Herpetological Conservation and Biology 19(2):189–208.
Submitted: 14 July 2022; Accepted: 31 May 2024; Published: 31 August 2024.

HABITAT QUALITY OF RESTORED WETLANDS IN AGRICULTURAL SYSTEMS FOR FRESHWATER TURTLES

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Abstract.—**Freshwater turtles are important components of wetland ecosystems, but few studies have assessed the quality of created and restored wetlands for turtles. We determined whether habitat characteristics and abundance, body condition, adult sex ratio, and mean adult size of two turtle species, Painted Turtles (*Chrysemys picta*) and Snapping Turtles (*Chelydra serpentina*), differed between 16 restored and 16 reference wetlands in West Virginia, USA, and quantified the influence of habitat characteristics on abundance and body condition. At each wetland, we measured habitat characteristics and sampled turtle populations using hoop-net traps. We found that habitat characteristics were similar between the restored and reference wetlands and found no difference in abundance for either species between wetland types. Painted Turtle abundance was positively associated with the number of surrounding wetlands and amount of emergent vegetation cover around the periphery of the wetlands and negatively associated with density of surrounding roads. Snapping Turtle abundance was positively associated with water conductivity and dissolved oxygen. We found no difference in body condition between wetland types for Snapping Turtles but did find evidence that body condition was lower in restored wetlands for Painted Turtles. This result appeared to be driven by a negative relationship between body condition and the number of surrounding wetlands. We found no difference in mean body size between wetland types, but adult sex ratio differed for Painted Turtles. Overall, our study indicates that habitat quality of restored wetlands in West Virginia for our focal species was similar to surrounding wetlands associated with agricultural land.**

Key Words.—abundance; ACEP; Agricultural Conservation Easement Program; *Chelydra serpentina*; *Chrysemys picta*; habitat; Painted Turtle; Snapping Turtle; Wetlands Reserve Program; WRP

INTRODUCTION

Nearly 40% of naturally occurring wetlands in the U.S. have been drained since European settlement (Fluet-Chouinard et al. 2023). Prior to the 1970s, the removal of wetlands was supported by federal agencies, which promoted conversion to agricultural land (Vileisis 1997). The Clean Water Act of 1977 was the first legislation that offered protection for remaining wetlands in the U.S. (National Research Council 2001). The U.S. Environmental Protection Agency adopted a federal policy of no net loss of wetlands in 1989 (Vileisis 1997; Mitsch and Gosselink 2000; Robertson 2000). The Swampbuster provision in the 1985 Farm Bill removed incentives to farm converted wetlands (Brady 2000). Then, to facilitate wetlands restoration on private land in the U.S., the Wetlands Reserve Program (WRP) was created as part of the Farm Bill of 1990. The WRP provided funding to restore wetlands and pay easement fees to private landowners to facilitate the restoration of farmland back to wetlands (Despain 1995). The WRP was absorbed into the Agricultural Conservation Easement Program (ACEP) with the Agricultural Act of 2014.

The goal of wetland restoration projects completed through the WRP/ACEP program is to return wetlands to their pre-disturbance condition and restore their functional integrity (Natural Resources Conservation Service 2010). This includes restoring and maintaining the appropriate hydrology, hydric soil, native vegetation, and ecosystem services of wetlands (Bryzek et al. 2024). Essential ecosystem services sought through restoring wetlands include water filtration and recharge, nutrient recycling, and flood mitigation (Facelli and Pickett 1991; Costanza et al. 2008; Ballantine and Tanner 2010). Wetland sediments, vegetation, periphyton, and algae are responsible for removing and retaining nitrogen and phosphorus, two nutrients often sourced from agricultural runoff that can be detrimental in large quantities to aquatic systems (Reddy et al. 1999; Ballantine and Tanner 2010). Invertebrates play an integral role in nutrient cycling by decomposing plant litter in wetlands, influencing primary productivity and prey composition (Knight and Gibbons 1968; Anderson et al. 2000; Gingerich et al. 2015). Wetlands also function as permanent or temporary habitat for a wide variety of vertebrates, including many fish, amphibian, reptile, bird, and mammal species (Gibbs 1993; Semlitsch and Bodie 1998; Babbitt and Tanner 2000; Keddy et al. 2009; Lewis et al. 2019).

Wetland restoration goals are generally assessed by quantifying wetland area at the landscape level and evaluating the quality of individual wetlands (Environmental Protection Agency [EPA] 2002). Traditional functional assessments focused on hydrology, biogeochemical processes, and physical habitat of the wetlands; the ability to support plants and wildlife was a separate assessment (EPA 1998). Regarding their wildlife value, contemporary wetland assessments often focus on use by waterfowl or amphibians (Leschisin et al. 1992; McKinstry and Anderson 2002; Petranka et al. 2003). Freshwater turtles are also important members of wetland communities, however, contributing to nutrient cycling, storage, and transfer between terrestrial and aquatic systems (Dreslik et al. 2005; Sterrett et al. 2015; Lovich et al. 2018), and serving as apex predators in these systems (Ernst 1986; Rowe and Parsons 2000; Spotilla and Bell 2008).

Several studies have investigated freshwater turtle use of created or restored wetlands, with the majority of previous research focused on documenting colonization, including in the U.S. states of Florida (Weller 1995), Illinois (Palis 2007), Missouri (Nickerson et al. 2019), New York (Kiviat et al. 2000; Hartwig and Kiviat 2007), and Pennsylvania (Hepler 2014), and Ontario, Canada (Dupuis-Desormeaux et al. 2018). Hughes et al. (2016) assessed abundance-habitat relationships among created wetlands in Pennsylvania and found that Snapping Turtle (*Chelydra serpentina*) abundance was positively correlated with large wetlands with little vegetation, and Painted Turtle (*Chrysemys picta*) abundance was positively associated with small wetlands with abundant vegetation. Benson et al. (2018) concluded that species richness and relative abundance of freshwater turtles were similar between restored and reference wetlands in New York. Hollender and Ligon (2021) compared species richness and relative abundance of turtle species between natural and strip mine-associated lakes in Kansas, USA, and determined that mean richness was higher in the strip mine lakes, but relative abundance patterns differed across species. Dudley et al. (2015) found that restored streams with riparian wetlands in North Carolina, USA, had greater diversity and relative abundance of turtle species than reference streams. Similarly, Nowalk (2010) found that restored streams in the North Carolina Piedmont had greater relative abundance of turtles than natural streams and characterized the natural areas as exhibiting more habitat degradation.

