



Influence of Wetland and Landscape Characteristics on Freshwater Turtle Relative Abundance and Movement Patterns in West Virginia, USA

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Abstract

Wetland management practices often alter habitat characteristics to improve the function of the wetland (e.g., removing emergent vegetation for aesthetics or dredging for fish stocking), potentially at the cost of reducing habitat quality for wetland-dependent species such as freshwater turtles. We identified wetland and surrounding landscape characteristics related to painted turtle (*Chrysemys picta*) and snapping turtle (*Chelydra serpentina*) relative abundance and snapping turtle movement among wetlands. We surveyed turtles at 29 wetland sites (0.04–1.71 ha) in a mixed-use watershed in north-central West Virginia, USA, where hardwood forests and wetlands have been heavily fragmented by agriculture and roads. We also applied radio transmitters to 33 adult snapping turtles (17 females and 16 males) across 17 wetlands. Snapping turtle relative abundance was best estimated with mean substrate depth, mean wetland depth, and minimum distance from roads. Painted turtle relative abundance was best estimated with the null model. We documented movement among wetlands for 22 snapping turtles (67%), including 10 females and 12 males. The probability of inter-wetland movement decreased with increased minimum distance from wetlands. Our results suggest that the focal turtle species readily used shallow, mucky wetlands with deep substrate and that increasing the density of wetlands could increase snapping turtle population connectivity. Managers could consider restoring a diversity of wetland types that result in reduced travel distance between wetlands and that collectively have characteristics conducive to multiple species.

Keywords Appalachia · *Chelydra serpentina* · *Chrysemys picta* · Habitat · Radio Telemetry

Introduction

Wetland-level factors such as turbidity, pH, dissolved oxygen, and vegetative cover can directly influence assemblages of biotic communities such as fish (Brazner and Beals 1997; Kaller et al. 2013), macroinvertebrates (De Szalay and Resh 2000; Anderson et al. 2013b), and amphibians (Sacerdote and King 2009; Clipp and Anderson 2014; McPherson et al. 2020). Surrounding landscape characteristics such as road density, agriculture, and other anthropogenic land uses can increase sediment and nutrient loading through runoff (Gleason and Euliss 1998; Drohan et al. 2006; Duan et al. 2012; Hedrick et al. 2013), potentially leading to lower abundances of taxa due to increased environmental stressors (Houlahan and Findlay 2003; Babbitt et al. 2009). Landscape conversions further affect wetland-dependent taxa as they are supported by adjacent upland areas (Veselka et al. 2010; Quesnelle et al. 2015). Semi-aquatic turtles, for instance, are important high-order predators in wetland systems (Silliman

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and Bertness 2002; Lindsay et al. 2013). Wetland population carrying capacity is likely influenced by habitat characteristics required to fulfill life-history requirements such as basking habitat (Lindeman 2000; Anthonysamy et al. 2014), foraging sites (Zadnik et al. 2009; Vance et al. 2012; Anderson et al. 2013a), nesting sites (Markle and Chow-Fraser 2014), and hibernacula (Strain et al. 2012). Thus, understanding how local and landscape factors influence turtle abundance in wetlands can improve our understanding and management of wetland systems.

Painted turtles (*Chrysemys picta*) and snapping turtles (*Chelydra serpentina*) are semi-aquatic, freshwater turtle species with broad ranges throughout the eastern United States (Ernst and Lovich 2009). These are typically the dominant wetland turtle species within their ranges (Zadnik et al. 2009; Phu 2010; Buchanan et al. 2018). While both species are considered habitat generalists, densities are highly variable among wetlands (Flaherty et al. 2008; Anthonysamy et al. 2014; Buchanan et al. 2018; Mota et al. 2021), indicating that habitat characteristics likely strongly influence wetland carrying capacity. Previous studies suggest that both local and landscape features could influence wetland-level abundances of these species (Bowne et al. 2006; Zadnik et al. 2009; Anthonysamy et al. 2014; Braun and Phelps 2016; Hughes et al. 2016).

At the local scale, wetland-level factors such as size (i.e., perimeter, depth, and surface area) and structure (e.g., herbaceous cover and substrate) affect turtle populations as they can provide habitat for food (Zadnik et al. 2009; Anderson et al. 2013a; Hughes et al. 2016), temperature regulation (DonnerWright et al. 1999), and predator evasion (Ernst and Lovich 2009). Canopy cover can also influence turtle abundance (Braun and Phelps 2016), where regularly basking species such as painted turtles tend to favor habitats with lower canopy cover (Cosentino et al. 2010). Although snapping turtles are less likely to bask, changes in canopy cover could influence habitat preferences (Rizkalla and Swihart 2006; Attum et al. 2008; Aresco 2009).

Surrounding landscape characteristics such as upland soil composition and anthropogenic land use types can also affect turtle populations (Joyal et al. 2001; Milam and Melvin 2001; Attum et al. 2008; Ryan et al. 2008; Strain et al. 2012). Soil composition (i.e., percent clay, silt, or sand; Christens and Bider 1987) influences nest habitat quality, where snapping turtles nest in sandier soils than nearby random areas (Thompson et al. 2017). Alternatively, painted turtles favor clay soils when nesting (Christens and Bider 1987), and an increased percentage of sand decreases hatchling survival (Hughes and Brooks 2006). Movement between wetlands of different sizes and types alters local populations through female-biased road mortality because of upland nesting behavior (Aresco 2005; Price et al. 2013; Reid and Peery 2014; Crump et al. 2016; Dupuis-Desormeaux et al. 2018).

