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10 **Occupancy of Freshwater Turtles Across a Gradient of Altered Landscapes**

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

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

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

39 Human-induced landscape alteration is often implicated as compromising vertebrate biodiversity,
40 with habitat loss and degradation widely recognized as the leading causes of a loss of population
41 stability across taxa (Gibbons et al. 2000, Brooks et al. 2002). New England, in the northeastern
42 United States, has experienced substantial shifts in landscape composition since the time of
43 European settlement. Deforestation associated with agriculture and logging peaked in the mid-
44 nineteenth century when as much as 80% of the landscape had been cleared. Beginning around
45 1850 agriculture shifted to states farther west, ushering in a period of reforestation lasting
46 approximately 100 years (Foster and Aber 2004). In Rhode Island, USA, this period was
47 followed by another phase of deforestation for urban and suburban development. Total forested
48 land area in Rhode Island has been decreasing since at least 1953, when an estimated 65% of the
49 state was forested (Butler and Payton 2011). A recent estimate suggested that approximately

50 54% of the state is forested (Butler 2013). This extreme landscape alteration in a relatively short
51 period of time has certainly led to changes in the distribution and abundance of wildlife, but the
52 legacy of this change is poorly understood for many species, including freshwater turtles.

53 As a vertebrate group, turtles have an extremely high rate of extinction risk (Bohm et al.
54 2013). In the United States, freshwater turtles are of particular conservation concern largely
55 because of a significant loss in wetland area beginning in the eighteenth century. An estimated
56 37% of the wetlands in Rhode Island were drained, filled, or otherwise lost between 1780 and
57 1980 (Dahl 1990). Additional factors putting freshwater turtle populations at risk include the loss
58 of meta-population structure associated with terrestrial habitat loss and degradation (Dodd 1990,
59 Gibbs 2000), collection for pet, food, and medicine trades (Shiping et al. 2006, Luiselli et al.
60 2016), and life-history characteristics that include delayed sexual maturity and low recruitment
61 (Congdon et al. 1994, Heppell 1998). In Rhode Island, native freshwater turtles include the
62 common snapping turtle (*Chelydra serpentina*), eastern painted turtle (*Chrysemys picta picta*),
63 spotted turtle (*Clemmys guttata*), wood turtle (*Glyptemys insculpta*), and musk turtle
64 (*Sternotherus odoratus*). An additional species, the red-eared slider (*Trachemys scripta elegans*),
65 has been introduced to Rhode Island from the southern United States. The spotted turtle and
66 wood turtle have been identified as endangered by the International Union for the Conservation
67 of Nature (IUCN; van Dijk 2011, van Dijk and Harding 2011), and both are currently candidate
68 species under review for listing under the United States Endangered Species Act (U.S. Fish and
69 Wildlife Service 2015).

70 All freshwater turtle species use terrestrial habitats to some extent, using uplands to nest,
71 move between wetlands, and estivate, but the proportion of time spent on land varies among
72 species (Ernst and Lovich 2009). For example, spotted turtles move frequently between

73 temporary and permanent wetlands and estivate terrestrially, spending as much as 30% of their
74 time on land (Milam and Melvin 2001). The landscape adjacent to and between wetlands is
75 directly linked to many ecological processes of freshwater turtles (Joyal et al. 2001). Landscape
76 gradient analyses have been used for decades to investigate how changes in composition and
77 configuration of the landscape affect wildlife (Gibbs 1998, Riem et al. 2012). Typically, data are
78 collected based on some direct or indirect measure of varying anthropogenic intensity. For
79 certain taxa, these studies have led to broad generalizations about the relationships between
80 urbanization and patterns of distribution, abundance, and diversity (Marzluff 2001, McDonnell
81 and Hahs 2008). Very few studies, however, have examined patterns in reptile distributions
82 across urban gradients. A major review (McDonnell and Hahs 2008) of 201 studies investigating
83 organismal distributions along urbanization gradients published between 1990 and 2007 included
84 only 1 study of reptiles.