Previous studies indicate that freshwater turtles readily colonize created and restored wetlands and that restoration of degraded environments benefits turtle species. More robust research is needed, however, to determine the quality of created and restored wetlands relative to pre-existing local wetlands, including identifying habitat factors that influence relative habitat quality. The purpose of this study was to assess the quality of wetlands restored through the WRP/ACEP as habitat for two common and widely distributed freshwater turtle species, Snapping Turtles and Painted Turtles. Our objectives were to determine if abundance, body condition, and demographic characteristics of the focal turtle species differed between restored and reference wetlands and to identify and quantify the influence of important wetland habitat characteristics associated with abundance and body condition of each species to help guide future wetland restoration efforts.

MATERIALS AND METHODS

Study site.—We conducted this study at 32 wetlands spread across eight counties in West Virginia, USA (Fig. 1). Sixteen of the wetlands were restored through the WRP/ACEP, and the other 16 were corresponding reference wetlands. Restoration site activities consisted of restoring hydrology, controlling invasive plant species, fencing to remove grazing pressure from livestock, and planting native species. We selected reference wetlands that were near WRP/ACEP wetlands and were of similar size and surrounding land use (i.e., forested or agriculture). Reference wetlands were located 0.1 – 5 km from

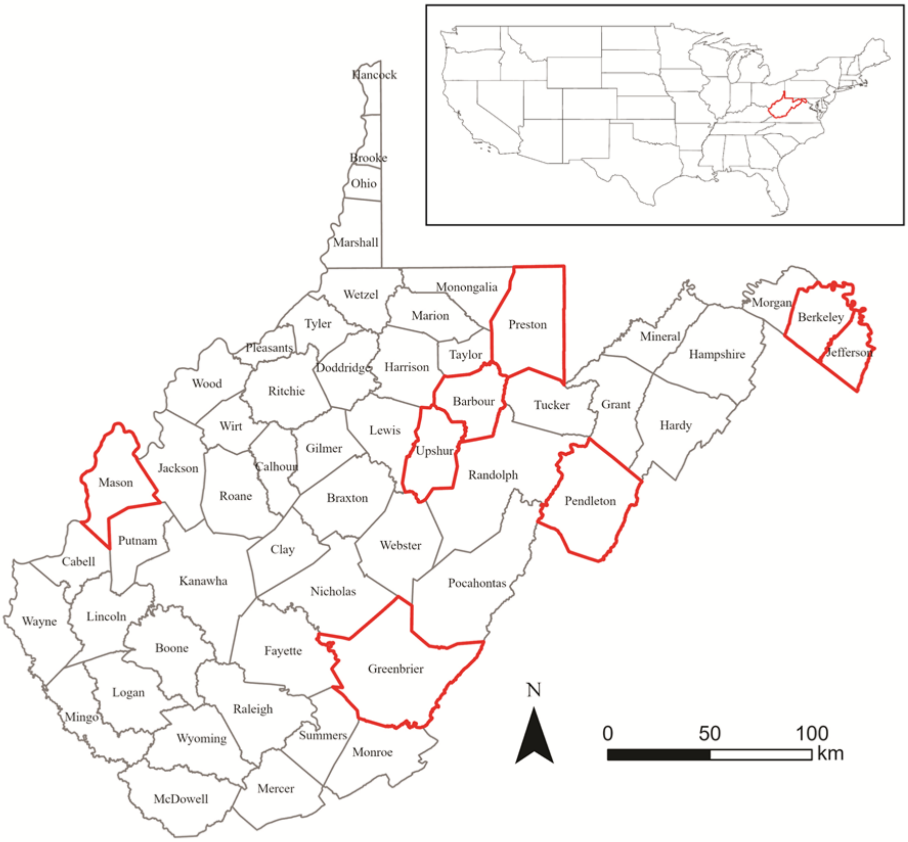

Figure 1. Counties (red outline) in West Virginia, USA, containing the 32 wetlands used in the study to assess habitat quality of wetlands restored through the Wetlands Reserve Program (WRP) and Agricultural Conservation Easement Program (ACEP) for two common freshwater turtles; Snapping Turtles (*Chelydra serpentina*) and Painted Turtles (*Chrysemys picta*). The counties included Barbour, Berkeley, Greenbrier, Jefferson, Mason, Pendleton, Preston, and Upshur. We sampled 22 of the wetlands between 16 July and 9 September 2016 and 10 of the wetlands between 3 June and 15 July 2017.

their corresponding WRP/ACEP wetland (mean = 1.3 ± 0.34 [standard deviation] km). All reference wetlands were located on private land except for one WRP/ACEP and one reference wetland located on a state wildlife management area, and one WRP/ACEP wetland located on publicly accessible land owned by the Audubon Society. Most reference wetlands were farm ponds that were created or maintained by private landowners outside of the WRP/ACEP program. Thus, the reference condition in this study represents pre-existing wetlands in an active agricultural landscape rather than pristine natural wetlands. The WRP/ACEP wetlands were restored between 1996 and 2011, and most were used for agriculture prior to restoration. None of the wetlands had apparent surface connections to flowing water. Median wetland size was 0.591 ha (range = 0.025–11.072 ha). Wetland edges were typically covered with cattail (*Typha* spp.), sedges (*Carex* spp.), rushes (*Juncus* spp.), Rice Cutgrass (*Leersia oryzoides*), or arrowhead (*Sagittaria* spp.). We detected Bluegill Sunfish (*Lepomis macrochirus*) and Channel Catfish (*Ictalurus punctatus*) in most wetlands.

Turtle sampling.—We sampled turtle populations from 16 July to 9 September 2016 (11 restored and 11 reference wetlands) and 3 June to 15 July 2017 (five restored and five reference wetlands). We sampled each wetland for five consecutive days using 10 baited hoop-net traps set around the perimeter at 3–20 m intervals, depending on wetland size. We standardized the number of trap days among wetlands because a previous study found that the number of turtles captured at their study sites was equivalent between high and low trap densities if the total number of trap days was consistent (Brown et al. 2011*b*). We assumed that even at our largest sites, individual turtles had a high probability of encountering a trap during the sampling period because previous studies have documented movement rates of several hundred meters per day during the summer months for both of our focal species (e.g., Brown and Brooks 1993; Rowe 2003). At each wetland, we used five 0.76 m and five 0.91 m diameter hoop-net traps and alternated placement of the two trap sizes (Gulette et al. 2019). All hoop-net traps were approximately 1.8 m long and included three steel hoops and a single mouth with a circular throat (Memphis Net and Twine Company, Memphis, Tennessee, USA). Traps were held taut using two wood posts connected to the terminal hoops, and mouths were held open by tightening, then knotting, the rope that opens them. This design allowed our traps to float and did not require that a ground stake be used to keep the mouth open. We placed flotation devices in all traps to prevent drowning of captured turtles. We baited traps with a half-can of sardines in oil, placed in plastic bottles containing holes to allow for scent dispersal but not bait consumption (Ernst 1965; Jensen 1998; Mali et al. 2012). We checked traps and changed bait daily.

