

Community structure and differential responses of aquatic turtles to agriculturally induced habitat fragmentation

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Abstract Several studies have shown that wetland loss and habitat fragmentation can alter diversity and abundance of herpetofauna, but taxonomic attention has been skewed towards amphibians. We assessed responses of aquatic turtles to features at multiple spatial scales in an intensively farmed region of the Midwestern United States. Spatially hierarchical sampling was conducted from 2001 to 2003 in 35 randomly selected 23-km² cells throughout the upper Wabash River basin in Indiana. Hoop nets were used at wetlands to capture common snapping turtles (*Chelydra serpentina serpentina*) ($n=258$), midland painted turtles (*Chrysemys picta marginata*) (151), eastern spiny softshells (*Apalone spinifera spinifera*) (70), red-eared sliders (*Trachemys scripta elegans*) (59), northern map turtles (*Graptemys geographica*) (27), false map turtles (*Graptemys pseudogeographica pseudogeographica*) (6), Blanding's turtles (*Emydoidea blandingii*) (3), and stinkpot turtles (*Sternotherus odoratus*) (3). We examined the degree to which these aquatic species were nonrandomly distributed in 14 landscapes. Assemblages of turtles generally were random and the extent of nestedness was influenced by the

diversity of landcover, the proportion of grassland, and the total length of roads in each landscape. The occurrence and abundance of several species also were modeled to test hypotheses regarding the importance of site, patch, and landscape-level variables. Red-eared sliders appeared to be most sensitive to habitat fragmentation, whereas painted turtles, snapping turtles, map turtles, and spiny softshells were less affected. Factors at multiple spatial scales affect turtle distributions, suggesting differential responses to landscape fragmentation.

Keywords Abundance · Fragmentation · Northern map turtle · Nestedness · Occupancy · Midland painted turtle · Red-eared slider · Common snapping turtle · Eastern spiny softshell

Introduction

Wetlands have been destroyed at an alarming rate in the Midwestern United States, primarily due to agricultural activities (Dahl 1990). Indiana's wetlands have been reduced by 86% since the mid-1800s (Hartman 1994). In addition to habitat loss, remnant wetlands may further be degraded by fragmentation, pollution, sedimentation, introduced species, or altered hydrology (Johnson et al. 2002). Modeling of future land-use scenarios consistently predicted greater risk of extinction for herpetofauna dependent

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on wetlands compared with other taxa (White et al. 1997). Unfortunately, our understanding of the potential costs imposed by loss, fragmentation, and degradation of natural wetlands on native herpetofauna is decidedly uneven. For instance, the response of amphibians to fragmentation has been increasingly well-documented (Johnson et al. 2002; Knapp et al. 2003; Kolozsvary and Swihart 1999; Swihart et al. 2003; Weyrauch and Grubb 2004). In contrast, the response of turtles to fragmentation is poorly understood, even though many species reportedly are in decline (Lovich 1995). The life history of turtles, which includes delayed sexual maturity and low reproductive success, potentially could accentuate negative consequences of habitat alteration (Lovich 1995). Here we report results of a study designed to identify correlates of turtle abundance and occurrence at multiple spatial scales within an agricultural landscape of the Midwest.

The ability of aquatic turtles to disperse in a fragmented landscape is not well-studied, and thus, wetland connectivity requirements are unknown. Galat et al. (1998) found higher turtle species richness in connected wetlands but higher abundance in remnant wetlands, suggesting that birth rates are not affected by isolation but dispersal and colonization rates might be. Other factors related to fragmentation which could affect reptile assemblages include water quality, local characteristics such as hydroperiod, vegetation or available basking sites and characteristics of the surrounding landscape such as road density and forest cover (Bodie et al. 2000; DonnerWright et al. 1999; Findlay and Houlahan 1997; Russell et al. 2002). Importantly, terrestrial habitat may be just as critical as wetlands in maintaining viable populations, because many turtle species nest in uplands within 1 km of a wetland (Mitchell and Klemens 2000). Adult males also rely on terrestrial habitat when they move between wetlands and search for mates (Gibbons 1970; Rowe and Moll 1991).

The scale of analysis can have major implications for determining relationships between species distributions and habitat variables (Turner et al. 1989). The Upper Wabash Ecosystem Project is a large-scale ecosystem inventory focused in the upper basin of the Wabash River. Spatially hierarchical sampling was conducted from 2001–2003 to determine the response of vertebrates to fragmentation. Here, our goal is to

determine whether turtle species are nonrandomly distributed. Species distributions within fragmented habitat have been shown to exhibit nested patterns (Wright et al. 1998). In a nested system, species-poor sites support a proper subset of the species present at successively more species-rich sites and consequently presents a predictable order of species extinction. We also examined which local and landscape features have the greatest ability to predict turtle species occurrence and abundance. Ultimately, models that incorporate patch and landscape features can be used to predict species' responses to potential land-use change (i.e., Schumaker et al. 2004).

Methods

Study areas were located in the upper Wabash River basin in north-central Indiana (Fig. 1). The basin includes about 200 million hectares, or 21% of the state, and encompasses eight watersheds associated with the Wabash River, the longest free-flowing river in the United States east of the Mississippi River (Swihart and Slade 2004). Approximately 88% of the area is under agricultural use, primarily for corn and soybeans, approximately 8% is forested, and 2.5% is classified as wetland.

