

Wetland hydrology, area, and isolation influence occupancy and spatial turnover of the painted turtle, *Chrysemys picta*

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Abstract Habitat area and isolation have been useful predictors of species occupancy and turnover in highly fragmented systems. However, habitat quality also can influence occupancy dynamics, especially in patchy systems where habitat selection can be as important as stochastic demographic processes. We studied the spatial population dynamics of *Chrysemys picta* (painted turtle) in a network of 90 wetlands in Illinois, USA from 2007 to 2009. We first evaluated the relative influence of metapopulation factors (area, isolation) and habitat quality of focal patches on occupancy and turnover. Next, we tested the effect of habitat quality of source patches on occupancy and turnover at focal patches. Turnover was common with colonizations ($n = 16$) outnumbering extinctions ($n = 10$) between

the first 2 years, and extinctions ($n = 16$) outnumbering colonizations ($n = 3$) between the second 2 years. Both metapopulation and habitat quality factors influenced *C. picta* occupancy dynamics. Colonization probability was related positively to spatial connectivity, wetland area, and habitat quality (wetland inundation, emergent vegetation cover). Extinction probability was related negatively to wetland area and emergent vegetation cover. Habitat quality of source patches strongly influenced initial occupancy but not turnover patterns. Because habitat quality for freshwater turtles is related to wetland hydrology, a change from drought to wet conditions during our study likely influenced distributional shifts. Thus, effects of habitat quality of source and focal patches on occupancy can vary in space and time. Both metapopulation and habitat quality factors may be needed to understand occupancy dynamics, even for species exhibiting patchy population structures.

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Introduction

Metapopulation theory has been instrumental in guiding research on population dynamics in systems with spatial structure (Hanski and Gaggiotti 2004).

Whereas early metapopulation models ignored effects of patch attributes and isolation on species occupancy dynamics (Levins 1969), spatially-realistic models focus explicitly on the geometry of suitable habitat patches in the landscape. For example, the widely used incidence-function model (IFM) predicts that patch extinction probability is related negatively to patch area, and patch colonization probability is related negatively to patch isolation (Hanski 1994). Although these predictions have become central ideas in the conservation of species in fragmented landscapes (e.g., McCullough 1996), recent analyses indicate that empirical support for the area-isolation paradigm is not widespread (Baguette 2004; Pellet et al. 2007; Prugh et al. 2008).

Habitat quality factors can influence species occupancy and turnover dynamics in systems in which area and isolation are poor predictors (e.g., Fleishman et al. 2002; Franken and Hik 2004). Whereas metapopulation theory emphasizes the threat of stochastic extinction in small patches (i.e., patches with small population sizes), habitat quality can affect extinction probability deterministically by directly influencing individual survival, fecundity, and growth (Thomas 1994). Local habitat quality can also influence patch colonization probability if dispersers actively assess quality during the transfer and settlement stages of dispersal (Lima and Zollner 1996; Bêlisle 2005). Although the metapopulation and habitat views have generally been perceived as alternative hypotheses on factors driving occupancy dynamics (Thomas and Hanski 2004), an integrated approach is commonly supported in patchy systems (Hokit et al. 1999; Thomas et al. 2001; Armstrong 2005; Jaquière et al. 2008; Schooley and Branch 2009).

Although it has become more customary to assess how habitat quality of focal patches influences occupancy and turnover in metapopulation models, fewer studies consider how the quality of surrounding patches (i.e., source patches) affects dynamics (but see Jaquière et al. 2008; Schooley and Branch 2009). If high-quality patches produce more emigrants than low-quality patches, sites within dispersal distance of high-quality sources may have greater occupancy and colonization probabilities than those near low-quality sources. The likelihood of rescue effects (Brown and Kodric-Brown 1977) may also depend on spatial proximity to high-quality sites (Schooley and Branch

2007). Connectivity (i.e., the inverse of isolation) metrics based on the IFM typically account for distances to and areas of potential source patches, but for systems in which area is a poor predictor of number of emigrants, incorporating an index of source quality may be more effective for predicting incidence patterns.