We identified, measured, determined the sex, marked using unique individual carapace notches (Cagle 1939), and released all turtles we captured. We measured midline carapace length (MCL; Iverson and Lewis 2018) and plastron length to the nearest 1.0 mm using calipers (Haglof, Madison, Mississippi, USA). We weighed individuals < 1,000 g to the nearest 10 g and individuals > 1,000 g to the nearest 20 g using spring scales (Pesola, Baar, Switzerland). We determined sex using secondary sexual characteristics (Ernst and Lovich 2009).

Habitat variables.—We considered 10 wetland-level habitat variables as potentially important predictors of turtle abundance, with field measurements taken at the time of turtle sampling (Appendix Table 1). We estimated the perimeter length (m) and size (ha) of each wetland using 2016 National Agriculture Imagery Program (NAIP) aerial imagery and a geographic information system (ArcGIS 10.3; Esri, Redlands, California, USA). We obtained water depth at the deepest point of each wetland using a meter stick. We quantified vegetation characteristics by sampling 10 random points on the perimeter of each wetland. We estimated canopy cover (%) at each point using a spherical densiometer and used a 1 m² frame to estimate edge emergent vegetation (%). In addition, we visually estimated total emergent vegetation (%) for each wetland. We measured pH, dissolved oxygen (mg/L), and conductivity (uS/cm) at each random point using a YSI Professional Plus meter (YSI Incorporated, Yellow Springs, Ohio, USA). We estimated average percentage sand in the soil of each wetland using the Soil Survey Geographic Database (10–18 cm depth, 6–32 m resolution; http://websoilsurvey.nrcs.usda.gov/). Sand content influences both soil moisture and strength, which are important components of turtle nesting habitat quality (Christens and Bider 1987; Feaga et al. 2013; Frye et al. 2017).

To assess the potential influence of surrounding landscape characteristics on turtle abundance and body condition, we created 100 m and 1,000 m buffers around each wetland. We selected 100 m to represent the area adjacent to the sampled wetland and 1,000 m to represent the area of the surrounding landscape with high potential for use by our focal turtle species. While overland movement patterns vary among species, individuals, and study areas, previous studies suggest that movements up to 1,000 m from occupied wetlands are common for Snapping Turtles (Congdon et al. 1987; Pettit et al. 1995) and Painted Turtles (Bowne and White 2004; Bowne et al. 2006). Dominant land uses surrounding our sites were primarily deciduous forest or agricultural (i.e., cultivated crops or pasture/hay; Lewis et al. 2020). For each buffer, we calculated the percentage of area that was forested using the 2016 National Land Cover Database (hereafter forest cover; Wickham et al. 2021) and the density of roads (i.e., total length of all roads [m] within the buffer) using the U.S. Census Bureau 2011 roads database (hereafter road density; https://www.census.gov/geographies/mapping-files/time-series/geo/tiger-line-file.html). We z-score transformed road density values to facilitate model convergence. Finally, we calculated the number of surrounding wetlands within 1,000 m of each site using the National Wetlands Inventory (hereafter wetland count; https://www.fws.gov/program/national-wetlands-inventory).

Survey variables.—We recorded mean daily water temperature during the sampling period at each wetland using HOBO Pendant Temperature Data Loggers (model UA-001-68; Onset Computer Corporation, Pocasset, Massachusetts, USA). We attached a single logger to a trap approximately 0.2 m below the surface of the water and recorded water temperature at 1-h intervals for the duration of the trapping period. We computed mean water temperature for each trap day using a 24-h period from 1200 to 1200. Data loggers malfunctioned during the last trap day at three of the sites and we replaced the missing values with the mean temperature values from the previous trap day. To account for the potential effect of trap density on capture probability, we tested total trapline distance (m) and proportion of wetland perimeter sampled (trapline distance/perimeter length) as detection covariates.

Statistical analyses.—We assessed if wetland characteristics differed by wetland type (i.e., restored or reference) using a Redundancy Analysis (RDA), which is an extension of Principal Components Analysis (PCA) to include explanatory variables (Legendre and Legendre 2012). Specifically, for RDA, each response variable is regressed on each explanatory variable and then a PCA is performed on the matrix of fitted values (McCune and Grace 2002). We standardized the response variables (i.e., zero mean and unit variance) because they were recorded on different scales. We tested the effect of wetland type on habitat variables using a Permutation test with 10,000 replications. We visually assessed relationships between individual wetland characteristics and wetland type using a correlation biplot, where angles between the habitat variables and between habitat variables and wetland type reflect their correlations (Borcard et al. 2011).

We used Multinomial *N*-mixture Models with a removal (i.e., depletion) sampling observation process to determine important habitat characteristics and model abundance-habitat relationships (Royle 2004*a*, 2004*b*). *N*-mixture models use both spatial and temporal replication of count data to jointly estimate abundance and detection probability (*p*), and thus, they explicitly account for observed numbers being a product of both ecological and observational processes (Kéry and Royle 2016). We chose to use the *N*-mixture class of models rather than individual-level capture-recapture models because these models could accommodate our sites with low capture and recapture data. We chose to use removal models because, at most sites, we had low recapture rates and number of captures generally decreased as sampling days progressed, indicating the turtles likely developed a trap-shy response after initial capture (Mali et al. 2014; Tesche and Hodges 2015; Hollender et al. 2023), and thus *p* estimates for binomial *N*-mixture models would likely be biased (Riddle et al. 2010).

To delineate important covariates for *p* and abundance of the focal species, we performed a three-stage model selection, with each model selection containing a null model and candidate predictor variables, and variables ranked using Quasi Akaike Information Criterion corrected for small-sample size (QAICc; Symonds and Moussalli 2011; see below for explanation of using QAICc). For each stage, we first ranked each variable individually and then created candidate additive models when individual variables had support (ΔQAICc < 7 and more support than the null model; Burnham et al. 2011). For the first stage, we assessed the importance of survey variables for *p* and retained the most parsimonious *p* model for subsequent analyses (Kéry and Royle 2021). We then determined which surrounding landscape extent (100 m or 1,000 m) was more supported for forest cover and road density and retained this extent for the abundance model selection. Finally, we ranked the influence of the 10 wetland-level habitat variables, three surrounding landscape variables, and wetland type on abundance.

To assess model goodness-of-fit, we used the most complex candidate model and a 10,000-replication parametric bootstrap of the Pearson Chi-square statistic (Kéry and Royle 2016). This test indicated high overdispersion for the Painted Turtle model ($\hat{c}$= 3.20) and minor overdispersion for the Snapping Turtle model ($\hat{c}$=1.63). To account for this overdispersion, we ranked candidate models using QAICc as well as inflated model confidence intervals, using $\hat{c}$ as the variance inflation factor (Symonds and Moussalli 2011; Kéry and Royle 2016). For the most supported models, we computed the 85% confidence intervals (CI) of the beta coefficients (Arnold 2010). We considered there to be strong support for an effect when CIs did not overlap zero (Halsey 2019).