Vertebrate sampling was conducted in 35 randomly selected 23-km² (4.8 × 4.8 km) landscapes throughout the basin from May–August 2001–2003. Because sampling was conducted under two concurrent projects, the majority of landscapes occurred in the southwest region of the basin (Swihart and Slade 2004); however, the stratified selection algorithms for both projects were based on capturing the range of variation in landcover. Across the 35 landscapes, the proportion of wetland cover ranged from 0.43 to 9.07%. Wetland cover, and thus sampling availability, was higher in the east. Therefore, almost 2/3 of the landscapes occurred in the southwest, but only half of the sample wetlands occurred in this region. Sampling locations were randomly assigned to each landscape according to the relative proportion of each land cover class (see below). Two hundred twenty-eight sites at 159 wetlands each were sampled for 5 days for aquatic turtles with hoop nets using mark-recapture methods. Two hoop nets were placed in wetlands less than 0.08 ha. Wetlands between 0.08 and 0.28 ha had

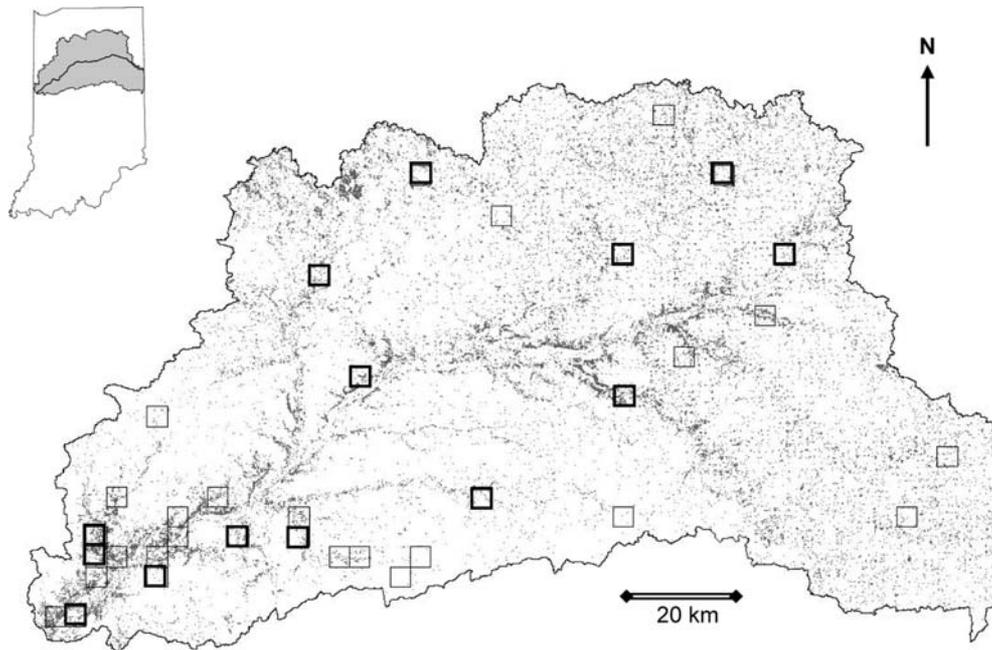


Fig. 1 Map of the upper Wabash River basin in Indiana, showing the distribution of wetlands and locations of 35 23-km² study landscapes. Landscapes outlined in bold indicate those used in the nestedness analysis

four nets, and at least eight nets were placed at wetlands greater than 0.28 ha. Hoop nets were baited with sardines and creamed corn. Upon capture, sex and carapace length were recorded. Adult turtles were marked with unique notches on the marginal scutes, whereas juvenile turtles and softshelled turtles were marked by claw clipping (Cagle 1939). All individuals were released at the site of capture.

Because we were interested in a landscape approach to predicting species distributions, we chose to maximize the number of wetlands sampled rather than examine numerous wetland characteristics such as water quality or food availability. We focused our effort on quantifying the density of emergent vegetation at each site. Vegetation provides an important food source and structural component of habitat, and may be indicative of areas suitable for nesting (Moll and Moll 2004; Sexton 1959). We measured the number of stems for woody species and percentage cover for herbaceous species. Due to the varied availability of vegetation at each wetland, three to five transects were positioned perpendicular to the shore. Within each transect, three 1-m² quadrats were sampled, spaced evenly to cover the vegetated area. Stem number and percentage herbaceous cover were

averaged across quadrats at each site for analysis (Table 1).

Landscape data

Nine landcover classes (forest, grassland, shrubland, wetland, urban, agriculture, treed corridor, herbaceous corridor, and road) for each 23-km² landscape plus a surrounding 1.6 km buffer were digitized with 1-m resolution using 1998 digital aerial ortho quads. The buffer allowed for accurate estimation of metrics for patches near the edge of a landscape. Wetland type and permanency were characterized for each patch from the National Wetland Inventory (Cowardin et al. 1979). We used Arcview 3.2 (ESRI, Redlands, CA) to measure the proportion of each landcover class within 100, 400, and 800 m buffers surrounding a target wetland. Additionally, heterogeneity in landcover types within each buffer was summarized using the Shannon Diversity Index

$$\text{Shan} = -\sum(p_i * \ln(p_i))$$

where p_i is the proportion of landcover class i . The total length of paved and gravel roads was measured

Table 1 Description of site, patch and landscape variables included in model development

<i>Site variables</i>	
LNSTEMS	Log transformation of # woody stems
HERB	Percent herbaceous cover
<i>Patch variables</i>	
WETLAND	Wetland type: Impoundment, Marsh, Lake, Stream
PERMANENCY	Temporary, Seasonal, Semi-permanent, Permanent
LNAREA	Log transformation of patch area (ha)
LNSHAPE	Log of patch shape
LNNPROX	Log of proximity index: normalized by area of 400 m search radius
LNAG100 (400, 800)	Log of proportion agriculture in a 100 (400, 800) m buffer
LNFOR100 (400, 800)	Log of proportion forest in a 100 (400, 800) m buffer
LNGR100 (400, 800)	Log of proportion grassland and shrubland in a 100 (400, 800) m buffer
LNURB100 (400, 800)	Log of proportion urban in a 100 (400, 800) m buffer
LNWET100 (400, 800)	Log of proportion wetland in a 100 (400, 800) m buffer
SDIV100 (400, 800)	Shannon diversity index for landcover in a 100 (400, 800) m buffer
<i>Wetland class/landscape variables</i>	
LNMNAREA	Log of mean patch area (ha)
LNMEDAREA	Log of median patch area (ha)
MNSHAPE	Mean patch shape
LNMNPROX	Log of the mean normalized proximity index
LNMEDPROX	Log of the median normalized proximity index
SHANDIV	Shannon diversity index
% GRASS	Total proportion of grassland and shrubland
% FOR	Total proportion of forest
ROADS	Total length of roads in the landscape (mi)