First, we used 3 years of occupancy and turnover data to examine how metapopulation (i.e., area and isolation) and habitat quality factors influence spatial population dynamics in the freshwater turtle *Chrysemys picta* in northern Illinois. *Chrysemys picta* likely exhibits a patchy population structure (*sensu* Harrison 1991; see Bowne et al. 2006) in which extinction and colonization dynamics may be more related to habitat selection than stochastic demographic processes (Marsh 2001). Habitat quality for freshwater turtles is strongly tied to wetland hydrology. Individuals rely on permanent water sources to forage during drought, whereas temporary wetlands provide high-quality forage when inundated (Roe and Georges 2007; Roe et al. 2009). Thus, we predicted that habitat quality factors related to wetland hydrology (e.g., hydroperiod and inundation) would have a strong influence on occupancy dynamics. Next, we compared spatially implicit and explicit approaches to habitat quality by assessing support for two connectivity measures. The first measure was an area-based metric typical of the IFM. The second measure was similar except that it incorporated an index of habitat quality of source patches. We predicted that wetlands connected to high-quality sites would have greater occupancy and colonization probabilities, and lower extinction probabilities, than wetlands near low-quality sites. Since our study occurred during a transition period from drought to wet conditions, we emphasize the important effects of both spatial and temporal variation in habitat quality on occupancy and turnover dynamics.

Methods

Study species and site

Chrysemys picta (painted turtle, Emydidae) occurs in both shallow wetlands with aquatic vegetation and slow-moving lentic systems (Ernst et al. 1994). Individuals are active from March to October in northern Illinois, and nesting occurs from May to July

(Phillips et al. 1999). Hatchlings overwinter in upland nests and move to wetlands during the following spring. Males become sexually mature at 3–5 years, and females mature at 6–10 years (Ernst et al. 1994). *Chrysemys picta* is omnivorous and foraging is confined to aquatic habitat, although terrestrial aestivation may occur during drought (Bowne 2008). Among-wetland movements by juveniles and adults occur seasonally, especially in response to water level changes in early spring and late fall (Sexton 1959; McAuliffe 1978).

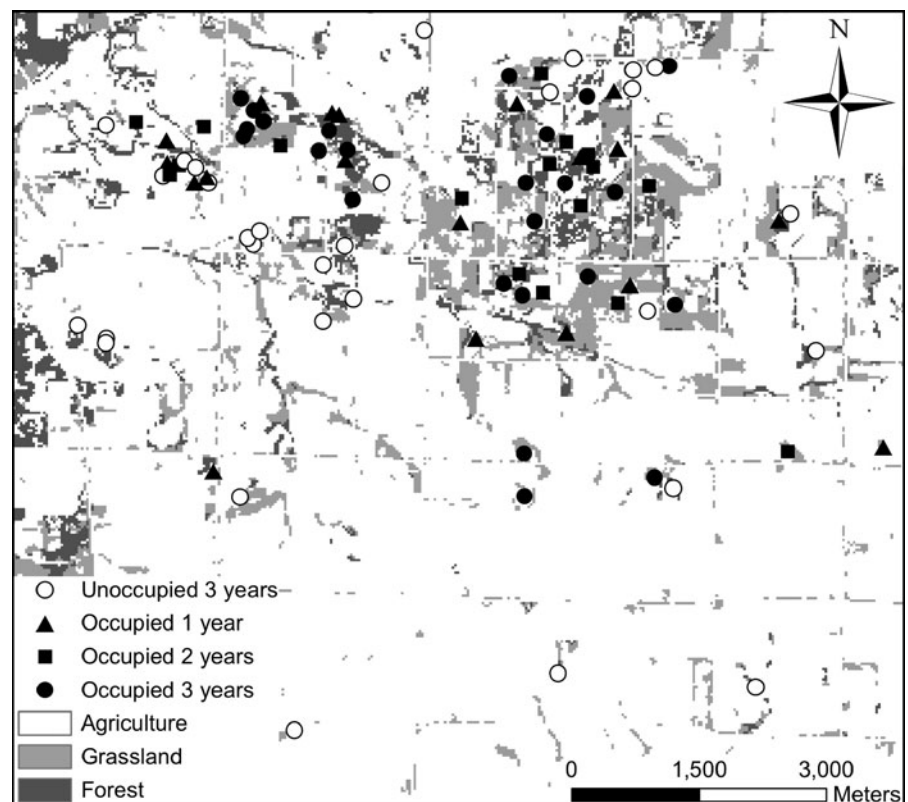
Our study was conducted at a 9268-ha area in northern Illinois centered at the Richardson Wildlife Foundation (RWF) property (West Brooklyn, IL; 41°42′26.6″ N, 89°11′25.0″ W). Although the landscape is dominated by row-crop agriculture (corn, soybean) and patches of prairie and forest, RWF is managed for sand prairie (Fig. 1). Suitable habitat for *C. picta* in this landscape consisted of freshwater wetlands with variable hydroperiods, which represented only 0.8% of the landscape. We documented the occupancy status of *C. picta* in 90 wetlands (average area = 1.03 ha; range = 0.01–5.29 ha) on