In addition to including wetland type as a candidate predictor of abundance in the *N*-mixture models, we also computed number of unique Painted Turtles and Snapping Turtles captured at each wetland and tested whether there was a difference between wetland types using paired randomization tests with 10,000 iterations (Sokal and Rohlf 1995), with each restored plot paired with its corresponding reference plot. When sample sizes are relatively small, such as in our study (n = 32 sites), randomization tests are an appropriate alternative to t-tests because the statistical distribution is derived from the randomized data rather than assuming the data follow an underlying parametric distribution (Sokal and Rohlf 1995). The *P*-values for randomization tests are also intuitive, representing the proportion of trials with a mean difference between samples that are as or more extreme than what we obtained in the study.

To investigate if body condition of Painted Turtles

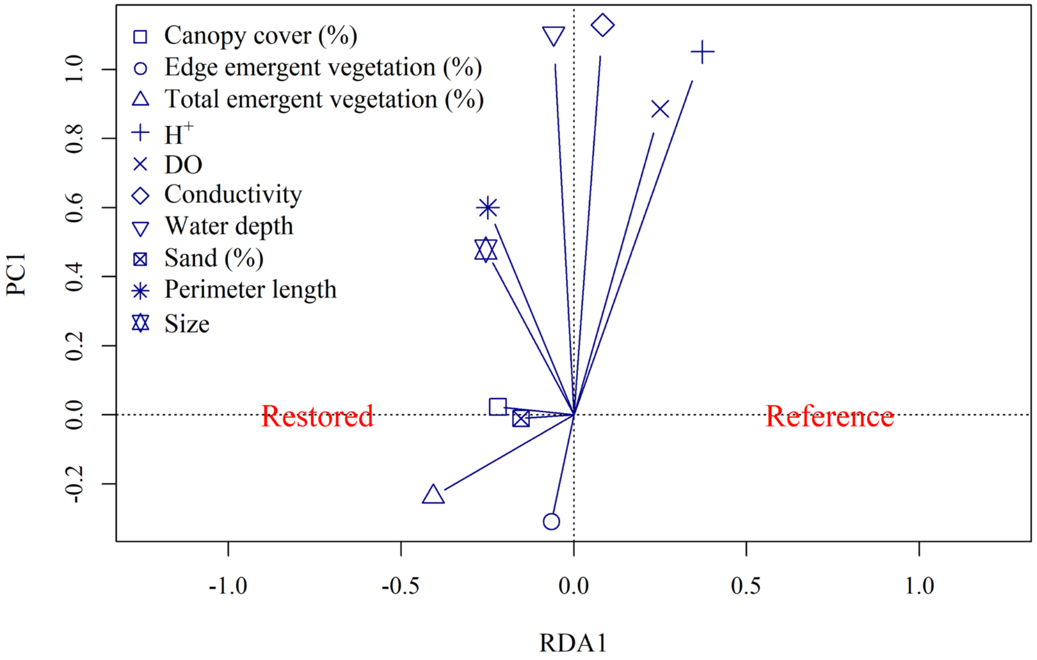

Figure 2. Correlation biplot from a Redundancy Analysis (RDA) used to assess differences in habitat characteristics between restored and reference wetlands in West Virginia, USA. We measured environmental characteristics at 22 of the wetlands 16 July to 9 September 2016 and 10 of the wetlands 3 June to 15 July 2017. Habitat variables that are further from the intercept and closer to the x-axis are more closely associated with restored (-) and reference (+) wetlands, respectively.

and Snapping Turtles was influenced by wetland type and habitat variables, we computed a Body Condition Index (BCI) score for each unique turtle using the residuals of log-transformed MCL-weight regressions for each species (Green 2001; Litzgus et al. 2008). We used Linear Regression models and AICc model selection to determine the most parsimonious model explaining variation in BCI scores, following the same approach as the abundance analyses. We assessed assumptions of normality using quantile–quantile plots and homoscedasticity using residual plots (Zuur et al. 2010). We removed one Painted Turtle and two Snapping Turtle observations to satisfy the assumption of normality. We also performed randomization tests to determine if mean BCI score at each wetland differed by wetland type. We did not pair wetlands for this analysis because the focal turtle species were not captured at all wetlands.

Finally, for each focal species, we assessed if sex ratio and size of adults differed between wetland types using randomization tests. The number of juveniles captured was too low to assess if age class ratios differed between wetland types. For the sex ratio analysis, we computed the observed adult sex ratio at each wetland and determined if there was a difference between wetland types using unpaired randomization tests. For sites where only one sex was captured, we added one capture to each sex to allow the sex ratio to be estimated. For the size analysis, we computed mean MCL at each wetland for each focal species and sex, and determined if there was a difference between wetland types using unpaired randomization tests. We considered Painted Turtles and Snapping Turtles to be adults at plastron lengths ≥ 70 and 145 mm, respectively (White and Murphy 1973; Ernst and Lovich 2009) and we acknowledge that we likely included larger sub-adults as adults in the analysis.

To align with support for variables in the AICc model selections (i.e., approximately = 0.15; Arnold 2010), we considered support for the RDA and randomization tests at $\alpha = 0.15$. We performed all statistical analyses using program R (version 4.1.1; The R Foundation for Statistical Computing, Vienna, Austria). We used the package vegan (version 2.6-2) for the RDA, unmarked (version 1.2.5) for *N*-mixture models, AICmodavg (version 2.3-1) for model selections and *N*-mixture model CIs and predictions, MASS (version 7.3-57) for linear model CIs, and

EnvStats (version 2.8.1) for randomization tests. We plotted results using the R packages ggplot2 (version 3.3.6) and cowplot (version 1.1.1).

RESULTS

We captured 286 unique Painted Turtles (202 in restored wetlands and 84 in reference wetlands). The number of unique individuals ranged from 0–116 (mean = 12.6) across restored wetlands and 0–41 (mean = 5.3) across reference wetlands. We captured 102 unique Snapping Turtles, including 61 and 41 in restored and reference wetlands, respectively. The number of unique individual Snapping Turtles ranged from 0–18 (mean = 3.8) and 0–7 (mean = 2.6) across restored and reference wetlands, respectively. We captured both species at 14 sites, only Snapping Turtles at 13 sites, only Painted Turtles at two sites, and no turtles at three sites. In addition to the focal species, we captured low numbers of four additional turtle species, including Eastern Spiny Softshell (*Apalone spinifera*; two captures at one restored wetland), Eastern Musk Turtle (*Sternotherus odoratus*; five captures at two restored wetlands), Red-eared Slider (*Trachemys scripta elegans*; three captures at two restored and one reference wetland), and Northern Red-bellied Cooter (*Pseudemys rubriventris*; eight captures at one reference wetland). There was no significant community-level difference in habitat conditions between restored and reference wetlands (adjusted $r^2 < 0.01$, $P = 0.415$). The strongest individual variable associations were canopy cover (%) and sand in soil (%), which were positively associated with restored wetlands (Fig. 2). Minimum and maximum values of habitat variables for restored and reference wetlands displayed substantial overlap (Appendix Table 1).