This pattern may also be biased toward slower, larger-bodied species such as snapping turtles (Gibbs and Shriver 2002). Alternatively, road density can increase species abundance through the degradation of water quality (i.e., painted turtles; DeCatanzaro and Chow-Fraser 2010) or lead to male-skewed populations (i.e., painted turtles and snapping turtles; Steen and Gibbs 2004; Reid and Peery 2014). In some studies, population dynamics shifted, but neither roads (Steen and Gibbs 2004; Attum et al. 2008; Langen et al. 2012; Dorland et al. 2014) nor agricultural land use (Rizkalla and Swihart 2006) appeared to impact snapping turtle or painted turtle abundance significantly.

Although landscape effects on turtle abundance are well-documented for these species, only some studies concurrently investigated the effects of habitat structure and landscape factors on abundance and wetland site fidelity. Our study aimed to 1) improve our understanding of the effects of wetland characteristics on the relative abundance of snapping turtles and painted turtles and 2) assess inter-wetland movement patterns of snapping turtles within a mixed-use watershed. We identified important habitat characteristics, estimated their influence on the relative abundance of turtles, and identified environmental characteristics associated with the probability of a snapping turtle moving between wetlands to aid in the conservation and management of wetlands and turtles. Regarding relative abundance, we hypothesized that increased mean substrate depth would increase the relative abundance of both focal species, while increased canopy cover would decrease painted turtle relative abundance. Concerning snapping turtle inter-wetland movement, we hypothesized that reduced distance between wetlands would increase movement. In contrast, a higher average percentage of sand within 30 m of wetlands would decrease female snapping turtle movement.

Methods

Study Area

We performed this study in the 7,778 ha Upper Deckers Creek watershed in Preston County, West Virginia, USA (centroid latitude: 39°31'12.8061"N; longitude: 79°48'34.6437"W). This mixed-use watershed is in the Appalachian Mountains, which range from southeastern Canada to the southeastern United States. The climate in the study area is moderate (Hartman 2000), where mean annual temperature and precipitation at the nearest weather station were 12.68 ± 1.67 °C and 107.52 ± 0.12 cm from 2019–2020, respectively (Morgantown Municipal-Hart Field, approximately 36.2 km from the study area). Deciduous forests and freshwater wetlands (emergent [18%], unconsolidated bottom [42%], forested/shrub wetlands [25%], and

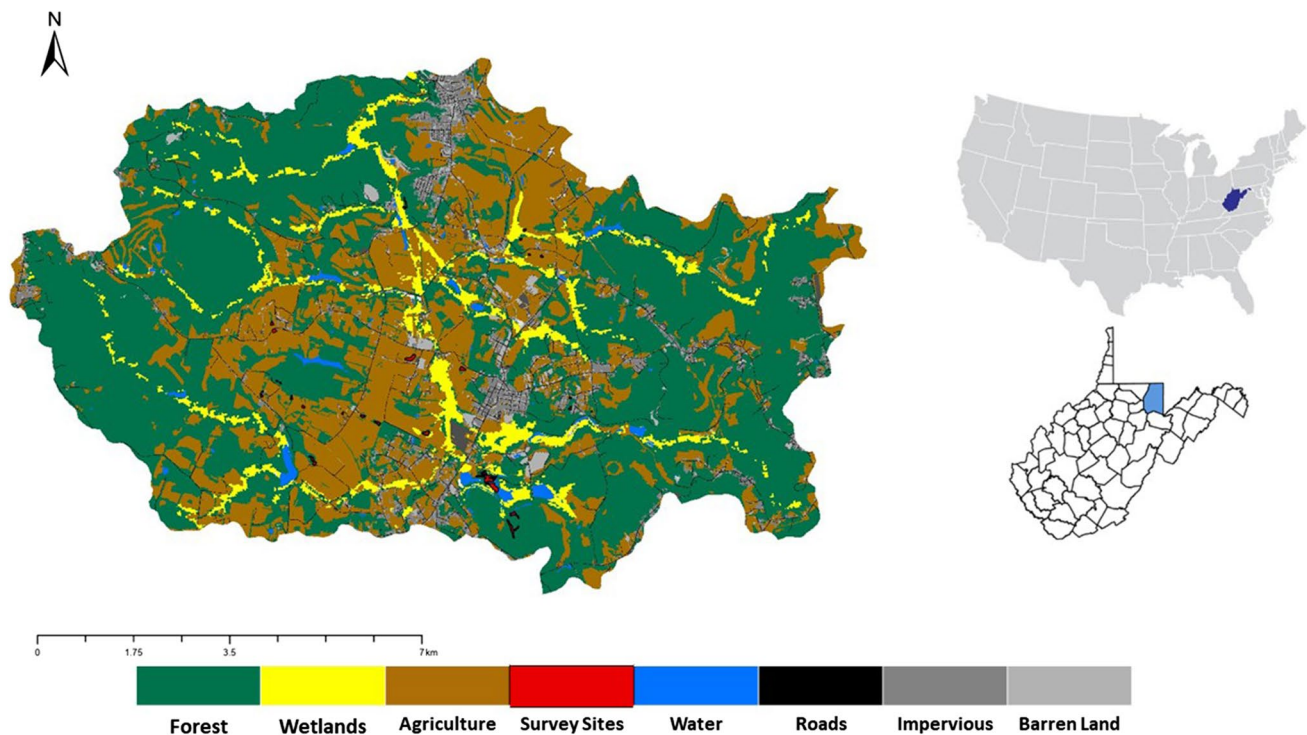


Fig. 1 Wetlands in Preston County, West Virginia, USA, where snapping turtles (*Chelydra serpentina*) and painted turtles (*Chrysemys picta*) were surveyed to investigate the influence of habitat characteristics on relative abundance and inter-wetland movement. We

sampled turtle populations at 29 wetlands and tracked the movement dynamics of 33 adult snapping turtles from 17 wetlands between 2019 and 2020

riverine systems [15%]) in the watershed have been substantially fragmented by agricultural production (Becker et al. 2022; Fig. 1). Development-associated fragmentation in the watershed includes northern (i.e., Masontown) and central (i.e., Reedsville) residential hubs.