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

93 **STUDY AREA**

94 Our study was conducted throughout the state of Rhode Island (excluding Block Island) from
95 2013 to 2015. At approximately 2,700 km² (when excluding coastal waterways), Rhode Island is

96 the smallest state geographically in the United States but ranks second highest in human
97 population density. The highest levels of land development and human population densities
98 occur along the south coast and around Narraganset Bay in the eastern part of the state. Mean
99 elevation is approximately 60 m with a highest point of 247 m. The Wisconsin glaciation, which
100 reached a maximum extent approximately 25,000 years ago and retreated completely from the
101 area 10,000–12,000 years ago, is responsible for the dominant parent materials found in Rhode
102 Island. These include glacial till, glacial outwash, and windblown silts (eolian mantle). Till soils
103 are typically associated with higher elevation landforms, whereas outwash materials are located
104 in valley landscape positions. A mantle of windblown silt can be found across various landscapes
105 throughout the state (Rector 1981). Long-term (1981–2010) average annual temperature in
106 Kingston, Rhode Island was 10.5 °C and long-term average annual precipitation was 134.3 cm.
107 Long-term average monthly temperatures ranged from –1.4°C in January to 22.1°C in July
108 (National Centers for Environmental Information [NCEI] 2016). Rhode Island consists of a
109 matrix of different land use types and hosts a diverse assemblage of flora and fauna (RIDEM
110 2015).

111 **METHODS**

112 **Site Selection**

113 We used ArcGIS version 10.1 (Environmental Systems Research Institute, Redlands, CA, USA)
114 to identify all freshwater wetlands ≤ 2 ha in size throughout the state. We then selected candidate
115 wetland sites for sampling using a stratified random design to capture statewide variability in
116 landscape composition. To minimize confounding factors among sites, we focused our sampling
117 on relatively small (0.1–2.0 ha), isolated (i.e., discrete, non-riparian) wetlands. To further

118 minimize potential confounding variables, we excluded wetlands that were within 500 m of the
119 coastline, within 300 m of a federal or state highway, or within 10 m of a local road.

120 We grouped retained wetlands as small (0.1–0.4 ha) or large (>0.4–1.8 ha) using a 0.4 ha
121 breakpoint, which was the approximate median of wetland size for all retained wetlands. We
122 calculated percent forest cover within buffers of 300 m and 1 km from the wetland edge of all
123 retained wetlands. We selected these distances to represent a core scale (Burke and Gibbons
124 1995, Semlitsch and Bodie 2003) and a more encompassing scale, respectively (Mitchell and
125 Klemens 2000). We assigned wetlands into 1 of 8 hierarchically assembled forest cover classes,
126 which we binned at the 300-m scale into increments of 10% (excluding 0–10% and 70–80%),
127 and binned at the 1-km scale into 4, partially overlapping larger increments (0–40%, 20–60%,
128 40–80%, 80–100%) such that each value at the 300-m scale was encompassed within a value at
129 the 1-km scale (Table 1). These cover classes created a near-continuous gradient of sites with
130 different forest conditions that captured much of the variation in the landscape statewide. We
131 identified 1,665 potential wetlands, assigned each wetland a random number, sorted them by
132 random number in ascending order, and contacted property owners or land managers in that
133 order until we received permission to sample the desired number of wetlands in each forest cover
134 and size class. Our intent was to sample approximately 10–12 wetlands in each of the 10% forest
135 cover classes and an equal number of wetlands in each size class.

136 **Turtle Sampling and Data Collection**

137 In 2013–2015 we sampled turtles from May–October, sampling approximately 30 wetlands per
138 year. We sampled each wetland for only 1 year but surveyed each up to 4 times within that year,
139 hydroperiod allowing. For each survey, we trapped turtles for an approximately 48-hour period,
140 with trap checks every 24 hours, totaling 2 trapping sessions per survey. We sampled sites using

141 small (30.5-cm-diameter collapsible minnow traps; Promar Nets, Gardena, CA, USA) and large
142 (91.4-cm single throated hoop traps; Memphis Net and Twine, Memphis, TN, USA) traps baited
143 with sardines placed inside perforated plastic containers. Alternating between small and large
144 traps, we placed traps approximately 30 m apart around the perimeter of wetlands (within 10 m
145 of the edge) such that the perimeter of each wetland determined the number of traps deployed.
146 We opportunistically hand-captured a small number of turtles (<15) that were encountered when
147 working with traps.