private land in and around RWF in 2007, 2008, and 2009. Nearest-neighbor distances between wetlands averaged 371 m (range = 36–2830 m). Wetlands were identified using 1:24000 National Wetland Inventory quadrangles and aerial photographs, and all agricultural drainage ditches and temporary pools (i.e., typically those pools that held water only after heavy rains for <30 days) were excluded from sampling. Wetland emergent vegetation was dominated by *Alisma subcordatum*, *Eleocharis* spp., *Phalaris arundinacea*, *Polygonum* spp., *Pontederia cordata*, *Sagittaria* spp., *Scirpus* spp., and *Typha* spp. Other turtles encountered during surveys included *Chelydra serpentina* and *Emydoidea blandingii*.

Wetland surveys and habitat quality

All wetlands were surveyed for up to four consecutive days between late May and early August in each year. Logistical constraints prevented sites from being sampled randomly. Instead, wetlands were grouped by spatial proximity, and we randomized the sequence of groups surveyed each year. We used hoop traps

Fig. 1 Naïve occupancy dynamics of *Chrysemys picta* among 90 wetlands surveyed for 3 years (2007–2009) in northern Illinois, USA. Turtles were absent from wetlands in all years (open circles), present in 1 year (closed triangles), present in 2 years (closed squares), or present in all 3 years (closed circles)



baited with sardines to detect *C. picta* presence at each wetland. Traps were set on the perimeter of each site within 10 m of the shoreline, and sampling effort was standardized by wetland area.

We collected data on habitat characteristics thought to influence wetland occupancy by *C. picta*. During each survey, we used an ordinal rank to record emergent vegetation cover and canopy cover in each wetland: 1 (<5%), 2 (5–25%), 3 (26–50%), 4 (51–75%), 5 (76–95%), 6 (>95%). Aquatic vegetation is an important food source for *C. picta* (Sexton 1959; McAuliffe 1978; Marchand and Litvaitis 2004), and we assumed that canopy cover is related positively to the abundance of floating limbs potentially used as basking sites. Yearly estimates of emergent vegetation and canopy cover were averaged due to minimal variation among years. As an index of water quality, water pH was recorded within 1 m of the shoreline in 2007 using a portable water quality meter (850081, Sper Scientific, Scottsdale, Arizona, USA). Finally, wetland quality for freshwater turtles can vary in space and time depending on hydroperiod and water levels. Permanent wetlands function as stable refuges, but ephemeral wetlands offer high-quality foraging opportunities when water is present (Roe and Georges 2007; Roe et al. 2009). To account for spatial and temporal variation in habitat quality related to hydrology, we used an ordinal rank ranging from one to four to record hydroperiod for each wetland (1 = most ephemeral, 4 = most permanent). Hydroperiod ranks were based on observations during repeated visits to each site over 3 years, and one overall rank was assigned to each wetland. Additionally, wetland inundation level was recorded during each survey using the same ordinal rank used for emergent vegetation and canopy cover.