We surveyed 29 wetlands on or near the JW Ruby Research, Education, and Outreach Center (REOC), Reedsville, West Virginia. The REOC was the focal point of a larger study evaluating wildlife responses to stream and wetland restoration (Becker et al. 2022; MacKenzie et al. 2023). Study sites included other wetlands on the REOC and nearby wetlands where landowners granted access to their properties. Most sites ($n=18$) were classified as palustrine unconsolidated bottom wetlands; six sites were classified as palustrine emergent, one was palustrine scrub-shrub, and four were palustrine aquatic bed (Cowardin et al. 1979; Lozon 2021). Wetlands varied from 0.04–1.71 ha (mean: 0.37 ha) and perimeter length from 70.5 to 1,263.4 m (mean: 300.1 m). Wetlands were surrounded (i.e., within 1 km) by predominantly forest or agricultural land (Fig. 1). Soil composition primarily consisted of silt loam or loam types (Natural Resources Conservation Service 2016). Sites with agriculture as the predominant land use within 1 km were associated mainly with the REOC (Becker et al. 2022) or private farms where the land was used for hay and pasture.

Turtle Abundance Sampling

We sampled aquatic turtle populations using baited hoop net traps, one of the most commonly used sampling approaches for freshwater turtles (reviewed by Mali et al. 2014). We used two trap sizes, 0.76 m diameter and 0.91 m diameter, because a previous study compared these trap sizes and found that trap size influenced painted turtle and snapping turtle capture success (Gulette et al. 2019). We baited each trap with sardines in a perforated container so the scent could escape, but the bait could not be consumed (Mali et al. 2014). We replaced bait after each trap day to minimize the influence of bait freshness on capture success (Brown et al. 2011). We also included a flotation device in each trap to ensure captured individuals had constant access to air.

In 2019, we sampled 20 wetlands in spring (18 April to 19 May), summer (1–31 July), and fall (5 October to 1 November). Trapping effort was consistent among sites and seasons, ranging from 27–30 trap nights per trapping session. In 2020, we sampled 9 wetlands in spring (11–29 May) and summer (30 June to 15 July), but we did not conduct fall surveys due to low fall capture success in 2019 (Table 1). Wetlands sampled in 2020 were chosen with the goal of reducing the distance between wetlands surveyed, particularly for the movement component of the study. For each

sampling session, we set 10 traps ≥ 10 m apart and sampled for 3 consecutive days, with hoop nets checked every 24 h. We cleaned traps, boots, and equipment between sites to avoid the potential spread of invasive species and diseases among wetlands (Bryzek et al. 2022).

For each turtle captured, we used secondary characteristics (i.e., foreclaw and tail lengths for painted turtles; precloacal tail and posterior plastral scute lengths for snapping turtles) to determine sex (Mosimann and Bider 1960; Ernst and Lovich 2009). We also uniquely marked the carapace of each individual using a hand file or rotary tool (Cagle 1939; Ernst et al. 1974). Turtles were released near their capture site after processing.

Inter-wetland Movement

To assess the inter-wetland movement of snapping turtles, we applied very-high frequency transmitters (RI-2B, Holohil Systems LTD, Ontario, Canada) to 33 captured adult snapping turtles. We assured that individuals weighed ≥ 300 g to keep transmitters $\leq 5\%$ of biomass to minimize impacts on mobility (Seburn 2012). We chose turtles to track based on the sex of the individual (15 male, 17 female) and the dominant land use (i.e., agriculture (16), forest (12), mixed (5)) surrounding its resident site. We relocated turtles during daylight hours every 2–5 days between April and October 2019 and 2020 and once per month from November to March 2019 and 2020 using an R2000 series receiver (Advanced Telemetry Systems, Isanti, MN) with an F152-3FB model antenna (AF Antronics, Inc., Urbana, IL).

When turtles were in inaccessible locations (e.g., deep water, private land), we estimated their location via triangulation and point projection (Garmin eTrex Legend Cx model, Garmin, Olathe, KS). For each turtle relocation, we recorded landscape type and turtle behavior, if possible, from several

meters away so the natural behavior of the turtle was not disturbed (Baldwin et al. 2004). The mean number of days snapping turtles were tracked was 282.67 ± 29.03 days.

Environmental Characteristics

Local Characteristics

For each site, we measured substrate depth (cm) and compaction (kg/cm^2) at both ends of each trap ($n=2$ readings per trap location) with a meter stick and soil compaction tester (Dickey-John Corporation, Auburn, Illinois, USA), respectively. We also measured water depth across each wetland using a metered weighted line (Doody et al. 2002), where depth at 15 equidistant points across the longest length of the wetland was measured to the nearest 0.5 cm. We measured 15 additional points along a transect perpendicular to the first transect at the widest breadth of the wetland.

We estimated the percent cover of herbaceous vegetation (emergent, floating, floating-leaved) with 1 m^2 frames centered on each water depth location ($n=30$; Marchand and Litvaitis 2004) and used categories defined by Daubenmire (1968) and Cosentino et al. (2010): 1 ($<5\%$), 2 (5–25%), 3 (26–50%), 4 (51–75%), 5 (76–95%), and 6 ($>95\%$). To calculate the mean wetland vegetation cover for each wetland across each trapping session, we used midpoint values for the respective category at each measurement location (i.e., 2.5, 15, 37.5, 62.5, 85.5, and 97.5). Wetland area (ha) and perimeter (m) were measured with ortho imagery in ArcGIS (version 10.7, ESRI, Redlands, CA, USA). To quantify potential nesting area quality, we calculated the average percent sand in soil within 30 m of each wetland using the Soil Survey Geographic Database (Baldwin et al. 2004; Natural Resources Conservation Service 2016).