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

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

170 **Statistical Analysis**

171 We estimated relative abundance for each species at each wetland by calculating the total
172 number of unique individuals caught divided by the total number of trap nights. We used
173 canonical correspondence analysis (CCA) to summarize relationships between species relative
174 abundance and the environmental covariates measured at each wetland. We were primarily
175 interested in using CCA as an exploratory technique to identify the major structure in the data
176 and to identify the most important covariates associated with abundance (Everitt and Hothorn
177 2011). We built a correlation matrix consisting of all site-level covariates (Table 2; excluding
178 geographic location and only considering landscape covariates at the 300-m scale) and the
179 corresponding relative abundances for each species, at each site. We conducted the CCA using
180 the vegan package in R (R Foundation for Statistical Computing, Vienna, Austria) using the
181 scaling option, which standardized all data to a mean of zero and standard deviation of 1. We
182 constructed a plot of the first 2 constraints with ellipses drawn around mean values for each
183 species and representing 95% confidence ellipses based on the corresponding standard error. We
184 used a permutation test with 999 permutations to assess the significance of constraints.

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

204 We conducted the following modeling procedure for each species. We first modeled the
205 probability of detection by keeping the occupancy parameter constant and allowing detection to
206 vary as a function of the survey-level covariates. For each covariate, we considered both a linear
207 and quadratic functional form when building models. For model selection, we considered all

208 subsets and used BIC to identify the most supported model. We retained the most supported
209 model to serve as the detection parameter for all subsequent models for that species.

210 Next, to model the probability of occupancy, we built an initial additive global model
211 consisting of the retained detection parameter and linear terms for each site-level covariate (for
212 landscape covariates these included only the 300-m scale). We considered all subsets and
213 identified the most supported models using BIC. When assessing subsets, we limited the number
214 of occupancy parameters (excluding the intercept) in any model to 5 to limit the ratio of
215 parameters to sample size (MacCallum et al. 2001). We retained all site-level covariates included
216 in any model within 2 BIC units of the top model and used these to build a secondary global
217 model. To determine which functional form to include in the secondary global model, for the
218 appropriate covariates, we then built separate, single-covariate linear and quadratic models and
219 compared them using BIC. We retained the term from the most supported model. If the covariate
220 was a landscape covariate, we compared both functional forms at both spatial scales (i.e., linear
221 300 m, quadratic 300 m, linear 1 km, and quadratic 1 km) and retained the term from the most
222 supported model. If 2 remaining covariates were highly correlated (≥ 0.9 Pearson correlation
223 coefficient), we compared single covariate models containing each term using BIC and retained
224 the term from the more supported model. With these retained terms, we then built the secondary
225 global model, evaluated all subsets, and considered the most supported model as our top model.
226 To assess fit of each top model, we used a MacKenzie-Bailey goodness-of-fit test with
227 parametric bootstrapping employing 1,000 simulations to approximate the distribution of the test
228 statistic (MacKenzie and Bailey 2004). We used ArcGIS 10.1 to visualize spatial data.

229 The Institutional Animal Care and Use Committee of the University of Rhode Island approved
230 our methods (protocol #12-11-005). All work was carried out under scientific collecting

231 permits (numbers 2013–12, 2014–25, and 2015–5) of the Rhode Island Department of
232 Environmental Management.

233 **RESULTS**

234 We sampled 88 wetlands over 3 years (Fig. 1, Tables S1 and S2, available online in Supporting
235 Information). Traps were deployed for a total of 5,824 trap nights yielding 1,661 unique
236 individuals consisting of 5 species (Table 1). We conducted 4 surveys at 79.5% (70/88) of
237 wetlands and <4 at the remaining wetlands. The average number of days between surveys was
238 38.9 ± 0.77 (SE; $n = 228$). Painted turtles were the most abundant species and were detected in
239 84.1% of wetlands (1,369 individuals; 74/88 wetlands). We detected snapping turtles in 62.5% of
240 wetlands (207 individuals; 55/88 wetlands), red-eared sliders in 10.2% of wetlands (21
241 individuals; 9/88 wetlands), spotted turtles in 7.9% of wetlands (52 individuals; 7/88 wetlands),
242 and musk turtles in 4.5% of wetlands (12 individuals; 4/88 wetlands). We did not capture any
243 wood turtles because we did not sample riparian wetlands. We did not detect turtles in 10.2% of
244 wetlands (9/88 wetlands).

245 Relative abundance of painted turtles was highest at the lowest forest cover class and
246 generally decreased with increasing forest cover. Relative abundance of spotted turtles was
247 substantially higher in the highest forest cover class and we detected only 1 individual below the
248 60–70% forest cover class. Relative abundance of snapping turtles exhibited minor variation
249 across most of the gradient of forest cover (Fig. S1). Non-native red-eared sliders did not occur
250 in cover classes >50–60% forest cover.