For local predictor variables that exhibited multicollinearity (canopy cover, emergent vegetation cover, hydroperiod, and pH; $r > 0.4$), we used principal components analysis (PCA) in R 2.9.1 (R Development Core Team 2009) to ordinate the data (Supplementary material, Table 1). The first two axes explained 81% of the variation, and PCA scores for these axes were used in subsequent analyses. The first axis (L1) was positively correlated with emergent vegetation cover and negatively correlated with hydroperiod and pH. The second axis (L2) was negatively correlated with canopy cover and positively correlated with emergent vegetation cover.

Area and isolation metrics

Patch area was measured with ArcGIS 9.3 (ESRI, Redlands, California, USA) after digitizing wetlands using aerial photographs from 2007. We considered a measure of wetland area that incorporated potential nesting habitat within 300 m of each wetland, but a measure of basin area alone explained more variation in occupancy patterns (B.J. Cosentino, unpublished data). Thus, basin area was used in all analyses. Patch isolation was measured using PATHMATRIX in ArcView 3.2 (Ray 2005). To measure connectivity of each wetland, we used a patch connectivity metric typical of the IFM that includes a negative exponential dispersal kernel and accounts for the distances to and area of all potential source wetlands (Hanski 1994; Moilanen and Nieminen 2002). The connectivity (C_i) of wetland i was defined as

$$C_i = \sum_{j \neq i} \psi_j \exp(-\alpha d_{ij}) A_j^b$$

where ψ_j is the probability of occupancy of source wetland j , α is a parameter scaling the effect of distance on dispersal ($1/\alpha$ is the average dispersal distance), d_{ij} is the Euclidean distance between target wetland i and source wetland j , A is the area of source wetland j , and b is a parameter scaling the relationship between abundance and source area.

Prugh (2009) found that the effectiveness of C_i as a predictor of patch occupancy and colonization is sensitive to changes in α , but relatively insensitive to changes in b . We assessed the performance of three connectivity metrics to explain occupancy patterns when α was set to represent the mean ± 1 SD (1695 ± 871 m) of *C. picta* dispersal distances reported by Bowne (2008). A metric with α set as 0.0012 (average dispersal distance = 824 m) was a better predictor of occupancy patterns than the alternative metrics (B.J. Cosentino, unpublished data). We used this value in all subsequent analyses. Because emigration is unlikely to scale linearly with wetland area, we set b as 0.5 (Moilanen and Nieminen 2002).

Weighting of source patches: naïve occupancy

Connectivity was calculated separately for each transition period between years: 2007–2008 and

2008–2009. Since inter-pond movement may occur during fall or spring, we first calculated C_i by setting ψ_j equal to 0 for source wetlands in which *C. picta* was undetected in both years of the transition period, 0.5 for source wetlands occupied in either year of the transition period, and 1 for source wetlands occupied in both years of the transition period.

Weighting of source patches: modeled habitat quality

Our first connectivity metric did not directly account for variation in habitat quality of source wetlands, which may influence the number of emigrants from sources. Hence, we parameterized an alternative connectivity metric in which ψ_j was an index of source-patch quality. To do so, we used occupancy models that account for imperfect detection (MacKenzie et al. 2006) to assess how wetland occupancy probability was a function of factors thought to represent local habitat quality. Program PRESENCE (2.4) was used to build single-season occupancy models (MacKenzie et al. 2006) to estimate wetland occupancy probability (ψ) and detection probability (ρ) for *C. picta* in each year (Supplementary material, Table 2). Specifically, we used a logit link function to model among-wetland variation in ψ as a function of habitat covariates. The Akaike Information Criterion corrected for small sample size (AIC_C) was used to rank the support of 23 candidate models with different combinations of wetland-specific covariates. Detection probability was modeled as a function of session day (day 1, 2, 3, or 4 of each sampling session) and Julian date for all candidate models for each year. We first constructed three models that included the first two axes of our PCA for local habitat characteristics (L1, L2, L1+L2). Next, we constructed eight models to assess whether wetland inundation influenced occupancy alone (I), additively with local habitat characteristics (I+L1, I+L2, I+L1+L2), or in interaction with local habitat characteristics (I+L1+I*L1, I+L2+I*L2, I+L1+I*L1+L2, I+L2+I*L2+L1). Models were restricted to one interaction term to minimize the number of parameters estimated. Finally, we constructed 12 additional models that included wetland area (A) alone or as an additive term in the previous 11 models. Akaike weights (w_i), which represent the probability of model i given the candidate set, were estimated for each model, and