***Turtle abundance*.**—For Painted Turtle abundance, the most supported *p* model included mean daily water temperature as a covariate (model weight [w_i] = 1), with a positive influence of temperature on *p*. The most supported surrounding landscape extent was 100 m for forest cover ($w_i = 1.0$) and 1,000 m for road density ($w_i = 1.0$). The initial abundance model selection determined that wetland count was strongly supported over all other variables ($w_i = 1$), and we conducted a second model selection using wetland count as the null model. The most supported abundance model included wetland count, edge emergent vegetation, and road density as covariates ($w_i = 1.0$; Appendix Table 2). Predicted abundance was positively associated with wetland count and edge emergent vegetation and negatively associated with road density (Fig. 3), and the CI did not overlap 0 for any of the variables. Wetland count + wetland type did not receive strong support (ΔQAICc = 23.74, $w_i < 0.01$). The paired randomization test also did not support a difference in Painted Turtle captures between restored and reference wetlands ($P = 0.44$).

For Snapping Turtle abundance, the most supported *p* model included trapline distance as a covariate ($w_i = 0.98$), with a positive influence of trapline distance on *p*. The most supported surrounding landscape extent was 100 m for forest cover ($w_i = 0.66$) and 1,000 m for road density ($w_i = 0.91$). The most supported abundance model included conductivity and dissolved oxygen as covariates ($w_i = 0.51$; Appendix Table 2). Predicted abundance was positively associated with both variables (Fig. 4), and the CIs did not overlap 0. Wetland type did not receive strong support (ΔQAICc = 16.54, $w_i < 0.01$). The paired randomization test also did not support a difference in Snapping Turtle captures between restored and reference wetlands ($P = 0.39$).

***Turtle body condition*.**—For Painted Turtles, the most supported surrounding landscape extent was 1,000 m for forest cover ($w_i = 1.0$) and 1,000 m for road density ($w_i = 0.60$). As with the abundance analysis, the initial body condition model selection determined that wetland count was strongly supported over all other variables ($w_i = 1$), and we conducted a second model selection using wetland count as the null model. The most supported body condition model included wetland count and wetland type as predictors ($w_i = 0.14$, $r^2 = 0.183$), with wetland count-only being the second most-supported model ($w_i = 0.14$, $r^2 = 0.177$; Appendix Table 2). Body condition was negatively associated with wetland count and lower at restored wetlands (Fig. 3). The CI did not overlap 0 for wetland count (β = -0.00095, CI = -0.00127 to -0.00064) but did overlap 0 for wetland type (β = -0.01523, CI = -0.03049 to 0.00003). The randomization test also supported a difference in mean Painted Turtle BCI score between restored and reference wetlands ($P = 0.099$). Mean BCI score at restored and reference wetlands was -0.013 and 0.031, respectively.

For Snapping Turtles, the most supported surrounding landscape extent was 1,000 m for forest cover ($w_i = 0.62$) and 100 m for road density ($w_i =$

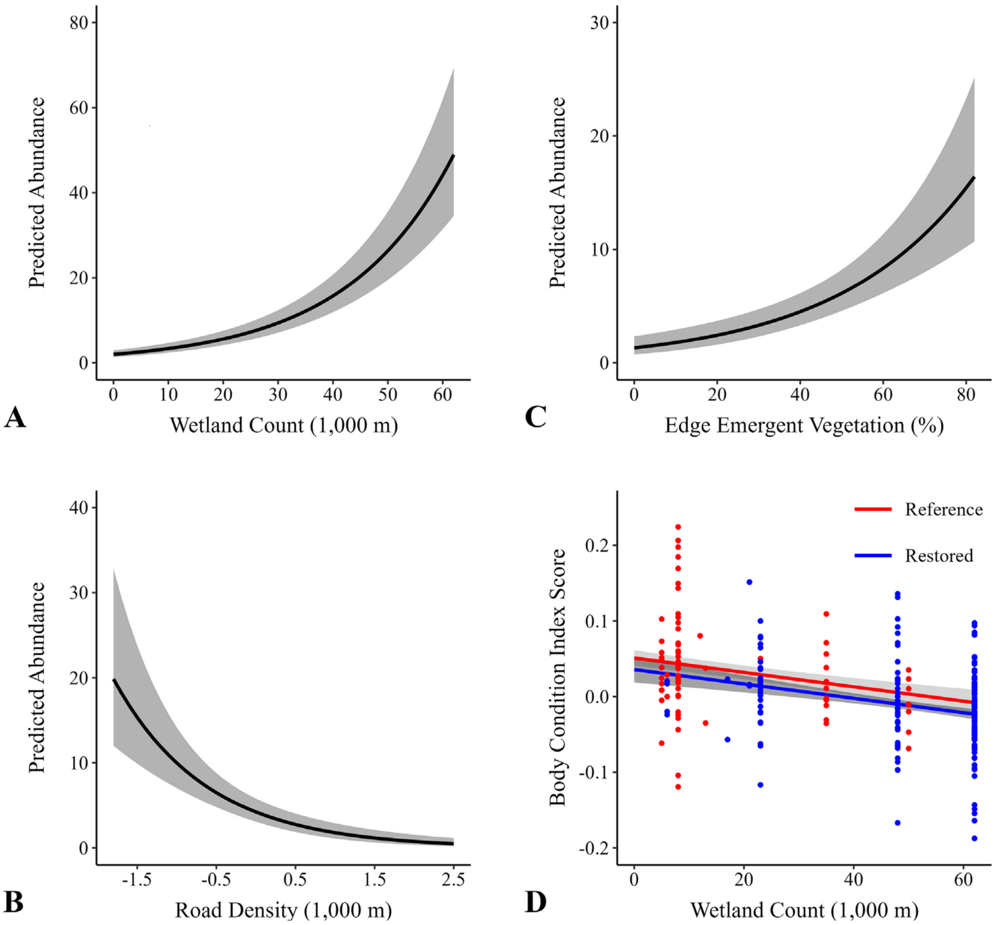

FIGURE 3. Influential environmental characteristics for abundance (A-C) and body condition index score (D) of Painted Turtles (*Chrysemys picta*) at restored and reference wetlands in West Virginia, USA. We sampled turtles and measured environmental characteristics at 22 of the wetlands 16 July to 9 September 2016 and 10 of the wetlands 3 June to 15 July 2017. We modeled abundance relationships using Multinomial *N*-mixture models with a removal (i.e., depletion) sampling observation process and body condition relationships using Linear Regression models. Wetland count represents the number of surrounding wetlands, and road density represents the total length of all roads within 1,000 m (standard deviation units from the mean), within 1,000 m of each sampled wetland. For each plot, we held non-focal variables at their mean value. Grey bands represent 85% confidence intervals. The points in (D) represent computed body condition index scores for individual Painted Turtles in restored (blue) and reference (red) wetlands.