251 For the first CCA axis, pH, woody vegetation, and forest cover accounted for the most
252 variation in relative abundance of freshwater turtles (Table S3). This axis accounted for 43.3% of
253 the total variation in the data. Total dissolved solids, wetland age, and road density accounted for

254 the most variation in the second axis, but this axis accounted for only 4.9% of the total variation
255 in the data. Ellipses for painted turtles and snapping turtles were both positioned towards the
256 center of the plot (Fig. 2). The spotted turtle ellipse was positioned towards the negative end of
257 the first axis (more forest cover and woody vegetation). The red-eared slider ellipse was
258 positioned farthest towards the positive end of the first axis (more development and higher pH)
259 and the negative end of the second axis (higher road density and total dissolved solids). The
260 CCA was marginally significant based on the permutation test P -value of 0.078.

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

277 and a negative logistic relationship with wetland depth. For red-eared sliders, the estimate of
278 detection was 0.407 ± 0.098 and the estimate of occupancy was 0.125 ± 0.042 in the null model.
279 The detection parameter of the top model included a positive logistic relationship with air
280 temperature, and a positive logistic relationship with road density at the 1-km scale for the
281 occupancy parameter (Fig. 3; Fig. S2).

282 **DISCUSSION**

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

295 There was strong evidence of an association between spotted turtles and forest cover.
296 Spotted turtles were absent, except for a single individual, from wetlands surrounded by <60%
297 forest cover, and relative abundance increased in wetlands with 90–100% forest cover. Similarly,
298 the top spotted turtle occupancy model indicated a positive relationship with forest cover at the
299 1-km scale. Forest cover at the 1-km scale was negatively correlated with road density (Pearson r

300 = -0.889) and development (Pearson $r = -0.901$; Table S4), indicating that human disturbances
301 are generally reduced in areas of higher forest cover. Although wetland age was not a significant
302 covariate in the occupancy models, all wetlands in which spotted turtles were detected belonged
303 to the oldest age class (pre-1939). These are wetlands that are less likely to have been created or
304 significantly altered by people. Occupancy models also indicated that spotted turtles prefer
305 shallow wetlands with abundant woody vegetation, results that are consistent with other studies
306 of spotted turtle habitat selection (Milam and Melvin 2001, Ernst and Lovich 2009, Rasmussen
307 and Litzgus 2010). In the northeastern United States, the creation and maintenance of early
308 successional vegetation communities is often a management priority for the management of rare
309 species and because the land cover type can be locally rare (Buffum et al. 2014). The techniques
310 most often employed include timber harvest, mowing, and fire, and have potential to negatively
311 affect populations of spotted turtles. We recommend sampling for spotted turtles at sites slated to
312 undergo the creation of early successional vegetation communities and urge extreme caution
313 when initiating these practices if spotted turtles are present (Buchanan et al. 2017).

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

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

335 Our top occupancy model for painted turtles suggests that they are associated with larger
336 wetlands with little woody vegetation. However, for this model the observed chi-square test
337 statistic is large relative to the bootstrapped distribution, suggesting lack of fit. Therefore, this
338 and other competing models for this species should be interpreted with caution, especially with
339 respect to the precision of the estimates. Given that the MacKenzie-Bailey goodness-of-fit test
340 has no power to assess heterogeneity in occupancy, the lack of fit probably stems from
341 unmodeled detection heterogeneity (MacKenzie and Bailey 2004, MacKenzie et al. 2006). One
342 can use the model overdispersion parameter (\hat{c}) to inflate parameter standard errors, thereby
343 adapting their biological inference (MacKenzie and Bailey 2004). We think it is likely that
344 larger, often more permanent, wetlands contain higher densities of painted turtles, which could
345 be influencing detection (and occupancy) probability from site to site. An alternative explanation

346 is simply that painted turtles are cosmopolitan in the study area and that none of the covariates
347 we measured adequately captured variation in occupancy or detection. Painted turtles are the
348 most widespread North American turtle and populations appear to be resilient to intense
349 alteration of habitats, perhaps owing to their ability to disperse and readily colonize modified and
350 created wetlands (Cosentino et al. 2010). Heavily modified land cover types (i.e., urban,
351 suburban, golf courses, and agriculture) may be beneficial to painted turtles by providing
352 enhanced nesting habitat, basking habitat, and increased aquatic plant production resulting from
353 nutrient runoff (Marchand and Litvaitis 2004, Failey et al. 2007, Foley et al. 2012, Price et al.
354 2013, Winchell and Gibbs 2016).