Site variables describe emergent vegetation at each wetland

for each landscape. We used Fragstats 3.0 (McGarigal et al. 2002) to calculate patch and landscape metrics. Patch metrics included area, shape and proximity for each wetland (Table 1). The shape index is a measure of the patch perimeter relative to the minimum perimeter of a maximally compact patch of the same area. The value of the index increases as a patch becomes more linear. The proximity index is the sum of surrounding patch areas divided by the squared edge-to-edge distance between the focal patch and all other patches within a specified search radius, 400 m in our case. We modified the proximity index by dividing the index for each patch by the area of the 400 m search buffer. This was to correct for the fact that larger patches contain more area within a given search radius than do smaller patches. The proximity index increases as surrounding patches become closer and larger. Landscape metrics included the mean and median of patch area, shape, and proximity, as well as the Shannon Diversity Index for the landscape. Logarithmic transformations were used as needed to reduce skewness. Any correlations between explanatory variables ($r > 0.7$) were eliminated by removing one of the paired variables from the dataset.

Statistical analysis

Nestedness

To test whether aquatic turtle species were nonrandomly distributed across wetlands within a landscape, incidence matrices were constructed for each landscape containing at least four occupied wetlands ($N=14$). Rows in an incidence matrix represent sites and columns represent species. Each matrix element contains a 1, indicating a species was present at that site, or a 0, indicating absence. The 14 matrices contained a range of 4–8 sites and 3–6 species. We computed nestedness of each landscape using the temperature metric T (Atmar and Patterson 1993). Temperature measures the relative order of species occurrence patterns, and varies from 0 to 100°. Cooler temperatures represent more nested systems. The temperature rises as the number of unexpected presences or absences increases. To assess statistical significance of T , the temperature calculator (Atmar and Patterson 1995) uses Monte Carlo simulations to calculate T for each of n randomized matrices, and compares the observed value of T to the distribution of temperatures generated by simulation. Thus it can be

determined, by calculating the left tail probability for the observed temperature, whether the observed distribution of species is likely to have been generated by a random process or whether the community appears structured. The simulations of Atmar and Patterson (1995) rely on the assumption that species are drawn from a uniform probability distribution (Wright et al. 1998), but this may overestimate significance as an artifact of passive sampling (Fischer and Lindenmayer 2002). We conducted simulations for each landscape under the hypothesis that species are drawn with probabilities proportional to their incidence. Temperatures from 500 randomizations were computed for each landscape in Matlab 7.0 (DeWoody et al., unpublished manuscript). Temperatures were converted to z -scores to enable analysis of nestedness across landscapes. Z -scores were calculated as

$$(T_O - T_M)/SD_M$$

where T_O is the temperature of the observed matrix. T_M and SD_M are the mean temperature and standard deviation from the 500 randomized matrices. Linear regression was used to test which landscape factors were associated with system nestedness. Because we could compute nestedness for only 14 landscapes, models were limited to 2–3 variables. The best model was selected with Akaike's Information Criterion (AIC) (Akaike 1973). Analysis was conducted in R 1.9.1.

Occupancy

To model occupancy of each species, we began by constructing logistic models of different spatial scales: site, patch with 100, 400, or 800 m buffers, landscape, and all combinations thereof. Site variables included number of woody stems and percent herbaceous cover. Patch variables included wetland type, permanency, area, shape, proximity, and landcover surrounding each patch in each of the three buffers. Landscape variables included mean and/or median area, shape, and proximity for all patches within the landscape, Shannon Diversity Index for landcover, the proportions of grassland and forest, and total length of roads. All road types were included and weighted equally. AIC with a bias-correction term (AIC_c) and AIC_c weights (w) were used for model selection (Burnham and Anderson 2002). Once the best model

was selected, the candidate set of variables was reduced further to those within the best 10 models in SAS 8.0 using Proc Logistic and the SCORE criterion.

Although logistic regression is commonly used to model species occupancy, it assumes that during sampling a species is detected at all sites it occupies (i.e., detectability = 1). Failure to detect a species during sampling can result in serious errors in subsequent logistic regression models (Gu and Swihart 2004). To address the issue of nondetection error, we subjected the reduced set of models to further analysis using program PRESENCE 2.05 (MacKenzie et al. 2003). This software implements estimation of site-occupancy rates (ψ) and species detectability (p) when $p < 1$ according to the model developed by MacKenzie et al. (2002). The model uses a likelihood approach to estimate the probabilities of detection and occupancy, based on encounter histories. Detectability may be a function of site variables or environmental conditions, which vary on each trapping occasion. We used daily high temperature and precipitation as sampling covariates. Models again were evaluated with AIC_c weights, and goodness-of-fit was tested by comparing the observed χ^2 -test statistic to that from 100 parametric bootstrap simulations. Model accuracy was assessed using receiver operating characteristic (ROC) curves. Area under the curve (AUC) provides a measure of accuracy where 0.5 indicates no difference between classification of true- and false-positives, and 1.0 indicates a perfect fit to the data (Fielding and Bell 1997). Generally, we considered $AUC > 0.7$ as acceptable.

Abundance

To model abundance of each species, we proceeded in a similar manner to the occupancy models, constructing Poisson regression models of different scale and selecting the best model with AIC_c weights. The candidate set of variables was reduced further in SAS using Proc Reg and the AIC criterion. The best 10 models were then fit using zero-inflated negative binomial (ZINB) models and AIC in SAS. The Poisson distribution is often used to model counts, however, we chose the negative binomial due to inflated variance. ZINB models control for additional variation in the data due to imperfect detectability by applying a mixture of a Bernoulli distribution and a negative binomial distribution to the response

(Lambert 1992; Long 1997; Welsh et al. 1996). The negative binomial distribution is applied to the positive count responses. The Bernoulli distribution is applied to the zero responses to model the probability of absence (approximately $1 - \psi$). We tested those covariates that were shown to influence occupancy in the PRESENCE models. Model accuracy was assessed by determining the proportion of observed values occurring within 95% prediction intervals.