0.88). The most supported body condition model for Snapping Turtles included road density within 100 m of the wetland as a predictor ($w_i = 0.30$, $r^2 = 0.074$; Appendix Table 2), and BCI score was positively associated with road density (Fig. 4). The CI for road density did not overlap 0 ($\beta = 0.00996$, CI = 0.00471 to 0.01521). Wetland type received less support than the null model as a predictor of BCI score ($w_i = 0.02$; Appendix Table 2), and the randomization test did not support a difference in mean Snapping Turtle BCI score between restored and reference wetlands ($P = 0.690$).

Turtle sex ratio and size.—For Painted Turtles, adult female-male ratio ranged from 0.3–1.9 at restored wetlands (mean = 1.1 females per male) and from 1.0–5.5 at reference wetlands (mean = 2.5 females per male). For Snapping Turtles, adult female-male ratio ranged from 0.3–4.0 at restored wetlands (mean = 1.3 females per male) and from 0.5–5.0 at reference wetlands (mean = 1.8 females per male). The randomization tests indicated the proportion of females was higher at reference wetlands for Painted Turtles ($P = 0.025$) but did not differ by wetland type for Snapping Turtles ($P = 0.395$). Mean MCL for female Painted Turtles was 133.2 mm and 142.5 mm, and for male Painted Turtles was 123.5 mm and 126.5

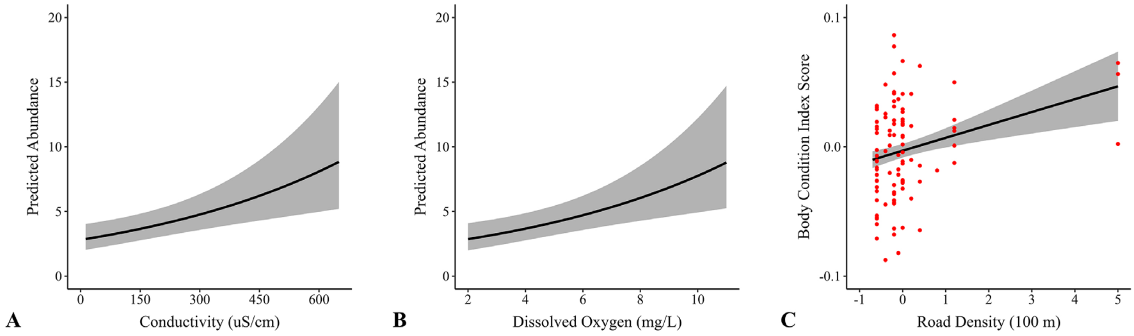

Figure 4. Influential environmental characteristics for abundance (A-B) and body condition index score (C) of Snapping Turtles (*Chelydra serpentina*) at restored and reference wetlands in West Virginia, USA. The points in (C) represent computed body condition index scores for individual Snapping Turtles. We sampled turtles and measured environmental characteristics at 22 of the wetlands 16 July to 9 September 2016 and 10 of the wetlands 3 June to 15 July 2017. We modeled abundance relationships using Multinomial *N*-mixture models with a removal (i.e., depletion) sampling observation process and body condition relationships using Linear Regression models. Mean conductivity (uS/cm) and dissolved oxygen (mg/L) were positively correlated among sites (Pearson $r = 0.45$). Grey bands represent 85% confidence intervals. Road density represents the total length of all roads within 100 m (standard deviation units from the mean).

mm, at restored and reference wetlands, respectively. Mean MCL for female Snapping Turtles was 262.6 mm and 263.3 mm, and for male Snapping Turtles was 277.5 mm and 264.9 mm, at restored and reference wetlands, respectively. The paired randomization tests did not support a difference in mean MCL between restored and reference wetlands for female Painted Turtles ($P = 0.207$), male Painted Turtles ($P = 0.760$), female Snapping Turtles ($P = 0.965$), or male Snapping Turtles ($P = 0.450$).

Discussion

Wetlands in West Virginia restored through the WRP/ACEP had habitat characteristics similar to those of surrounding wetlands on private agricultural land, and both wetland types provided habitats for two widespread turtle species. Thus, our study supports previous findings that some freshwater turtle species can persist in agriculturally dominated landscapes, provided the landscapes contain suitable wetland complexes (e.g., Bowne et al. 2006; Failey et al. 2007; Brown et al. 2011*a*). Our study also supports previous research that indicated freshwater turtles naturally colonize created and restored wetlands (e.g., Weller 1995; Palis 2007).

Based on the site and landscape variables we tested, the strongest predictor of abundance for Painted Turtles was a surrounding landscape variable, wetland count. Similarly, Marchand and Litvaitis (2004) found that abundance of Painted Turtles was positively correlated with proximity to other wetlands, and Roberts et al. (2023) reported that abundance of Painted Turtles was positively related to diversity of surrounding wetlands. Painted Turtles and many other freshwater turtles readily move among wetlands, likely to maximize habitat quality for survival, growth, and reproduction (Sexton 1959; Bowne et al. 2006; Cosentino et al. 2010). Thus, landscapes with greater availability and diversity of wetlands often support more robust turtle populations (Joyal et al. 2001; Roe and Georges 2007; Roberts et al. 2023).

Snapping Turtle abundance was most influenced by two wetland variables, conductivity and dissolved oxygen, which displayed a positive relationship with abundance and a positive correlation among the study wetlands (Pearson $r = 0.45$). While conductivity is generally stable, dissolved oxygen can fluctuate widely throughout the diel cycle and is typically highest around mid-day when our measurements were taken (Reeder 2011; Dubuc et al. 2017). Adult Snapping Turtles can tolerate a wide range of water quality conditions and have a higher tolerance of anoxic conditions than many other freshwater turtle species (Albers et al. 1986; Galbraith et al. 1988; Ultsch 2006). Tolerance for low oxygen levels is reduced in hatchling Snapping Turtles (Reese et al. 2002), which could impact abundance through reduced recruitment. We also speculate that these water quality relationships could reflect differences in food resource availability among sites, which likely influences the carrying capacity of the wetlands for Snapping Turtles (Galbraith et al. 1988; Brown et al. 1994), although additional research is needed to robustly assess relationships between water chemistry and biological communities in our study system. More productive freshwater wetlands often have higher conductivity (Wu et al. 2020; Zhang et al. 2022), potentially reflecting sites with greater agricultural runoff (Harwell et al. 2008). Dissolved oxygen is often positively correlated with abundance and diversity of animals and submerged plants in mesotrophic wetlands (Ogbeibu and Oribhabor 2002; Caraco et al. 2006; Croijmans et al. 2021).