Landscape Characteristics

We standardized land use types by calculating percentages within 250 m, 500 m, and 1 km of the perimeter of each wetland to account for indirect land use effects on relative abundance and overland movement (Findlay and Houlihan 1997; Joyal et al. 2001; Marchand and Litvaitis 2004; Attum et al. 2008). Land use data were retrieved from the 2011 National Land Cover Data Set (Strager 2012). Distance to nearby wetlands and roads (m) was measured with ortho imagery in ArcGIS.

Statistical Analyses

Relative Abundance

We estimated the influence of habitat characteristics on the relative abundance of painted turtles using linear

Table 1 The number of sites within the Upper Deckers Creek watershed in Preston County, West Virginia, USA, where snapping turtles (*Chelydra serpentina*) and painted turtles (*Chrysemys picta*) were captured from 2019–2020. Turtles were surveyed from 20 wetland sites in 2019 from 18 April to 19 May (spring=SP) and 1–31 July (summer=SU), and 5 October to 1 November (fall=FA), while 9 wetland sites were surveyed in 2020 from 11–29 May (spring) and 30 June to 15 July (summer). Two wetlands were not sampled in the fall of 2019 due to low water levels prohibiting trapping

Species	2019			2020	
	SP	SU	FA	SP	SU
Snapping turtle only	4	5	1	3	1
Painted turtle only	3	3	5	1	2
Both	8	7	1	5	4
None	5	5	11	0	2
Total sites	20	20	18	9	9

mixed-effects models. For painted turtle candidate models, we included wetland sites as a random effect to account for the repeated sampling of sites. Due to convergence issues, we ran linear models without random effects for snapping turtle candidate models. We used catch-per-unit effort (CPUE) as the response variable. To account for differing trapping efforts across sites and seasons (i.e., 27–30 trap days per session), we calculated CPUE as the number of unique individuals captured per trap day within each site and sampling period. All continuous variables were standardized (i.e., centered and scaled) to facilitate model convergence.

We included all habitat variables as fixed effects and used season-specific habitat measurements because these variables were dynamic across time. We first ranked each variable individually using Akaike Information Criterion corrected for small-sample size (AICc) (Burnham and Anderson 2002). Then, we created candidate additive models for individual variables that had more support than the null model (Burnham et al. 2011). We calculated variance inflation factors (VIF) for each variable in the top candidate models, compared any variables with a $VIF > 5$ (Kim 2019), and removed the variable with the lower predictive power. For the most parsimonious models, we computed the beta coefficients' 85% confidence intervals (CI; Arnold 2010). We considered there to be strong support for an effect when CIs did not overlap zero (Halsey 2019). We deemed models to have strong support if $\Delta AICc < 2$ and some support if $\Delta AICc < 7$ (Burnham and Anderson 2002; Burnham et al. 2011). We made inferences for the direction and strength of relationships based on coefficient, and CI estimates from individual models rather than using a model averaging approach due to the potential for misestimation of coefficient relationships when averaging values across models (Cade 2015; Banner and Higgs 2017). We also report variance explained (r^2) for each candidate model. We computed adjusted r^2 for the linear regression models and restricted r^2 to the fixed effects portion of the mixed-effects models (Nakagawa and Schielzeth 2013).

Inter-wetland Movement

Using logistic regression, we estimated the influence of habitat and surrounding landscape characteristics on the probability of a snapping turtle leaving its original capture site. We tested the following predictors: sex of the turtle, percent agriculture coverage within 1 km, minimum wetland distance from roads and other wetlands, average percent sand within 30 m, and wetland size (Attum et al. 2008; Patrick and Gibbs 2010). We followed the same data standardization, model selection, and model assessment approaches as the relative abundance analysis. We estimated the explanatory power of the candidate logistic regression models using pseudo- r^2 (Nakagawa and Schielzeth 2013). We used

a Kruskal–Wallis test to determine if there was a difference in movements between the sexes. We performed all statistical analyses using program R (version 4.1.1; R Core Team (2020)). We used the package lme4 (version 1.1–23) to construct linear mixed-effects models, car (version 3.0) to test for multicollinearity in additive candidate models, stats (version 4.2.1) to build linear and logistic regression models and perform Kruskal–Wallis tests, robustHD (version 0.7.4) for data standardization, StatisticalModels (version 0.1) and DescTools (version 0.99.52) to calculate r^2 and pseudo- r^2 values for linear mixed effect models and logistic regression models, respectively, and AICcmodavg (version 2.3–1) to rank candidate models.

Results

Wetland Habitat Characteristics

The mean percent canopy cover across sites was 25.84% (range: 0–88.75%; Appendix 1). Mean herbaceous cover was 9.62% (range: 2.5–31.38%; Appendix 1), where the dominant species present across sites were yellow pond lily (*Nuphar lutea*), duckweed (*Lemna minor*), and broadleaf cattail (*Typha latifolia*). Palustrine unconsolidated bottom wetlands tended to have a lower herbaceous cover (range: 2.5–16.78%; mean: 5.66%), whereas palustrine aquatic bed wetlands were predominantly covered by pond lilies, which resulted in higher herbaceous cover (range: 20.63–31.38%; mean: 24.58%). Distance from roads ranged from 0–418.9 m (mean: 99.2 m), and distance from the nearest wetland ranged from 4.6–238.8 m (mean: 64.9 m).