Multilevel models

When data are hierarchically structured, such as these wetlands nested within landscapes, performing site-level analyses may violate assumptions of independence and result in biased standard errors (Raudenbush and Bryk 2002). Hierarchical generalized linear models account for the multilevel structure by partitioning the appropriate degrees of freedom. They also may estimate random effects to determine whether landscapes have a unique effect on the site-level response beyond the explanatory variables. We used HLM 5.0 to evaluate the occupancy and abundance models with overdispersion for a hierarchical effect using logistic and Poisson regression, respectively. Note that these hierarchical models do not incorporate detection error.

Let η_{ij} be the response of a species at site i in landscape j with the appropriate link function (logit for logistic regression and log for Poisson regression). The level-1 model for site or patch is

$$\eta_{ij} = \beta_{0j} + \beta_{1j}X_{1ij} + \dots + \beta_{Qj}X_{Qij} + r_{ij},$$

where r_{ij} is the level-1 standard error. The level-2 model for landscape is

$$\beta_{0j} = \gamma_{00} + \gamma_{01}W_{1j} + \dots + \gamma_{0S}W_{Sj} + u_{0j},$$

$$u_{0j} \sim \text{Normal}(0, \tau_{00}),$$

where γ_{00} is the average response across landscapes, γ_{0S} is the level-2 slope coefficient for landscape-level variable W_S , and u_{0j} is the unique random effect of the landscape. The level-2 variance component τ_{00} is tested with a χ^2 statistic to determine its significance. If $\tau_{00} \neq 0$, we conclude that each landscape has a unique effect on the site-level response.

Results

Eight aquatic turtle species and 577 individuals were detected over the sampling period (Table 2). Common snapping turtles (*Chelydra serpentina serpentina*) were most abundant, occurring at almost half of the wetlands sampled. Midland painted turtles (*Chrysemys picta marginata*) were found at about a quarter of the wetlands. Northern map turtles (*Graptemys geographica*), red-eared sliders (*Trachemys scripta elegans*), and eastern spiny softshells (*Apalone spinifera spinifera*) occurred at less than 20% of the wetlands. Blanding's turtles (*Emydoidea blandingii*), false map turtles (*G. pseudogeographica pseudogeographica*), and stinkpot turtles (*Sternotherus odoratus*) were rarely detected.

Nestedness

Temperatures for the landscapes ranged from 1.31 to 36.46° (Table 3), however only one landscape was

Table 2 Total turtle detections at 228 wetland sites sampled May–August 2001–2003 in the upper Wabash River basin

Common name	Scientific name	N	Sex ratio			# Sites
			M	F	U	
Eastern spiny softshell	<i>Apalone spinifera spinifera</i>	70	34	12	24	39
Common snapping turtle	<i>Chelydra serpentina serpentina</i>	258	152	88	18	104
Midland painted turtle	<i>Chrysemys picta marginata</i>	151	49	96	6	66
Blanding's turtle	<i>Emydoidea blandingii</i>	3	2	0	1	3
Northern map turtle	<i>Graptemys geographica</i>	27	5	22	0	16
False map turtle	<i>Graptemys pseudogeographica pseudogeographica</i>	6	6	0	0	4
Stinkpot turtle	<i>Sternotherus odoratus</i>	3	2	1	0	3
Red-eared slider	<i>Trachemys scripta elegans</i>	59	26	30	3	21

N = total individuals of each species captured, M = number males, F = number females, U = sex unknown.

Table 3 Values of nestedness temperature (T) for 14 landscapes and their significance

Landscape	# Sites	# Species	T	p -Value	Avg T	SD	z -Score
Monticello	4	6	1.31	0.016	23.53	10.39	-2.14
Webster	6	3	3.79	0.906	1.48	1.76	1.31
Kokomo	5	3	6.59	0.785	4.14	3.11	0.79
Covington	7	4	14.08	0.513	13.84	7.10	0.03
Manchester	8	6	15.07	0.335	18.32	7.63	-0.43
Carbondale	7	3	15.25	0.934	7.23	5.32	1.51
Huntington	4	3	16.51	0.667	12.76	8.68	0.43
Dayton	4	3	17.34	0.711	11.68	10.20	0.56
Mississinewa	5	5	22.19	0.077	34.60	8.68	-1.43
Williamsport	4	4	30.23	0.761	21.09	12.91	0.71
Vine	4	3	32.06	0.983	14.29	8.35	2.13
Shadeland	5	3	32.67	0.907	18.13	11.01	1.32
Lockport	5	5	36.41	0.916	23.38	9.44	1.38
Rochester	7	4	36.46	0.999	12.82	7.47	3.16

Temperatures were transformed to z -scores for further analysis, based on the average temperature and standard deviation of 500 randomized matrices

considered significantly nested. Nestedness z -scores were influenced by landcover diversity, proportion of grassland, and roads ($F_{3,13} = 4.33$, $p = 0.0337$, $R^2 = 0.56$). A negative relationship of z -scores with the Shannon diversity index ($\beta = -3.71$, $SE = 2.18$) indicated that as landcover diversity increased, the relative level of nestedness increased (T decreased). A positive relationship of z -scores with grassland ($\beta = 0.51$, $SE = 0.15$) indicated that as the proportion of grassland increased, relative levels of nestedness declined (T increased).

Occupancy

Due to low observed occupancy, models were not developed for Blanding's, false map, or stinkpot turtles. Most of the wetlands in which these species were found were in close proximity to other wetlands. Generally, Blanding's turtles were found in large lakes and marshes (0.5–156 ha) in the northern portion of the basin, corresponding to the southern boundary of their geographic range. False map turtles were found in very large lakes (> 70 ha) and a stream. Stinkpots occurred in lakes and impoundments greater than 7.9 ha, though one was captured in a very small (0.08 ha) impoundment. The ability to effectively establish statistical relationships for rare species is difficult, but the error becomes evident when occupancy falls below 5% (Cunningham and Lindenmayer 2005). Observed occupancy rates for the remaining

five species, for which models were developed, ranged from 7 to 45.6%.