model-averaged estimates of ψ_j were calculated for each source wetland j in each year using all models in the candidate set (Burnham and Anderson 2002). To incorporate the habitat quality of source patch j in our connectivity metric for each transition period, we averaged ψ_j across both years of the transition. This method has the advantage of explicitly using habitat data to model variation in occupancy probability while accounting for imperfect detection. Occupancy can be a reliable measure of habitat quality, especially for species in which turnover is common (Sergio and Newton 2003).

Modeling of occupancy and turnover

We used a multiple-season occupancy modeling framework that accounts for imperfect detection probability (ρ) to assess how metapopulation and habitat quality factors influenced initial occupancy probability (ψ_{2007}), colonization probability (γ), and extinction probability (ε) for *C. picta*. A multi-season framework was used in this case to focus explicitly on turnover processes (colonization and extinction). All analyses were conducted in program PRESENCE (2.4) using a logit link function to model effects of covariates on among-wetland variation for each rate parameter. We conducted initial analyses to select a model accounting for variation in ρ while holding ψ_{2007} , γ , and ε constant. Potential effects on detection included survey day within sampling session, Julian date, and year. Next, we modeled ψ_{2007} , γ , and ε sequentially, starting with ψ_{2007} and ending with ε . The most-supported model for each rate parameter was used in subsequent model sets for the remaining parameters.

AIC_C was used to rank support for 87 candidate models representing the effect of different combinations of metapopulation and habitat covariates on ψ_{2007} , γ , and ε . The candidate set was the same for each rate parameter. The first 11 models included effects of local habitat characteristics (L1, L2, L1+L2), inundation level (I), or both factors together (I+L1, I+L2, I+L1+L2, I+L1+I*L1, I+L2+I*L2, I+L1+I*L1+L2, I+L2+I*L2+L1). We then added different combinations of metapopulation variables to the 11 habitat models: wetland area (A; models 12–22), connectivity using presence-absence of source wetlands only (C; models 23–33), connectivity using single season estimates of ψ_j as an index of habitat quality for source wetlands (“source quality

connectivity”, C_{SQ} ; models 34–44), additive effects of A and C (A+C; models 45–55), and additive effects of A and C_{SQ} (A+ C_{SQ} ; models 56–66). Next, we added an interaction effect of A*C and A* C_{SQ} to habitat models that did not have other interaction terms (models 67–73 and 74–80, respectively). Finally, we built 7 models that represented the effect of metapopulation variables only: A, C, C_{SQ} , A+C, A+ C_{SQ} , A+C+A*C, and A+ C_{SQ} +A* C_{SQ} . Akaike weights (w_i) were estimated for each model, and model-averaged estimates of ψ_{2007} , γ , and ε were calculated for each wetland in the candidate set (Burnham and Anderson 2002). To compare the support of C vs. C_{SQ} , we summed Akaike weights across all models within each candidate set (Burnham and Anderson 2002). Each connectivity metric was in 32 models for each candidate set.

Results

Chrysemys picta was detected at 42 wetlands (naïve occupancy = 46.7%) in 2007, 48 wetlands (53.3%) in 2008, and 35 wetlands (38.9%) in 2009. Using a constant model of ψ in single-season occupancy models, yearly occupancy probabilities after accounting for imperfect detection were 0.54 (SE = 0.07) in 2007, 0.64 (SE = 0.07) in 2008, and 0.46 (SE = 0.07) in 2009. Of the 90 sites, 30 sites (33.3%) were never occupied, 19 sites (21.1%) were occupied once, 17 sites (18.9%) were occupied twice, and 24 sites (26.7%) were occupied during all 3 years (Fig. 1). Turnover was common in both transition periods. Local colonizations ($n = 16$) outnumbered local extinctions ($n = 10$) between 2007 and 2008, and local extinctions ($n = 16$) outnumbered local colonizations ($n = 3$) between 2008 and 2009.