355 Snapping turtle abundance exhibited relatively little variation across the forest cover
356 gradient but was lowest in the lowest forest cover class. Snapping turtles are also widespread and
357 considered capable of occupying almost every kind of freshwater habitat (Ernst and Lovich
358 2009), but are large compared to most species of freshwater turtles and may be more vulnerable
359 to road mortality and collection in areas of high population density (Gibbs and Shriver 2002).
360 Though widespread and still abundant in many areas, snapping turtles are being harvested in the
361 United States at unprecedented rates to meet demands from Asian markets (Luiselli et al. 2016,
362 Colteaux and Johnson 2017). Exports of live snapping turtles have increased 3 orders of
363 magnitude since 1999, exceeding 1.3 million individuals in 2014, and approximately 16% of
364 these were wild caught (Colteaux and Johnson 2017). Small wetlands that occur in developed
365 landscapes are likely to play an increasingly important role in maintaining snapping turtle meta-
366 population structure if this demand persists.

367 Precise estimates of abundances of freshwater turtles are considered very difficult to
368 obtain, without longer-term mark-recapture studies, because of inherent variation in catchability

369 and observability (Dorland et al. 2014). Although we marked individuals, recapture rates for
370 most species (except for painted turtles) were too low to yield estimates of abundance via mark-
371 recapture modeling, particularly because we sampled each wetland for only 1 season.
372 Nonetheless, we report relative abundance estimates for descriptive purposes and to compare to
373 other studies. Occupancy modeling is more robust to these issues and can be interpreted in the
374 context of presence or absence and habitat selection. Although the utility of occupancy modeling
375 is limited in that it does not permit estimation of important population parameters such as
376 density, survival, or recruitment, the technique contributes to knowledge of geographic
377 distribution and allows for the identification of habitat features associated with a particular
378 species, especially when multiple species are compared (Nielsen et al. 2010).

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

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

389 **MANAGEMENT IMPLICATIONS**

390 Results from this study indicate that human development has influenced the distribution of
391 spotted turtles and red-eared sliders in Rhode Island, albeit in different ways. Identifying habitat

392 features at the landscape scale that are associated with species occurrence has long been an
393 objective in conservation biology. For spotted turtles, future work should aim to identify viable
394 populations in the region using these occupancy models as a way to narrow search effort. This
395 work also serves as a baseline for the current state of the invasion of red-eared sliders in Rhode
396 Island. With future sampling, wildlife managers may be able to assess whether existing
397 regulations intended to slow the invasion are proving effective.

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

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566 Figure Captions

567 Figure 1. Locations of wetlands sampled for freshwater turtles in Rhode Island, USA, 2013–
568 2015. An additional 7 sites are not pictured where we detected spotted turtles.

569

570 Figure 2. Canonical correspondence analysis ordination biplot for wetlands in Rhode Island,
571 USA, based on the relative abundance of 4 freshwater turtle species in 2013–2015 and
572 relativized values for 17 environmental covariates. Vectors indicate the direction and magnitude
573 of covariate scores. Ellipses are centered on the mean values for each species and represent 95%
574 confidence ellipses based on the corresponding standard error. Site-level covariates included
575 wetland age (Wetland.age), surface area of wetland (Hectares), maximum depth of wetlands
576 (Max.depth), pH (pH), total dissolved solids (TDS), dissolved nitrate (Nitrate), dissolved
577 phosphorous (Phos), percent of wetland surface containing graminoid vegetation (Graminoid),
578 percent of wetland surface containing herbaceous vegetation (Herbaceous), percent of
579 unvegetated wetland surface (Open.water), percent of wetland surface containing algae or
580 Lemnaceae (Surficial), percent of wetland surface containing woody shrubs and trees (Woody),
581 percent of forest within 300 m of wetland (Forest.300), percent of wetland area within 300 m of
582 wetland (Wetland.300), percent of developed area within 300 m of wetland (Develop.300),
583 percent of early successional vegetation within 300 m of wetland (ESH.300), road density within
584 300m of wetland (Road.dens.300).

585

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

589 Table 1. Occurrence and abundance of freshwater turtle species by forest cover class, Rhode Island, USA, 2013–2015.
 590

	Forest cover 1 km								Total number of wetlands (% of total)	Total number of individuals
	0–40%		20–60%		40–80%		80–100%			
	10–20%	20–30%	30–40%	40–50%	50–60%	60–70%	80–90%	90–100%		
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

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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 [<i>Decadon verticillatus</i>])
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

598 ^aIndicates that we considered both a linear and quadratic relationship.