Turtles differed in terms of the spatial scales at which models of occupancy received greatest support (Table 4). For spiny softshells, three models received nearly equal support: patch variables with an 800 m buffer ($w = 0.21$), patch variables (800 m buffer) and landscape variables ($w = 0.19$), and patch variables (400 m buffer) and landscape variables ($w = 0.17$). The best model for painted turtles included site and patch variables with an 800 m buffer ($w = 0.48$) and a 100 m buffer ($w = 0.38$). The best model for snapping turtles and red-eared sliders included site and landscape variables ($w = 0.77$ and 0.96, respectively). For map turtles the best model included patch variables with a 400 m buffer as well as landscape variables ($w = 0.62$). The landscape-only model received moderate support ($w = 0.17$). Where multiple models received support (painted, map, and spiny softshell turtles), all were tested in program PRESENCE.

PRESENCE results indicated that spiny softshell occupancy rates increased with patch area, the proportion of agriculture and urban within 800 m of a patch, and mean wetland proximity of the landscape (Table 5). Occupancy was negatively related to the proportion of grassland in the landscape. The overall estimated occupancy rate was 0.36 and AUC for the ROC plot was 0.83, indicating a good model. Painted turtle occupancy increased greatly in impoundments and marshes, with herbaceous vegetation, and with the proportion of agriculture and wetland within

Table 4 Model selection results for logistic models

Model	# Par	Spiny softshell		Painted turtle		Snapping turtle		Map turtle		Red-eared slider	
		ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i
S	2	11.55	0.00	35.61	0.00	4.90	0.07	35.33	0.00	12.02	0.00
P 100	15	9.95	0.00	13.32	0.00	25.72	0.00	18.67	0.00	18.32	0.00
P 400	15	2.22	0.07	18.24	0.00	14.04	0.00	21.56	0.00	22.91	0.00
P 800	15	0.00	0.21*	11.50	0.00	14.13	0.00	10.37	0.00	20.87	0.00
L	9	9.35	0.00	45.31	0.00	6.14	0.04	2.65	0.17*	14.25	0.00
S + P 100	17	7.04	0.01	0.47	0.38*	14.75	0.00	14.12	0.00	17.08	0.00
S + P 400	17	2.28	0.07	6.57	0.02	5.87	0.04	15.55	0.00	23.78	0.00
S + P 800	17	1.17	0.12	0.00	0.48*	5.18	0.06	8.68	0.01	20.12	0.00
S + L	11	5.75	0.01	39.63	0.00	0.00	0.77*	3.78	0.09	0.00	0.96*
P 100 + L	24	4.56	0.02	13.88	0.00	17.98	0.00	12.63	0.00	18.09	0.00
P 400 + L	24	0.50	0.17*	18.81	0.00	13.03	0.00	0.00	0.62*	25.09	0.00
P 800 + L	24	0.19	0.19*	19.20	0.00	16.85	0.00	15.75	0.00	17.61	0.00
S + P 100 + L	26	4.92	0.02	3.07	0.10	12.69	0.00	14.06	0.00	7.05	0.03
S + P 400 + L	26	2.66	0.06	8.42	0.01	7.12	0.02	3.67	0.10	16.10	0.00
S + P 800 + L	26	2.94	0.05	7.16	0.01	10.90	0.00	19.80	0.00	11.71	0.00

Asterisk indicates the models selected for further analysis with PRESENCE and HLM. S = Site variables; P 100, 400, 800 = Patch variables with 100, 400, or 800 m buffer; L = Landscape variables

800 m of a patch. Overall occupancy was estimated as 0.45 and AUC was 0.82. Snapping turtles responded positively at the landscape scale to mean shape, mean proximity, and proportion of grassland. They had a negative relationship with mean patch area. Estimated occupancy was 0.53 and AUC was 0.72, indicating a fair model. Map turtle occupancy showed a strong negative relationship to mean shape and proportion of grassland in the landscape, and a positive relationship to wetland patch area. Estimated occupancy was 0.13 and AUC was 0.94, indicating an excellent model. Finally, red-eared slider occupancy increased slightly with mean proximity and length of roads in the landscape, but showed a negative relationship with median area and the Shannon Diversity Index. Overall occupancy was estimated as 0.12 and AUC was 0.73. Chi-square tests showed that all models adequately fit the data (Table 5).

Landscape random effects in HLM were not significant for spiny softshells, map turtles, or painted turtles. Hierarchical binomial models were necessary for snapping turtles ($\tau_{00} = 0.53$, $\chi^2_{26} = 45.12$, $p=0.01$) and for red-eared sliders ($\tau_{00} = 4.48$, $\chi^2_{26} = 159.43$, $p < 0.001$). HLM parameter estimates and standard errors remained similar to those of the PRESENCE models. Validation of the models with ROC plots indicated that the models from PRESENCE were stronger in their predictive ability; AUC decreased from 0.72 to 0.70 for snapping turtles and from 0.73 to 0.58 for red-eared sliders.

Abundance

The most appropriate scales for modeling abundance also differed among turtle species (Table 6). For spiny softshells, the best model included site and patch variables with an 800 m buffer ($w = 0.45$), although adding landscape variables to this model also received support ($w = 0.33$). Both models were tested with ZINB in this case. The best model for painted turtles and red-eared sliders was the full model including site, patch with a 100 m buffer, and landscape variables ($w = 0.89$ and 0.98 , respectively). We selected the full model for snapping turtles also, but with an 800 m buffer at the patch level ($w = 0.99$). The best model for map turtles included patch variables with an 800 m buffer ($w = 0.90$).