Estimating quality of source patches

Single-season occupancy models for 2007 and 2008 included effects of survey day within session and Julian date on detection probability, and models for 2009 included an effect of Julian date on detection. Detection probability was greatest on the first day of each sampling period, and detection probability was negatively related to Julian date in 2007 and 2008. In 2009, detection probability was positively related to Julian date.

Strongly supported models ($\Delta AIC_C \leq 2$) of occupancy in 2007 included an additive effect of wetland area and an interaction between PCA axis L1 and wetland inundation (Supplementary material, Table 2). Occupancy in 2007 was positively related to both wetland area and the interaction between L1 and inundation level (beta estimate ± 1 SE for the top model, A = 0.85 ± 0.32 , L1*I = 5.96 ± 3.16). Competing models of occupancy in 2008 included additive effects of wetland area, wetland inundation, and PCA axis L2. Each predictor variable had a positive effect on occupancy in 2008 (A = 0.85 ± 0.50 , I = 1.25 ± 0.48 , L2 = 0.74 ± 0.36). Finally, competing models of occupancy in 2009 included additive effects of wetland area, PCA axis L1, and PCA axis L2. Occupancy in 2009 was positively related to wetland area, negatively related to L1, and positively related to L2 (A = 1.12 ± 0.39 , L1 = -0.88 ± 0.51 , L2 = 1.73 ± 0.94).

Multiseason occupancy and turnover models

The most supported model of detection probability in our multiseason models included effects of survey day within session, Julian date, and year (accounting for 5 estimated parameters). Specifically, detection probability was greatest on the first day of each sampling session in 2007 and 2008, but not in 2009. Julian date had a negative effect on detection probability in 2007 and 2008, and a positive effect on detection in 2009.

Strongly supported models of initial occupancy probability included additive effects of PCA axis L1 and source quality connectivity (Table 1). Initial occupancy was positively related to hydroperiod and pH, negatively related to emergent vegetation cover, and positively related to source quality connectivity (Fig. 2; beta estimate ± 1 SE for the top model, L1 = -2.13 ± 0.52 , $C_{SQ} = 1.79 \pm 0.51$). PCA axis L2 and wetland area occurred in competing models, but the addition of these variables did not substantially improve model fit (see log-likelihood values, Table 1). A model that only included additive effects of area and isolation on occupancy probability was not supported ($\Delta AIC_C = 31.47$).

Because there were only three colonizations between 2008 and 2009, we only modeled the effects of predictor variables on colonization probability for the transition between 2007 and 2008. After

Table 1 Model selection statistics for initial occupancy, colonization, and extinction probabilities of *Chrysemys picta* from 90 wetlands in northern Illinois

Rate parameter	Model	ΔAIC_c	ω_i	$-2l$	K
Occupancy ₂₀₀₇	L1+C _{SQ}	0.00	0.20	885.88	10
	L1+C _{SQ} +L2	1.24	0.11	884.94	11
	L1+C _{SQ} +A	1.45	0.10	885.16	11
Colonization ₂₀₀₈	Y+L2+I+A+C	0.00	0.17	844.64	15
	Y+L2+I+L2*I+A+C	0.82	0.11	843.20	16
	Y+L2+I+A+C+A*C	1.60	0.07	843.98	16
	Y+L2+I+A+C+L1	1.98	0.06	844.36	16
Extinction _{2008,2009}	L2+A	0.00	0.10	832.33	17
	L2+L1	1.03	0.06	833.35	17
	L2+A+I	1.19	0.06	831.21	18
	L2+A+L1	1.24	0.06	831.26	18
	L2	1.68	0.04	836.28	16
	L2+A+C _{SQ}	1.79	0.04	831.82	18
	L2+A+C	1.94	0.04	831.97	18

Years are indicated as subscripts for each rate parameter. Main effects include wetland area (A), connectivity (C), source quality connectivity (C_{SQ}), wetland inundation level (I), and PCA scores for two axes representing local habitat characteristics (L1 = emergent vegetation cover, wetland hydroperiod, and pH; L2 = emergent vegetation cover and canopy cover). A year effect (Y) indicates differences in the model intercept between the two transition periods. Summary includes relative difference between model AIC_C and AIC_C for the best model (ΔAIC_c), Akaike weights (ω_i), twice the negative log-likelihood ($-2l$), and number of parameters (K). Effects of survey day, Julian date, and year on detection probability were included in all models (5 parameters). Models with $\Delta AIC_c \leq 2$ are presented