Relative Abundance

We captured 338 turtles at least once during the study, including 63 snapping turtles and 160 painted turtles in 2019, 58 snapping turtles and 57 painted turtles in 2020, and one snapping turtle and four painted turtles in both years. In addition, we captured one red-eared slider (*Trachemys scripta elegans*) in 2019. We caught both painted and snapping turtles at some, but not all, wetlands each season (Table 1).

The most parsimonious model for snapping turtle CPUE ($w_i = 0.46$, $r^2 = 0.132$) included mean wetland depth (−0.00039, CI: −0.00065 – −0.00012), minimum distance from roads (0.00022, CI: 0.00008–0.00036), and mean substrate depth (0.00057, CI: −0.00013 – 0.00127; note the CI for this variable overlaps 0). Across the gradient of measured values, predicted CPUE was positively associated with minimum distance from roads and mean substrate depth, and negatively associated with mean wetland depth (Fig. 2). One additional environmental variable had some support, mean

percent sand within 30 m (Table 2). The model containing only this predictor estimated a positive relationship with snapping turtle CPUE (0.003, CI: 0.0005 – 0.005).

The most parsimonious model for painted turtle CPUE was the null model ($w_i=0.74$), but three environmental variables had some support (Table 2). Wetland area (-0.035, CI: -0.105 – 0.034) and wetland depth (-0.0005, CI: -0.001 – -0.0001) were negatively associated with CPUE, while mean herbaceous cover was positively associated with CPUE (0.003, CI: 0.0002–0.005).

Inter-wetland Movement

Out of the 33 adult snapping turtles tracked, 11 (7 females and 4 males) stayed within their resident wetland. The 22 remaining turtles (10 females and 12 males) moved to at least one other wetland, with 14 turtles using two wetlands, four turtles using three wetlands, three turtles using four wetlands, and one turtle using six wetlands. Road mortality was not observed during this study. The number of wetlands used differed slightly between sexes (Kruskal–Wallis: $\chi^2=2.17$, $df=1$, $p=0.14$; males: 2.31 ± 0.27 ; females: 1.88 ± 0.29). Females' estimated overland distance was 1.05 times longer than males.

The most parsimonious model for snapping turtle movement included distance to the nearest wetland (Table 3). The confidence interval did not overlap 0 (-0.018– -0.0014), but explanatory power was low (pseudo- $r^2=0.025$). The estimated probability of a snapping turtle leaving its resident site decreased by 0.0096 with every 1 m increase in minimum distance from the nearest wetland. The second most supported model ($\Delta AIC_c=0.53$) included distance to the nearest wetland and wetland area, and had approximately twice as much explanatory power (pseudo- $r^2=0.058$). This model estimated that probability of a snapping turtle leaving its resident site was negatively associated with distance to the nearest wetland (-0.01, CI: -0.018 – -0.001), and wetland size was positively associated with wetland size, but the confidence interval overlapped 0 (0.844, CI: -0.79 – 2.84).

Discussion

Our results suggest that, in our study area, both wetland and surrounding landscape characteristics had a strong influence on snapping turtle abundance. In contrast, they had a weak effect on painted turtle abundance. The positive

Fig. 2 The influence of three habitat characteristics on snapping turtle (*Chelydra serpentina*) catch-per-unit effort (CPUE) for 29 wetlands sampled in the Upper Deckers Creek watershed in Preston County, West Virginia, USA, from 2019–2020, including (a) mean wetland depth, (b) minimum distance from roads, and (c) mean substrate depth (note the coefficient confidence interval for this variable overlapped 0). For each modeled relationship, the other two variables were held at their mean value. Shaded gray areas indicate the 85% confidence intervals