ZINB results indicated that abundance of spiny softshells increased with the number of woody stems at the site level and mean wetland proximity in the landscape (Table 7). Abundance was negatively related to mean area of wetlands in the landscape. Accuracy was moderate; prediction intervals (95%) contained 88.5% of the observations. Painted turtle abundance increased in permanent wetlands and with increasing diversity within 100 m. A negative relationship existed with temporary wetlands, the proportion of agriculture within 100 m and the landscape Shannon Diversity Index. Accuracy was moderate with prediction intervals containing 83.5% of the observations. Snapping turtle abundance increased in

Table 5 Coefficient estimates, model fit, and ROC validation results for final PRESENCE models

Covariate	Spiny softshell		Painted turtle		Snapping turtle		Map turtle		Red-eared slider	
	β	SE	β	SE	β	SE	β	SE	β	SE
<i>p</i>										
Intercept	-5.46	0.59	-1.52	0.17	-0.83	0.11	-8.46	0.91	-5.85	1.98
TEMP	0.04	0.01					0.08	0.01	0.06	0.02
PRECIP	0.94	0.46								
<i>ψ</i>										
Intercept	6.36	2.59	-0.16	2.01	-4.48	1.25	13.22	5.05	-3.62	2.16
HERB			3.30	1.55						
WETLAND-IMPOUND			3.27	1.25						
WETLAND-MARSH			2.05	1.16						
WETLAND-STREAM			-2.78	1.35						
LNAREA	0.66	0.23					0.81	0.33		
LNSHAPE			0.41	0.61						
LNAG800	1.91	0.98	1.69	0.85						
LNURB800	0.82	0.43								
LNWET800			0.37	0.22						
LNMNAREA					-0.68	0.2				
LNMEDAREA									-0.90	0.35
MNSHAPE					1.20	0.43	-6.88	2.29		
LNMMNPROX	0.41	0.20			0.14	0.08			0.50	0.17
SHANDIV									-1.98	1.34
%GRASS	-0.41	0.18			0.23	0.07	-8.46	0.91		
ROADS									0.06	0.03
Model fit	χ^2 (<i>p</i> -value)	87.13 (1.00)	36.2 (1.00)		137.69 (0.9)		45.16 (0.42)		51.79 (0.66)	
Validation	AUC	0.833	0.816		0.722		0.937		0.731	
Estimated	occupancy rate	0.36	0.45		0.53		0.13		0.12	

p = Detectability, *ψ* = occupancy

impoundments and marshes. A slightly negative response occurred with the proportion of wetlands within 800 m and length of roads in the landscape. Accuracy was poor, with prediction intervals containing 68.4% of the observations. Map turtle abundance increased with patch area and decreased with patch shape and the proportion of urban within 800 m. Accuracy was poor; prediction intervals contained 67.1% of the observations. Finally, red-eared slider abundance was related to patch shape, the proportions of agriculture, urban, and wetland within 100 m, and median patch area. There was a negative relationship with the diversity index for landcover within 100 m and mean proximity. Accuracy was adequate, with prediction intervals containing 92.5% of the observations.

Hierarchical Poisson models were necessary for snapping turtles ($\tau_{00} = 0.49$, $\chi^2_{33} = 90.66$, $p < 0.001$), map turtles ($\tau_{00} = 2.59$, $\chi^2_{34} = 95.73$, $p < 0.001$) and red-eared sliders ($\tau_{00} = 3.14$, $\chi^2_{32} = 509.53$,

$p < 0.001$). Parameter estimates and standard errors remained similar to those of the ZINB models. Validation of the models by classification within the prediction intervals indicated that the hierarchical models were stronger than the ZINB models. Prediction intervals contained 92% of the observed snapping turtle counts, and 100% of map turtle and red-eared slider counts.

Discussion

Turtle species in the upper Wabash River basin showed a wide range of responses to habitat and landscape variables at multiple spatial scales. Of the species for which we were able to develop models, red-eared slider occupancy and abundance appeared to be negatively affected by habitat fragmentation, whereas painted turtles, snapping turtles, map turtles and spiny softshells were less affected by the dominance of

Table 6 Model selection results for Poisson models

Model	# Par	Spiny softshell		Painted turtle		Snapping turtle		Map turtle		Red-eared slider	
		ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i
S	2	66.97	0.00	104.45	0.00	113.10	0.00	14.58	0.00	151.49	0.00
P 100	15	22.08	0.00	31.62	0.00	115.94	0.00	7.44	0.02	47.68	0.00
P 400	15	25.50	0.00	36.79	0.00	97.10	0.00	9.82	0.01	104.78	0.00
P 800	15	2.42	0.13	38.18	0.00	105.56	0.00	0.00	0.90*	77.10	0.00
L	9	50.75	0.00	113.06	0.00	117.34	0.00	5.35	0.06	95.95	0.00
S + P 100	17	17.59	0.00	8.69	0.01	56.70	0.00	19.06	0.00	45.47	0.00
S + P 400	17	19.16	0.00	8.72	0.01	37.43	0.00	21.87	0.00	102.19	0.00
S + P 800	17	0.00	0.45*	15.03	0.00	41.19	0.00	11.36	0.00	68.15	0.00
S + L	11	40.31	0.00	95.04	0.00	46.24	0.00	16.81	0.00	87.47	0.00
P 100 + L	24	12.22	0.00	14.19	0.00	74.61	0.00	23.93	0.00	9.83	0.01
P 400 + L	24	14.99	0.00	28.17	0.00	76.83	0.00	24.63	0.00	67.09	0.00
P 800 + L	24	3.98	0.06	24.32	0.00	68.10	0.00	14.37	0.00	14.82	0.00
S + P 100 + L	26	7.69	0.01	0.00	0.89*	12.62	0.00	35.84	0.00	0.00	0.98*
S + P 400 + L	26	7.81	0.01	10.48	0.00	10.96	0.00	36.73	0.00	61.55	0.00
S + P 800 + L	26	0.61	0.33*	4.93	0.08	0.00	0.99*	24.58	0.00	8.99	0.01

* The models selected for further analysis with ZINB and HLM

S = Site variables; P 100, 400, 800 = Patch variables with 100, 400, or 800 m buffer; L = Landscape variables

agriculture. We do not have historical data for this region, and thus, do not know if any populations are declining. However, given that agricultural conversion occurred over the past 150 years, isolated populations appear to have been maintained. The relative rarity of Blanding's turtles, false map turtles, and stinkpots in our samples may have been a result of the bait we used, as their preferred foods include aquatic insects, mollusks, and crustaceans. Their rarity also is a likely consequence of this region being at the edge of their geographic range (Conant and Collins 1998; Swihart et al. 2006).