599 Table 3. Occupancy models (from secondary global model subset) within 2 Bayesian Information Criterion (BIC) units of top models,
 600 which show the strongest relationship between species presence and measured covariates in Rhode Island, USA, 2013–2015; p is
 601 detection parameter; Ψ is occupancy parameter; K is number of parameters in the model; MacKenzie-Bailey goodness-of-fit
 602 parameters are included for the top model of each species and include χ^2 , P -value, and \hat{c} as the overdispersion parameter.
 603

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

604 Survey-level covariates in top models included ordinal date (Ordinal) and air temperature (Temp). Site-level covariates in top models included wetland age
 605 (Wetland.age), surface area of wetland (Hectares), maximum depth of wetlands (Max.depth), pH (pH), dissolved nitrate (Nitrate), dissolved phosphorous (Phos),
 606 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
 607 wetland (Road.dens.1000).
 608

Figures

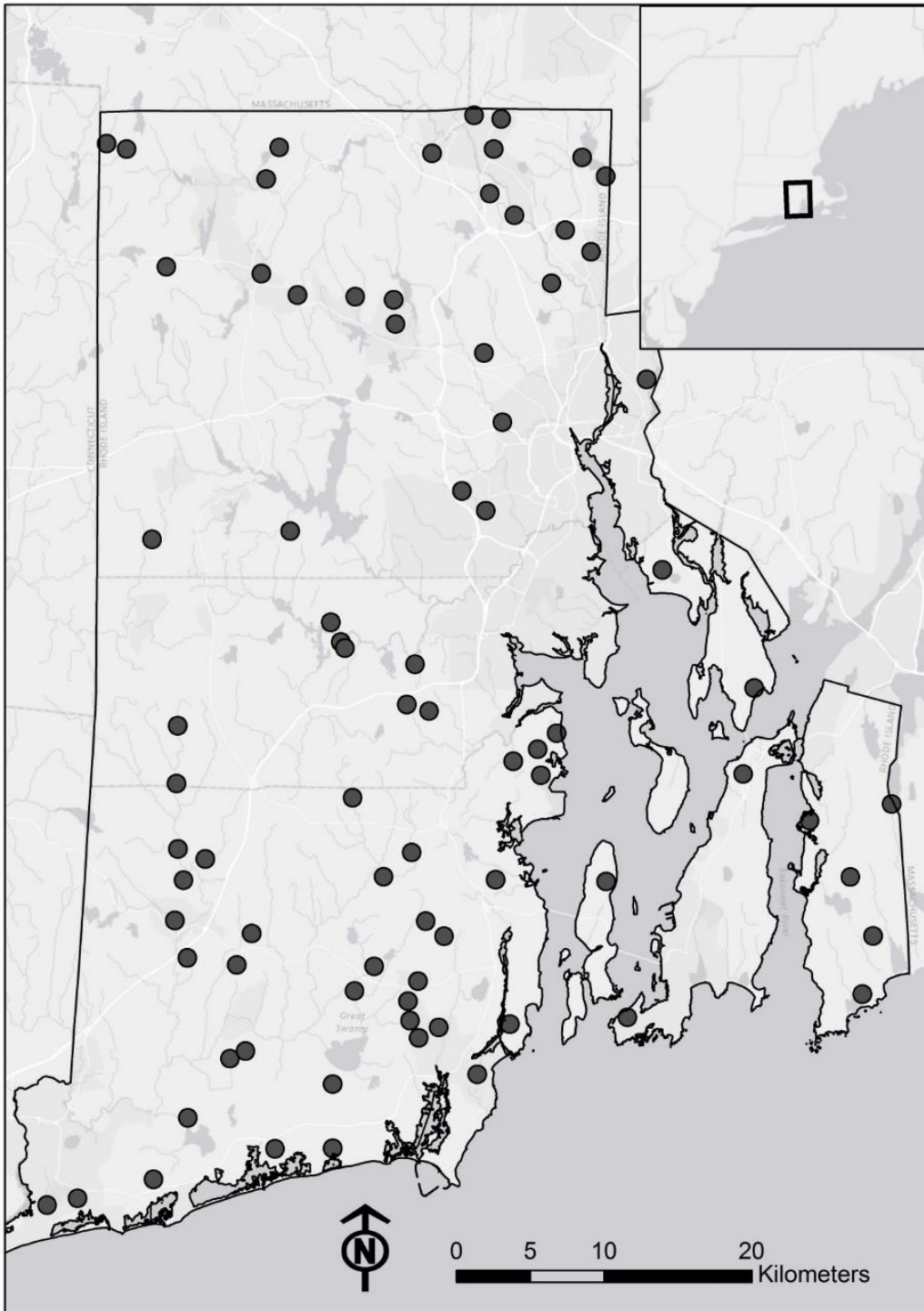


Figure 1. Locations of wetlands sampled for freshwater turtles in Rhode Island, USA, 2013–2015. An additional 7 sites are not pictured where we detected spotted turtles.