Interestingly, wetland count had a strong negative influence on Painted Turtle BCI score, and we also found some support that BCI was lower in restored wetlands (i.e., the model selection supported inclusion of wetland type, but the coefficient CI overlapped 0). We hypothesize that wetland count reflects the effect of intraspecific competition pressure (i.e., density-dependent effects) on body condition, given abundance increased with wetland count. Mean wetland count was also greater for restored wetlands than reference wetlands (19.8 and 14.3, respectively), potentially explaining why BCI scores were lower at restored wetlands despite our finding that environmental characteristics were generally similar between wetland types and there was not support for wetland type as a predictor of Painted Turtle abundance independent of wetland count. The effect of wetland type could also have been influenced by reference wetlands containing proportionally more adult females if many of those females were gravid at the time of capture (we did not determine gravidity), which could result in heavier individuals and thus higher BCI scores. While we did not detect a strong influence of wetland count on Snapping Turtle abundance or body condition, a comparable study in West Virginia found that Snapping Turtles often moved among wetlands (Becker et al. 2024) and a large regional study documented a positive relationship between Snapping Turtle abundance and diversity of surrounding wetlands (Roberts et al. 2023).

A previous study that combined body condition data from this and several other studies found that Painted Turtle BCI score was negatively associated with anthropogenic disturbance of the surrounding landscape (Mota et al. 2021). We did not detect a strong influence of surrounding road density on Painted Turtle BCI but did detect a negative influence of roads on Painted Turtle abundance at the 1,000 m scale. This finding suggests that road mortality could be negatively impacting Painted Turtle populations in our study area, which has been documented in other regions and is of general concern for freshwater turtles (Steen et al. 2006; Patrick and Gibbs 2010; Laporte et al. 2013). Surprisingly, Snapping Turtle BCI was positively correlated with surrounding road density at the 100 m scale. We hesitate to draw strong inferences from the estimated relationship due to the relatively low explanatory power (r^2 = 0.074) and lack of intermediate road densities in the data set.

In summary, we found that wetlands in West Virginia restored through the WRP/ACEP appear to be providing habitats for two common freshwater turtle species. The habitat characteristics we measured were generally similar between restored and reference wetlands, indicating that the restored wetlands likely serve as additional similar habitat, rather than as a new type of habitat, for our focal species. Our study suggests the benefits of wetland creation and restoration likely extends beyond creating new habitat to be occupied. By increasing the number of habitat patches and reducing the distance between habitat patches, habitat quality of the wetland complex improves. This is not only beneficial for freshwater turtles, but for other wetland-associated species, such as amphibians and waterfowl (Taft and Haig 2006; Petranka et al. 2007; Peterman et al. 2013; Mitchell 2016). In addition, our study suggests that planting native aquatic vegetation during wetland restoration could enhance habitat quality for Painted Turtles. We were unable to quantify and compare several important measures of habitat quality with our study design, including individual growth rates, fertility rates, and survivorship probabilities for the egg, hatchling, juvenile, and adult age classes. We recommend that additional research be conducted to address these information gaps and provide a more robust assessment of habitat quality of WRP/ACEP wetlands in West Virginia for freshwater turtles.

Acknowledgments.—This research was funded by the Natural Resources Conservation Service of the U.S. Department of Agriculture (USDA). This work was also supported by the U.S. National Institute of Food and Agriculture, McIntire Stennis projects WVA00117 (JTA), WVA00122 (DJB), WVA00812 (JTA), and WVA00820 (DJB), and the West Virginia Agricultural and Forestry Experiment Station. James Anderson was supported by the National Science Foundation under Cooperative Agreement No. OIA-1458952 during manuscript preparation. Donald Brown received additional support from the Northern Research Station and Pacific Northwest Research

Station of the U.S. Forest Service. We thank Ryan Wickiser, Kyle Levat, and Kylie Matthews for assisting with fieldwork. We are grateful to the West Virginia Division of Natural Resources, Potomac Audubon Society, and the many private landowners who graciously allowed us to use their property for several days or weeks. Capture and handling methods were approved by the West Virginia Division of Natural Resources (Permits 2016.173, 2016.174, 2017.013) and the Institutional Animal Care Use Committee of West Virginia University (Protocol 1603001197). Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official U.S. Department of Agriculture or U.S. Government determination or policy.

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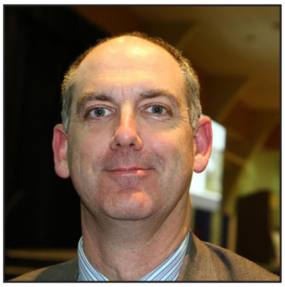

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APPENDICES

APPENDIX TABLE 1.—Variation in 10 wetland-level and three surrounding landscape characteristics for wetlands in West Virginia, USA, including all sampled wetlands, wetlands restored through the Wetlands Reserve Program (WRP) and Agricultural Conservation Easement Program (ACEP), and reference wetlands. We sampled 22 wetlands between 16 July and 9 September 2016 and 10 wetlands between 3 June and 15 July 2017.

Habitat variable	Mean	Minimum	Maximum
All wetlands			
Edge emergent vegetation (%)	37.86	0.00	82.00
Canopy (%)	17.48	0.00	89.90
Total emergent vegetation (%)	22.81	5.00	65.00
pH	7.12	6.08	8.29
Dissolved oxygen (mg/L)	4.73	2.03	10.99
Conductivity (uS/cm)	203.86	13.71	650.10
Water depth (m)	1.16	0.39	3.30
Wetland perimeter (m)	274.03	58.07	1,821.80
Wetland size (ha)	0.59	0.02	11.07
Sand in soil (%)	23.13	10.00	51.18
Forest cover (%; 100 m)	39.96	0.00	100
Forest cover (%; 1,000 m)	48.16	9.34	88.81
Road density (m; 100 m)	384.58	0.00	3,851.26
Road density (m; 1,000 m)	13,574.54	5,434.12	23,574.86
Wetland count (1,000 m)	17.03	5	62
Restored wetlands			
Edge emergent vegetation (%)	38.92	0.00	82.00
Canopy (%)	21.66	0.00	89.90
Total emergent vegetation (%)	27.19	5.00	40.00
pH	6.96	6.08	7.84
Dissolved oxygen (mg/L)	4.25	2.42	9.86
Conductivity (uS/cm)	192.73	13.71	548.70
Water depth (m)	1.18	0.43	2.20
Wetland perimeter (m)	349.10	58.07	1,821.80
Wetland size (ha)	0.96	0.02	11.07
Sand in soil (%)	24.25	10.00	46.68
Forest cover (%; 100 m)	39.79	0.00	87.88
Forest cover (%; 1,000 m)	46.58	9.34	88.81
Road density (m; 100 m)	485.31	0.00	3,851.26
Road density (m; 1,000 m)	13,630.52	5,434.12	19,247.34
Wetland count (1,000 m)	19.81	6	62
Reference wetlands			
Edge emergent vegetation (%)	36.80	3.00	65.50
Canopy (%)	13.29	0.00	71.80
Total emergent vegetation (%)	18.44	5.00	65.00
pH	7.28	6.50	8.29
Dissolved oxygen (mg/L)	5.20	2.03	10.99
Conductivity (uS/cm)	214.99	25.97	650.10
Water depth (m)	1.13	0.39	3.30
Wetland perimeter (m)	198.95	62.90	611.90
Wetland size (ha)	0.22	0.03	1.00
Sand in soil (%)	22.01	10.33	51.18
Forest cover (%; 100 m)	40.13	0.00	100
Forest cover (%; 1,000 m)	49.74	14.27	86.50
Road density (m; 100 m)	283.86	0.00	968.88
Road density (m; 1,000 m)	13,518	5,552.21	23,574.86
Wetland count (1,000 m)	14.25	5	50