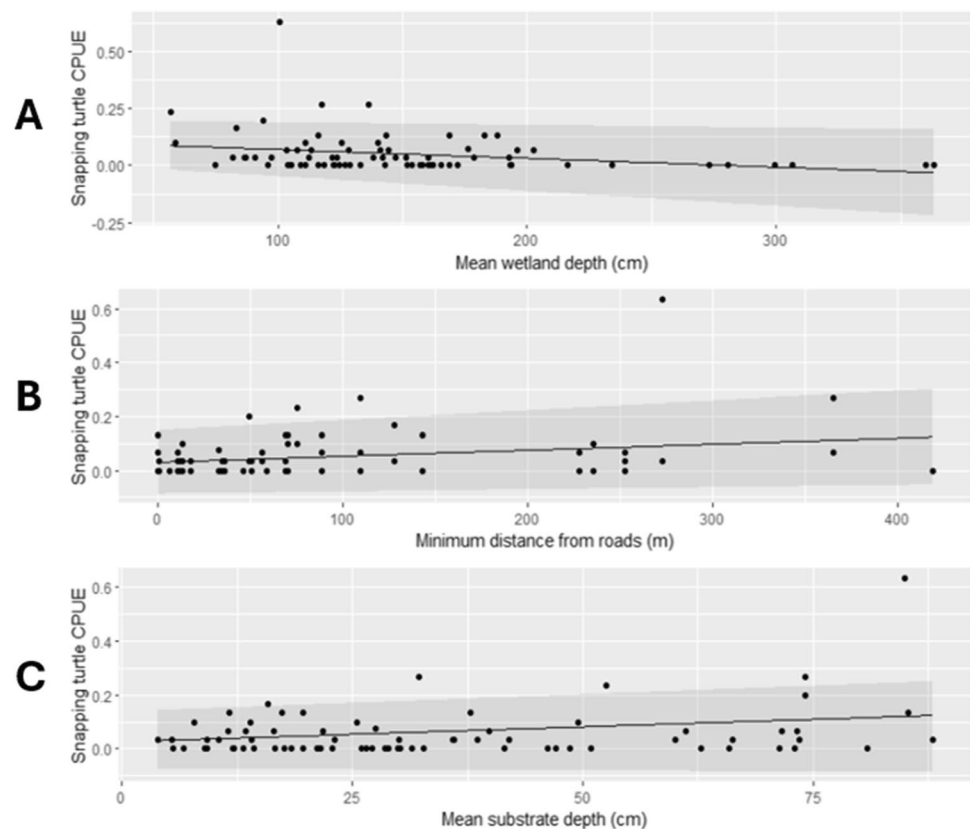


Table 2 Candidate environmental variable models for explaining relative abundance of snapping turtles (*Chelydra serpentina*) and painted turtles (*Chrysemys picta*) within the Upper Deckers Creek watershed in Preston County, West Virginia, USA, with corrected Akaike's Information Criterion (AICc) values, change in AICc from

the top model (ΔAICc), model weight (w_i), and model adjusted r^2 . We used linear regression models for snapping turtles and linear mixed effect models for painted turtles, with wetland treated as a random effect. Additive models were tested for individual variables that had greater support than the null model (.)

Model	AICc	ΔAICc	w_i	r^2
<i>Snapping turtle</i>				
Mean substrate depth + Mean wetland depth + Minimum distance from roads	-149.41	0.00	0.43	0.132
Mean substrate depth + Mean wetland depth + Minimum distance from roads + Mean percent sand within 30 m	-147.38	2.03	0.16	0.123
Mean substrate depth	-146.60	2.82	0.11	0.069
Mean substrate depth + Mean wetland depth	-146.41	3.01	0.10	0.082
Mean percent sand within 30 m + Minimum distance from roads	-145.51	3.90	0.06	0.071
Mean wetland depth	-144.93	4.48	0.05	0.049
Minimum distance from roads	-144.44	4.98	0.04	0.043
Mean percent sand within 30 m	-143.41	6.00	0.02	0.029
(.)	-142.29	7.13	0.01	-
Mean wetland herbaceous cover	-141.18	8.23	0.01	0.006
Wetland area	-140.78	8.63	0.01	-0.005
Minimum distance from wetlands	-140.37	9.04	0.00	-0.010
Mean substrate compaction	-140.13	9.29	0.00	-0.013
Mean percent canopy cover	-140.13	9.29	0.00	-0.013
Percent agriculture within 250 m	-140.12	9.29	0.00	-0.014
<i>Painted turtle</i>				
(.)	-59.91	0.00	0.74	-
Wetland area	-55.25	4.66	0.07	0.009
Mean wetland herbaceous cover	-54.53	5.39	0.05	0.033
Mean wetland depth	-54.14	5.77	0.04	0.037
Percent agriculture within 1 km	-52.84	7.07	0.02	0.018
Mean percent canopy cover	-52.49	7.42	0.02	0.015
Mean percent sand within 30 m	-52.10	7.82	0.01	0.008
Mean substrate depth	-51.82	8.10	0.01	0.005
Minimum distance from roads	-51.63	8.29	0.01	0.0004
Minimum distance from wetlands	-51.62	8.29	0.01	0.002
Mean substrate compaction	-51.45	8.46	0.01	0.0004

relationship between wetland substrate depth and snapping turtle CPUE is similar to what was found in the St. Croix River in Minnesota and Wisconsin, USA, where increased percent muck had a strong positive correlation with snapping turtle abundance (DonnerWright et al. 1999). In a previous study in the Ohio River, West Virginia, the percent silt in the substrate was positively correlated with snapping turtle CPUE (Anderson et al. 2013a). Snapping turtles are ambush predators, with deep, mucky substrate providing concealment from prey (Bodie et al. 2000; Van Meter et al. 2006; Ernst and Lovich 2009).

Despite the influence of aquatic vegetation on food availability (Graves and Anderson 1987), mean herbaceous cover did not have a strong relationship with either

species; however, mean wetland depth was related to snapping turtle CPUE, which can have a negative effect on vegetative growth. Increased vegetative density along the shallow edge of wetlands can serve as a food source, provide microhabitats for animal prey items such as small fish, tadpoles, and macroinvertebrates, and provide a direct food source for omnivorous turtles (Gibbons 1967; Punzo 1975; Aresco and Gunzburger 2007; Kimmons and Moll 2010). Turtles occasionally defecated seeds when we processed them (Becker pers. obs.), indicating turtles were feeding on wetlands plants at our study sites.

Although mean wetland depth was related to snapping turtle CPUE, wetland area was not strongly associated with either snapping turtle or painted turtle CPUE. This

Table 3 Candidate logistic regression models assessing the influence of habitat and surrounding landscape characteristics on the probability of a snapping turtle (*Chelydra serpentina*) leaving its original capture site, with corrected Akaike's Information Criterion (AICc) values, change in AICc from the top model (Δ AICc), model weight (w_i), and model pseudo- r^2 . We used radio telemetry to track movements of 33 adult snapping turtles (16 males and 17 females) from 2019–2020 within the Upper Deckers Creek watershed in Preston County, West Virginia, USA. The null model is shown as (.)