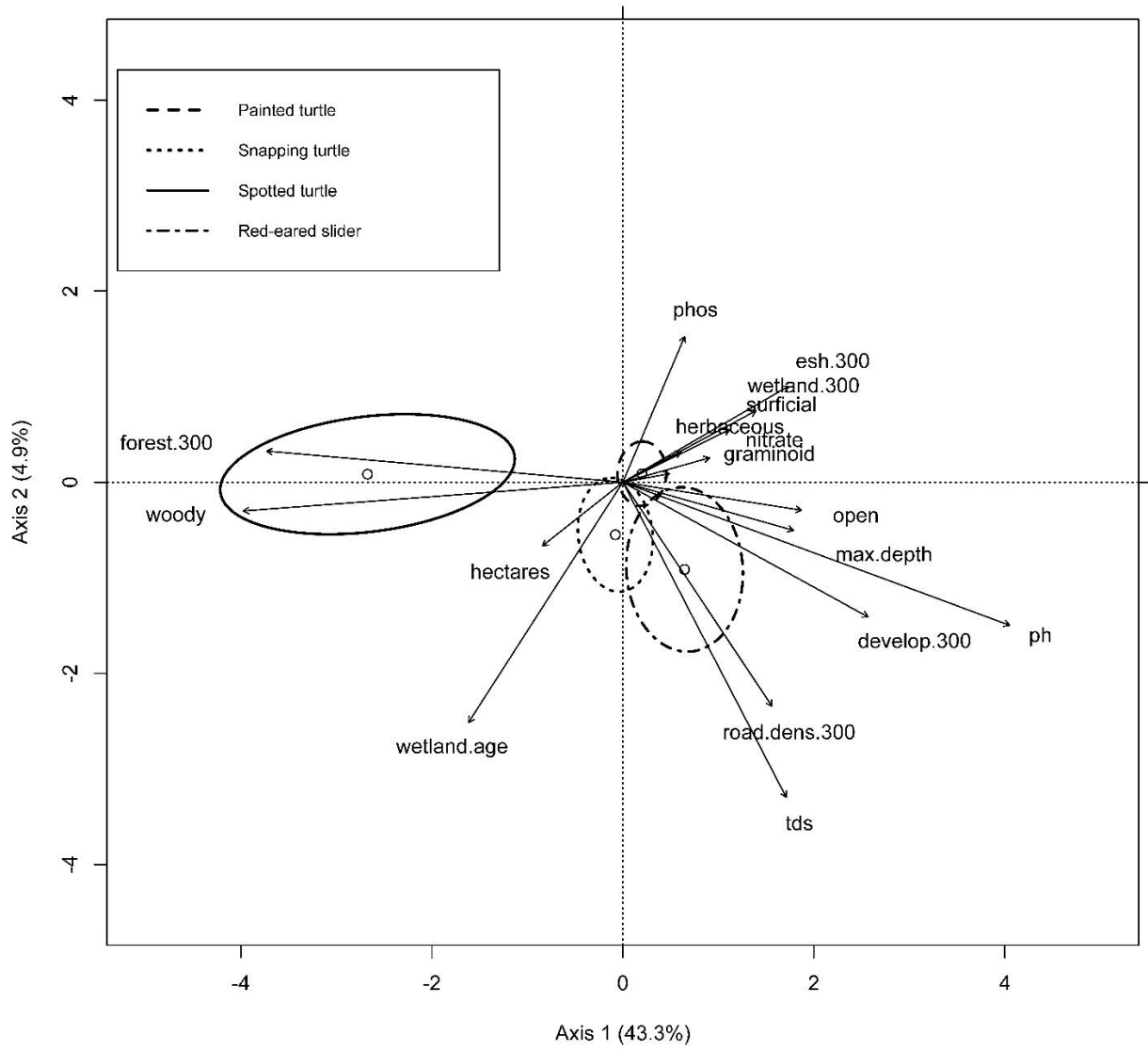


Figure 2. Canonical correspondence analysis ordination biplot for wetlands in Rhode Island, USA, based on the relative abundance of 4 freshwater turtle species in 2013–2015 and relativized values for 17 environmental covariates. Vectors indicate the direction and magnitude of covariate scores. Ellipses 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).