Appendix Table 2.—Final model selection results for environmental variables tested as predictors of Painted Turtle (*Chrysemys picta*) and Snapping Turtle (*Chelydra serpentina*) abundance and body condition at restored and reference wetlands (Wetland Type) in West Virginia, USA. We sampled turtle populations and collected environmental measurements at 22 wetlands between 16 July and 9 September 2016 and 10 wetlands between 3 June and 15 July 2017. Candidate wetland-level variables included dissolved oxygen in water (%; DO), water conductivity (uS/cm; Conductivity), water acidity (H^+), water depth (m; Depth), sand in soil (%; Sand), wetland perimeter length (m; Perimeter Length), canopy cover around the perimeter (%; Canopy Cover), emergent vegetation around the perimeter (%; Edge Emergent Vegetation), and total emergent vegetation (%). Candidate surrounding landscape variables included number of surrounding wetlands within 1,000 m of the focal wetland (Wetland Count), percentage of forest within 100 m or 1,000 m of the focal wetland (Forest Cover), and total length of all roads within 100 m or 1,000 m of the focal wetland (Road Density). Null models are shown as (.). We modeled abundance relationships using multinomial *N*-mixture models with a removal (i.e., depletion) sampling observation process, with models ranked using Quasi Akaike Information Criterion corrected for small-sample size (QAICc). We modeled body condition index scores using linear regression models, with models ranked using AICc. Model explanatory power (r^2) is provided for the regression models.

Model	Parameters	Δ(Q)AICc	w_i	r^2
Painted Turtle – Abundance				
Wetland Count + Edge Emergent Vegetation + Road Density	7	0.00	1.00	–
Wetland Count + Edge Emergent Vegetation	6	18.01	0.00	–
Wetland Count + Road Density	6	21.01	0.00	–
Wetland Count	5	22.11	0.00	–
Wetland Count + Canopy Cover	6	22.61	0.00	–
Wetland Count + Sand	6	23.43	0.00	–
Wetland Count + Depth	6	23.52	0.00	–
Wetland Count + Wetland Type	6	23.74	0.00	–
Wetland Count + Total Emergent Vegetation	6	23.75	0.00	–
Wetland Count + Size	6	24.16	0.00	–
Wetland Count + Conductivity	6	24.43	0.00	–
Wetland Count + DO	6	24.98	0.00	–
Wetland Count + H^+	6	25.02	0.00	–
Wetland Count + Forest Cover	6	25.10	0.00	–
Wetland Count + Perimeter Length	6	27.83	0.00	–
Snapping Turtle – Abundance				
Conductivity + DO	6	0.00	0.51	–
Conductivity	5	1.17	0.28	–
Conductivity + DO + Depth	7	2.87	0.12	–
DO	5	4.00	0.07	–
Depth	5	7.87	0.01	–
Canopy Cover	5	11.49	0.00	–
Forest Cover	5	12.71	0.00	–
Road Density	5	14.71	0.00	–
Sand	5	16.14	0.00	–
Wetland Type	5	16.54	0.00	–
(.)	4	16.64	0.00	–
Total Emergent Vegetation	5	17.70	0.00	–
H^+	5	18.48	0.00	–
Edge Emergent Vegetation	5	18.60	0.00	–
Perimeter Length	5	18.87	0.00	–
Size	5	19.38	0.00	–
Wetland Count	5	19.38	0.00	–
Painted Turtle – Body Condition				
Wetland Count + Wetland Type	4	0.00	0.14	0.183
Wetland Count	3	0.02	0.14	0.177
Wetland Count + Canopy Cover	4	1.14	0.08	0.179
Wetland Count + Forest Cover	4	1.30	0.07	0.179
Wetland Count + Total Emergent Vegetation	4	1.32	0.07	0.179
Wetland Count + Sand	4	1.49	0.07	0.178
Wetland Count + DO	4	1.64	0.06	0.178
Wetland Count + Road Density	4	1.89	0.06	0.177
Wetland Count + Perimeter Length	4	1.99	0.05	0.177

Appendix Table 2.—cont.

Model	Parameters	Δ(Q)AICc	w_i	r^2
Wetland Count + Size	4	2.02	0.05	0.177
Wetland Count + Depth	4	2.03	0.05	0.177
Wetland Count + Edge Emergent Vegetation	4	2.04	0.05	0.177
Wetland Count + Conductivity	4	2.07	0.05	0.177
Wetland Count + H^+	4	2.08	0.05	0.177
Snapping Turtle – Body Condition				
Road Density	3	0.00	0.30	0.074
Road Density + Size	4	1.77	0.12	0.077
Size	3	1.85	0.12	0.055
Road Density + Perimeter Length	4	2.17	0.10	0.074
Perimeter Length	3	3.29	0.06	0.041
Road Density + Size + Edge Emergent Vegetation	5	3.66	0.05	0.081
Road Density + Size + Edge Emergent Vegetation + Depth	6	4.68	0.03	0.093
Edge Emergent Vegetation	3	4.87	0.03	0.025
Depth	3	5.18	0.02	0.022
(.)	2	5.21	0.02	0.000
Conductivity	3	5.33	0.02	0.021
DO	3	5.39	0.02	0.020
Wetland Type	3	5.41	0.02	0.020
Sand	3	5.48	0.02	0.019
Total Emergent Vegetation	3	5.77	0.02	0.016
Canopy Cover	3	6.14	0.01	0.012
Forest Cover	3	6.15	0.01	0.012
Wetland Count	3	6.78	0.01	0.006
H^+	3	6.87	0.01	0.005