Model	AICc	Δ AICc	w_i	Pseudo- r^2
Minimum distance from wetlands	38.55	0.00	0.23	0.025
Minimum distance from wetlands + Wetland area	39.08	0.53	0.18	0.058
Wetland area	39.19	0.64	0.17	0.023
(.)	39.49	0.94	0.15	-
Sex	40.60	2.06	0.08	0.0003
Percent agriculture within 1 km	40.63	2.08	0.08	0.027
Minimum distance from roads	41.52	2.97	0.05	0.048
Mean percent sand within 30 m	41.77	3.22	0.05	0.0002

result differs from what Failey et al. (2007) observed with snapping turtles, painted turtles, yellowbelly sliders (*Trachemys scripta*), and eastern mud turtles (*Kinosternon subrubrum*) in golf course and farm ponds in North Carolina, where abundance increased as area increased in wetlands ranging from 0.03 to 1.02 ha. Our results are possibly influenced by the greater heterogeneity in our wetland types potentially masking effects of size since we studied wetlands ranging from farm ponds to natural scrub-shrub wetlands. One potential limitation of our study is that we treated the wetland area as a consistent value rather than measuring the area each season to account for fluctuating water levels. Future investigations could investigate the seasonal fluctuations of water levels and determine how the changing hydroperiod and extent of wetted perimeter affects inter-wetland movement and abundance, especially since we were unable to trap two sites in the fall 2019 trapping session due to the wetlands being dry.

Snapping turtle relative abundance was not influenced by percent canopy cover, which was expected (Paterson et al. 2012; Vance et al. 2012; Anthonysamy et al. 2014). The absence of a relationship between painted turtle CPUE and canopy cover was unexpected as painted turtles regularly bask, and thus we would expect a positive relationship (Cosentino et al. 2010; Anthonysamy et al. 2014). This result could have been due to canopy cover at our sites being greatest in shallow water, which painted turtles favor as a foraging habitat (Jaeger and Cobb 2012).

The direct impact of roads causing increased rates of turtle mortality is well-documented (e.g., Gibbs and Shriver 2002; Crump et al. 2016); however, the effects of roads on painted turtle relative abundance are variable. Previous studies indicated roads had a harmful (Price et al. 2013), positive (Winchell and Gibbs 2016), or no (Failey et al. 2007; Dorland et al. 2014) relationship with the relative abundance of painted turtles. The lack of association between painted turtle CPUE and roads in this study could be due to the rural area we surveyed. The positive effect on snapping turtle CPUE we observed is similar to Roberts et al. (2023) and different from Steen and Gibbs (2004), who found no effect on snapping turtle relative abundance between high ($> 1.5 \text{ km/km}^2$) or low ($\leq 1.5 \text{ km/km}^2$) road density within 1 km of wetlands. Winchell and Gibbs (2016) found snapping turtle relative abundance increased when the frequency of low-intensity (low-traffic) roads within 500 m of wetlands increased, and the distance to the nearest road increased, which would be expected due to the high traffic volumes near their study area (max: 25,409 vehicles per day; NYSDOT 2017) compared to the rurality of our study area (max: 9,500 vehicles per day; WVDOT 2019). Future studies could be conducted to indicate whether traffic speed and intensity are stronger predictors than the presence of roads alone, especially with large, slow-moving turtles that are more susceptible to road mortality.

Other studies have found similar use of wetlands between sexes in snapping turtle populations (Paterson et al. 2012; Ryan et al. 2014). The sites from where we captured and tracked turtles had multiple nearby wetlands that could have promoted inter-wetland movements, but the mean number of sites used was only one additional site for males, while females, on average, stayed at their resident wetland, with some females occasionally visiting another wetland. The reason for reduced movement to nearby wetlands is uncertain. Other studies observed reduced inter-wetland movement between July and August (Major 1975; Brown and Brooks 1993; Ryan et al. 2014), indicating males can be more sedentary while finding mates. Steen and Gibbs (2004) observed increased female road mortality due to overland movement to nesting areas. Still, we found that road proximity to wetlands did not strongly affect snapping turtle movement, which is potentially because female snapping turtles primarily move upland for nesting during times of the day that are associated with lower traffic density (i.e., early morning and late evening; De Solla and Fernie 2004). Although 69% of sites surveyed in our study were within 100 m of roads, road mortality appeared relatively low in our study area (i.e., we encountered two dead snapping turtles on roads that were not marked or being tracked during the study). The only observed inter-wetland movement was a female from FPR4 who was found resting along a chain-link fence next to a road. Still, she

was relocated again three days later, having successfully moved to a pond on the other side of the fence.

Conclusions

Increased wetland area does not necessarily correspond to increased habitat availability for all freshwater turtles. We found the wetland area only to show some support with painted turtle abundance, possibly due to the diversity of wetland types evaluated, resulting in smaller wetlands with diverse cover and larger wetlands with sparse cover, negating impacts of size. Meanwhile, snapping turtle relative abundance improved in shallow wetlands with deeper substrate that had increased distance from roads. Shallow, mucky shoreline edges provide environmental conditions suitable for snapping turtles to ambush their prey. Promoting cumulative wetland structure by creating or restoring a diversity of wetland types, including managed infrastructure (e.g., sediment ponds, rain gardens, drainage ditches) with multiple surrounding land uses, may be amicable for human-wildlife interfaces. A diversity of wetland types also could help mitigate potential negative consequences due to climate change. In our study, site fidelity increased as the distance between wetlands increased, and this information could aid in identifying areas that could inevitably have turtle crossings and need increased road advisories and reduce mortality in more urbanized environments.