Seasonality of turtle movements could cause sex-biased capture rates. As females move upland to nest, we would expect to capture more males. This potentially could result in an inaccurate assessment of the factors affecting turtle habitat since we did not sample nesting areas. Differences in movement between the sexes, however, are not consistent among different species. Bodie and Semlitsch (2000) reported that female false map turtles and red-eared sliders used more upland habitat than males and moved farther from the wetland during increasing temperature and decreasing water levels of the summer. Female painted turtles, however, were less likely than males to leave the wetland; males are generally thought to have greater vagility (Rowe 2003). We did not consistently capture more of one sex (Table 2) and therefore, did not perform any analysis on the capture rates. Of the

five species modeled, we captured more female painted turtles and more male snapping turtles and spiny softshells. By examining landscape correlates at multiple scales, we believe our analyses have effectively accounted for habitat used in sex-biased movement.

Painted turtles avoid deep water and strong currents (Anderson et al. 2002; Minton 2001); our results are consistent with this, as evidenced by their occurrence in impoundments and marshes. Herbaceous vegetation is positively correlated with occupancy, but this variable was not included in the final abundance model. Marchand and Litvaitis (2004) observed a negative relationship of abundance and vegetation and suggested movement may be restricted by dense vegetation. The elevated abundances we observed in some wetland remnants also may have resulted from low emigration rates. Painted turtles are abundant in wetlands immediately surrounded by a diversity of land-uses, but they are negatively affected by land-use diversity at the landscape scale. Land-use diversity will likely increase as agricultural lands are developed into residential areas. Because of the longevity of turtles, it may be some time before we can detect any change. However, a Kentucky population of painted turtles apparently has persisted over 30 years while being separated from its nearest neighboring population by 15 km (Lindeman and Scott 2001).

Table 7 Coefficient estimates and validation results for final ZINB models

Covariate	Spiny softshell		Painted turtle		Snapping turtle		Map turtle		Red-eared slider	
	β	SE	β	SE	β	SE	β	SE	β	SE
$1 - \psi$										
Intercept	-2.54	2.15	0.19	1.44	4.92	1.96	-5.89	3.17	12.40	3.99
HERB			-2.87	1.29						
WETLAND-IMPOUND			-2.65	0.89						
WETLAND-MARSH			-1.76	0.92						
WETLAND-STREAM			2.04	1.10						
LNAREA	-1.26	0.51								
LNAG800			-1.24	0.65						
LNWET800			-0.33	0.18						
LNMNAREA					0.49	0.25				
LNMEDAREA									2.52	0.79
MNSHAPE					-1.67	0.77				
LNMNPROX									-1.31	0.37
%GRASS	0.42	0.23			-0.25	0.10	0.60	0.31		
ROADS									-0.17	0.07
λ										
Intercept	-0.90	0.29	0.71	0.72	0.05	0.61	-8.59	1.55	14.41	3.57
LNSTEMS	0.30	0.10								
WETLAND-IMPOUND					0.85	0.49				
WETLAND-MARSH					0.49	0.53				
WETLAND-STREAM					-0.17	0.52				
PERMANENCY-PERMAN			0.55	0.46						
PERMANENCY-SEASON			0.15	0.50						
PERMANENCY-TEMP			-0.97	0.64						
LNAREA							0.90	0.16		
LNSHAPE							-0.34	0.45	0.69	0.23
LNAG100			-0.09	0.05					0.44	0.12
LNURB100									0.63	0.17
LNWET100									0.76	0.19
SDIV100			0.86	0.35					-5.74	1.55
LNURB800							-1.20	0.22		
LNWET800					-0.11	0.05				
LNMNAREA	-0.84	0.19								
LNMEDAREA									0.84	0.43
LNMNPROX	0.42	0.11							-0.59	0.23
SHANDIV			-1.15	0.51						
ROADS					-0.02	0.01				
% in 95% Prediction interval	88.5		83.5		68.4		67.1		92.5	

$1 - \psi$ = zero inflation, λ = abundance

Snapping turtles are considered wide-ranging and adaptable, with a preference for muddy shallows (Minton 2001). We observed higher occupancy rates in landscapes with smaller wetlands, and the highest abundance in impoundments. Large constructed wetlands in this region may not provide the microhabitat features (i.e., muddy shallows and stagnant water) that snapping turtles require. Snapping turtles have large home ranges and can migrate several kilometers, especially during nesting season, which may result in high road mortality (Haxton 2000; Pettit et al. 1995)

and male-biased sex ratios (Gibbs and Steen 2005; Steen and Gibbs 2004). Consistent with these observations, our models suggest that snapping turtles benefit from greater wetland connectivity and are adversely affected by high road density. Low colonization ability was suggested to explain a temporal decrease in abundance of snapping turtles in Alabama ponds (Stone et al. 1993). Snapping turtles were the most abundant species in this study; however, local populations may suffer in isolated wetlands where migration is impeded by roads. Just as we suggest

painted turtles may respond to future development and increasing diversity of land-use, snapping turtles may also be affected by urban growth, due to an increasing density of roads and intensification of traffic patterns.

Spiny softshells are considered common throughout their range but are decreasing in some localities (Anderson et al. 2002). They are intolerant of isolated and ephemeral wetlands, preferring rivers and streams and larger wetlands in open areas without aquatic vegetation (Minton 2001). We also observed this habitat association, although the correlation of abundance with woody stems and smaller wetlands on average suggests the species is capable of adapting to less suitable habitat. Galois et al. (2002) attributed long movements of spiny softshells to habitat fragmentation; the species is capable of high mobility in search of suitable habitat. A positive correlation of occupancy with proximity, agriculture and urban areas suggests that spiny softshells are able to persist in altered landscapes, given a shorter distance to adjacent wetlands. Indeed, softshell turtles may have benefited from forest clearing. Females tend to nest in full sunlight in early summer, before crops have attained significant height. Thus, agricultural lands offer the open upland habitat this species prefers.