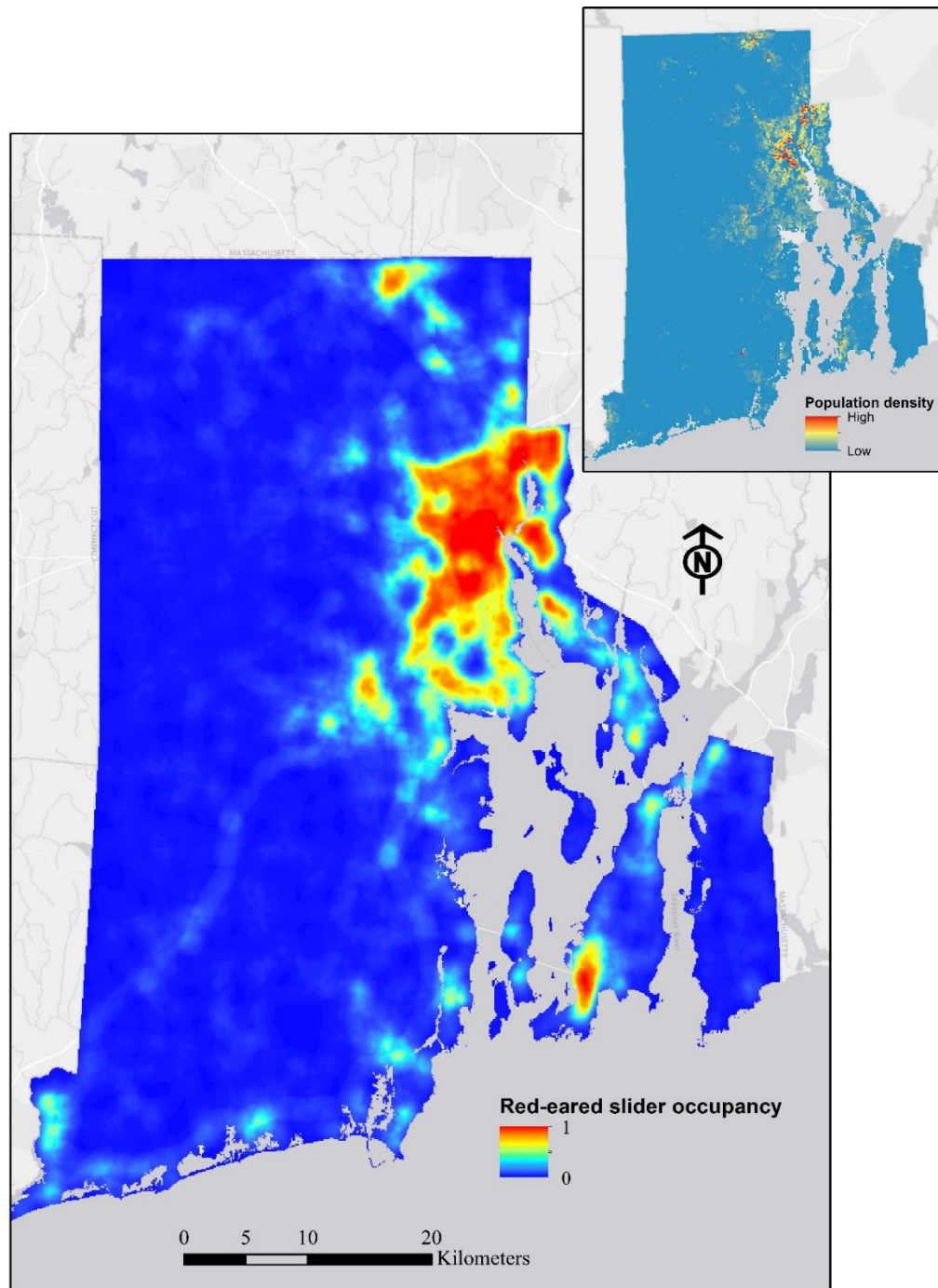


Figure 3. Predicted red-eared slider occupancy in Rhode Island, USA, developed from the top model at a 100-m cell size and based on detections from 2013–2015. Inset map shows human population density for comparison.