Appendix 1

Table 4 Measured predictors that were either constant (values reported, i.e., wetland area, wetland perimeter, minimum distance from roads or wetlands, percent sand within 30 m, and percent agriculture (Ag)) or variable (ranges reported, i.e., herbaceous wetland cover, canopy cover, substrate depth, substrate compaction, and wetland depth) for 29 wetland sites in Preston County, West Virginia, USA. Measurements were taken at each site per trapping session in 2019 ($n=20$ sites visited three times) and 2020 ($n=9$ sites visited twice)

Site	Vegetation cover	Canopy cover	Substrate depth	Substrate compaction	Wetland depth	Wetland area	Wetland perimeter	Road distance	Percent sand	Ag within 250 m	Ag within 500 m	Ag within 1 km
Adams	2.5	0	66.2–73.0	8.5–11.8	45.2–54.7	0.07	99.9	11.9	24.5	73.7	70.3	54.7
Anderson	2.5–8.8	19.9–75.85	5.4–15.9	3.2–5.9	8.9–57.8	0.21	601.2	127.9	32.6	7.8	19.3	37.4
Born1	2.5	6.46–20.75	9.3–21.2	6.2–9.5	40.0–54.0	0.13	186.8	10.4	19.6	68.4	63.4	41.8
Born2	2.9–39.8	6.82–35.9	5.6–14.0	6.2–11.6	38.7–46.0	0.04	85.4	235.1	29.4	68.5	47.8	43.8
Born3	2.5–5.2	47.49–76.94	9.3–14.1	6.2–12.1	36.3–45.6	0.05	90.9	35.9	20.4	32.0	49.6	44.6
Born4	27.2–47.1	88.75	27.2–47.1	5.1–8.0	24.5–52.2	0.06	112.3	45.9	20.4	28.3	43.1	44.3
Cedar Mdw	2.5	0	65.8–71.4	9.2–12.2	39.9–49.0	0.08	121.7	6.3	18.2	29.7	22.9	19.7
Farm1	4.5–14.1	12.40–67.87	25.5–47.1	8.6–12.0	14.7–41.3	0.30	268.6	69.8	16.9	70.5	38.7	63.6
Farm2	3.3–5.7	43.50–89.61	17.4–29.0	9.0–11.1	25.8–49.8	0.55	351.3	88.6	15.9	70.7	69.9	53.9
Farm3	4.7–21.5	14.02–23.34	11.7–39.9	7.1–9.1	29.6–41.0	0.25	197.2	0	22.4	71.5	54.9	50.8
Farm4	6.5–29.0	34.1–44.6	19.7–48.6	6.2–9.0	35.4–39.6	0.12	297.7	68.8	17.3	64.1	53.5	51.1
FPR2	2.5–10.3	25.6–77.8	12.1–41.5	3.5–8.3	46.2–69.0	1.71	1263.4	0	9.1	6.9	11.1	22.2
FPR3	2.5–15.6	0.5–100.0	7.9–31.5	5.8–9.5	33.5–42.2	0.33	441.8	12.9	9.1	12.0	12.3	22.6
FPR4	6.5–10.5	9.9–22.1	16.5–50.9	3.3–8.3	33.3–64.8	1.21	636.4	109.6	9.1	2.4	6.5	18.9
FPR7	2.5	68.8–88.2	9.0–30.0	4.2–7.5	31.1–61.8	0.56	529.6	418.9	9.1	1.9	1.3	10.7
FPR8	2.5–33.4	41.0–61.4	11.6–48.6	3.9–7.8	34.0–49.5	0.77	931.5	252.4	16.4	1.7	8.2	9.0
Hicks1	15.0–29.2	0	71.6–74.2	11.6–11.8	41.8–43.6	0.17	161.9	364.9	24.5	60.2	49.2	44.3
Hicks2	14.4–48.3	10.5–16.0	73.3–80.9	7.1–8.9	40.9–46.7	0.15	193.7	227.5	23.9	46.6	40.4	43.5
Hodges	3.3–4.5	0.0–2.7	18.4–32.7	6.9–8.2	48.5–144.0	0.03	70.5	58.8	22.7	16.3	22.9	16.9
Jesse	2.5–4.8	0.0–13.0	35.9–62.9	6.6–8.2	23.5–36.3	0.45	285.5	17.6	20.9	59.2	44.3	42.1
Keener1	2.5–10.7	0.0–5	3.9–19.7	6.1–9.4	28.7–38.0	0.62	184.9	50.1	26.3	79.6	43.1	46.1
Keener2	2.5–7.7	0	6.7–23.1	6.3–8.4	42.5–45.6	0.34	227.7	0.2	23.9	78.9	72.8	47.4
Ruby Pond	19.3–27.3	0	14.4–38.6	6.3–9.5	33.0–42.9	0.91	459.5	34.7	31.1	68.1	63.4	61.5
Turnley	9.3–31.9	41.1–57.7	73.5–74.2	7.9–10.5	29.7–34.9	0.22	213.8	48.9	23.1	78.5	75.3	60.5
Vernon1	8.1–13.2	2.7–6.9	49.5–52.6	9.5–10.5	30.4–39.2	0.13	136.9	74.9	21.7	64.5	36.4	24.4
Vernon2	17.2–24.7	0	60.1–61.2	7.6–9.2	58.0–82.8	0.07	105.1	55.9	20.3	52.4	34.9	26.4
Vernon3	2.5	6.6–9.4	46.2–85.3	10.8–11.3	49.0–60.2	0.08	109.8	142.5	33.3	21.9	29.9	31.7
Vernon4	2.5–5.6	23.9–48.0	84.9–88.0	6.5–7.5	44.1–54.1	0.14	158.9	272.7	34.7	15.0	27.5	32.1
Wolfe	2.5	0.0–10.4	21.6–27.5	9.2–10.2	31.6–52.5	0.19	178.6	32.6	18.2	27.8	16.1	33.6

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Data Availability Data are available by request to the corresponding author.

Declarations

Ethics Approval All animal experiments were approved by the West Virginia University Institutional Animal Care and Use Committee, reference number 1807015968.

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