. Canonical correspondence analysis ordination biplot for wetlands in Rhode Island, USA, based on the relative abundance of 4 freshwater turtle species in 2013–2015 and relativized values for 17 environmental covariates. Vectors indicate the direction and magnitude of covariate scores. Ellipses are centered on the mean values for each species and represent 95% confidence ellipses based on the corresponding standard error. Environmental covariates included wetland age (Wetland.age), surface area of wetland (Hectares), maximum depth of wetlands (Max.depth), pH (pH), total dissolved solids (TDS), dissolved nitrate (Nitrate), dissolved phosphorous (Phos), percent of wetland surface containing graminoid vegetation (Graminoid), percent of wetland surface containing herbaceous vegetation (Herbaceous), percent of unvegetated wetland surface (Open.water), percent of wetland surface containing algae or Lemnaceae (Surficial), percent of wetland surface containing woody shrubs and trees (Woody), percent of forest within 300 m of wetland (Forest.300), percent of wetland area within 300 m of wetland (Wetland.300), percent of developed area within 300 m of wetland (Develop.300), percent of early successional vegetation within 300 m of wetland (ESH.300), road density within 300m of wetland (Road.dens.300).

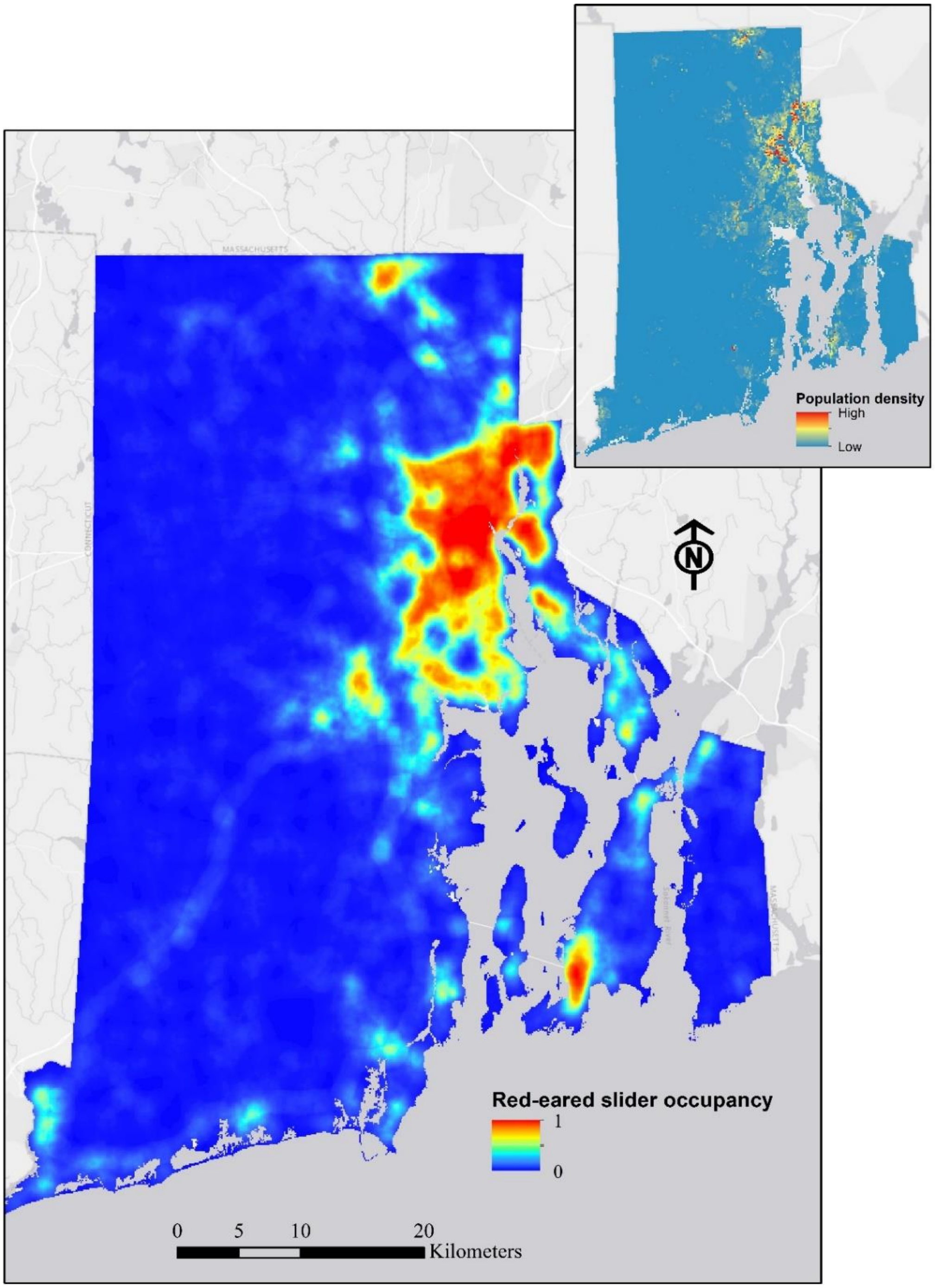


Figure 3. Predicted red-eared slider occupancy in Rhode Island, USA, developed from the top model at a 100-m cell size and based on detections from 2013–2015. Inset map shows human population density for comparison.