Red-eared sliders have a limited distribution in Indiana but can be locally common (Anderson et al. 2002; Minton 2001). Such observations of local abundance are supported by our models. Occupancy was most strongly determined by the diversity of land use at the landscape scale, limiting the presence of sliders to landscapes with low diversity. Local abundance was most negatively affected by land-use diversity within a 100 m neighborhood surrounding the wetland. Sliders in the upper Wabash River basin preferred smaller wetlands with high connectivity. Once present in such a wetland, populations appear to be inhibited only by land use in the upland immediately surrounding the patch.

Map turtles are considered common and able to adapt to habitat alteration, preferring rivers and lakes (Minton 2001). Map turtle occupancy rates and abundance increased in large wetlands, and in wetlands compact in shape, suggesting that lakes were highly preferred in this region. Occupancy also was strongly negatively related to the proportion of grassland-shrubland in the landscape. This metric was highly negatively correlated with the proportion

of agriculture in the landscape, and therefore, occupancy rates increased in highly agricultural landscapes. Abundance estimates, however, decreased in association with surrounding urban areas, suggesting a limit to the adaptability of the species.

The predictive ability of abundance models was less than acceptable for painted turtles and poor for map and snapping turtles, suggesting that one or more important variables were excluded. Unmeasured habitat variables, such as water depth, substrate, submerged vegetation and woody debris, may provide more explanatory power than patch and landscape metrics (Fleishman et al. 2002; Moll and Moll 2004). The availability of logs as basking sites has been deemed important to map and painted turtles, and as cover sites for snapping turtles (DonnerWright et al. 1999; Pluto and Bellis 1988). Incorporating chemical properties of the wetlands also might improve the models. The hierarchical models for map and snapping turtles suggest, however, that there is some unexplained landscape effect that correlates with observed abundance. These species may be responding at an even greater scale than what we measured, or to some unknown factor altogether. Direct anthropogenic effects might be considered: the snapping turtle is a game species in Indiana, and map and painted turtles are widely collected for the pet trade. The predictive ability of the remaining models was reasonable to good, and should prove useful in modeling the response of these species to alternative future land-use scenarios (Schumaker et al. 2004).

After controlling for passive sampling, nestedness may be caused by area, isolation, or habitat heterogeneity (Wright et al. 1998). Habitat heterogeneity is related to area in the sense that larger patches often contain a wider range of habitats, and theoretically should contain greater species richness due to the presence of both generalist and specialist species. We suggest that habitat heterogeneity may have contributed to the lack of nestedness in the turtle assemblage. Snapping turtles, red-eared sliders, and spiny softshells are considered generalists with an ability to thrive in altered environments (Moll and Moll 2000). Nonetheless, we demonstrated clear correlates of occupancy and abundance for these turtles. Because we considered an array of wetland types together, we would not expect to see all species represented in any one wetland, or a predictable ordering within landscapes. In

contrast, we would have expected a more nested pattern had we only looked at species occurring in marshes. Similarly, at least 17 turtle species occupy portions of the Mississippi River, but on average only 7 co-occur in specific habitats (Moll and Moll 2004).

Although the turtle assemblage was not significantly nested in most of the landscapes, the variation in nestedness among landscapes showed predictable relationships to land use and grassland cover. Nestedness z -scores significantly increased in landscapes with higher grassland cover. Grassland was positively correlated with wetland cover, and negatively correlated with agriculture. Thus, the loss of wetlands, or the loss of natural cover in general increased nestedness.

Idiosyncratic species are those which elevate the temperature of the matrix, implying that those species do not conform to a nested pattern of occupancy (Atmar and Patterson 1993). All eight species were idiosyncratic at least once, with spiny softshells, painted and snapping turtles most often (in seven, five and four landscapes, respectively). In these landscapes, these species may have been one of one or two species occupying a species-poor site, but did not occur at the more species-rich sites, as a nested pattern would predict. These generalist species have been shown to thrive in altered environments where specialist species have been extirpated (Moll and Moll 2004). Although there is no evidence of competitive exclusion among these turtle species, Dreslik and Phillips (2005) found species richness was poor where red-eared sliders were most abundant.

Swihart et al. (2006) found niche breadth and proximity to range boundary to be important predictors of tolerance to fragmentation. In our study, red-eared sliders and map turtles showed restricted occupancy patterns. Sliders are capable of relying on a broad array of food and habitat, but the upper Wabash River basin represents the northeast edge of their range. Naturally low abundance, relative to the core of their range, may magnify their response to fragmentation. Map turtles have the lowest niche breadth, and though they have a somewhat disjoint distribution, Indiana is also near the edge of their range. We only observed this species at 7% of sampled wetlands. Map turtles feed on mollusks and aquatic insects, and thus require clear, unpolluted water (Moll and Moll 2004). Map turtle abundance in an urban canal was attributed to the presence of

several species of freshwater snails (Conner et al. 2005). If the lakes in this region become unsuitable in the future, fragmentation may have a more detrimental effect on map turtles.

Widespread habitat alteration in the Midwest began in the 1800s, suggesting that species that remain today are tolerant of human activity (Swihart et al. 2003). The longevity of turtles, however, indicates that there likely is a lag in the response to alteration and wetland fragmentation. Additionally, while some species appear to have benefited from or adapted to an agricultural landscape, urban expansion implies further alterations to wetlands, with possible negative repercussions for some species (e.g. map turtles). Current policy in many states dictates the protection of wetland buffer zones, which have been criticized as being far too narrow to protect water quality (Houlahan and Findlay 2004) or to encompass terrestrial requirements of wetland species (Mitchell and Klemens 2000; Semlitsch 1998). Our combination of hierarchical models and models for low detection rates also demonstrate that aquatic turtles respond to factors at a variety of scales. Considering all species together, occupancy and abundance was related to vegetation at the site level, patch attributes and land use within 100 and 800 m, and attributes of the broader landscape. To maintain this turtle assemblage, it will be critical to consider effects of factors operating at multiple scales.

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