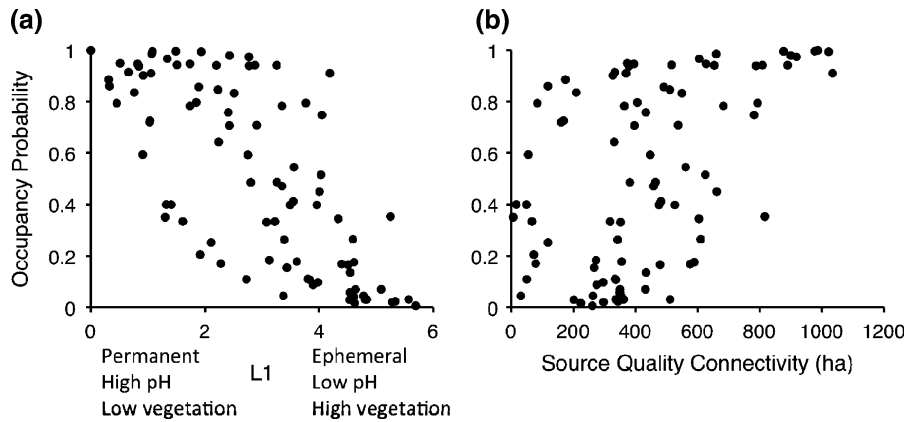


Fig. 2 Relationships of model-averaged, initial occupancy probabilities of wetlands by *Chrysemys picta* in 2007 to **a** L1 PCA scores, and **b** source quality connectivity. L1 values represent wetland hydroperiod, pH, and emergent vegetation cover

accounting for variation in model intercepts between the two transition periods, competing models of colonization probability between 2007 and 2008 included PCA axis L2, wetland inundation level, wetland area, and connectivity (Table 1). Colonized wetlands tended to have little canopy cover, high water levels, large areas, and high connectivity (beta estimate ± 1 SE for the top model, L2 = 1.28 \pm 0.65,

I = 3.61 \pm 1.86, A = 2.08 \pm 1.31, C = 3.22 \pm 1.55). There was some support for a positive interaction between L2 scores and wetland inundation, indicating effects of canopy cover and emergent vegetation on colonization were strongest when wetland inundation was high. A competing model also included a positive interaction between wetland area and connectivity, although model fit was not improved

substantially compared to the additive model including these variables.

Overall extinction probability was similar between years, and most competing models of extinction included effects of wetland area and PCA axis L2 (Table 1). Local extinctions were more common in small wetlands with high canopy cover and little emergent vegetation (Fig. 3, beta estimate \pm 1 SE for the top model, $A = -0.78 \pm 0.40$, $L2 = -1.48 \pm 0.86$). There was marginal support for a positive effect of PCA axis L1, suggesting extinctions also were more common in short hydroperiod ponds with low pH and high emergent vegetation cover. One competing model also included a negative effect of wetland inundation level on extinction probability. Extinction models with connectivity generally were not supported.

Connectivity and source-patch quality

Models with connectivity metrics that incorporated habitat quality of source patches had substantially more support than models with a simpler connectivity metric for predicting patch occupancy (Fig. 4). In contrast, the metric without source quality outperformed the metric with source-patch quality for predicting colonization probability, and both metrics had similar support for extinction probability (Fig. 4).

Discussion

Measures of patch geometry characteristic of spatially-realistic metapopulation models—area and isolation—were effective at explaining some variation in initial and subsequent distributions of *C. picta*

Fig. 3 Relationships of extinction probability of *Chrysemys picta* in wetlands between 2007–2008 (open circles) and 2008–2009 (closed circles) to **a** L2 PCA scores and **b** wetland area. L2 values represent canopy cover and emergent vegetation cover. Data for wetland area are plotted on a log scale

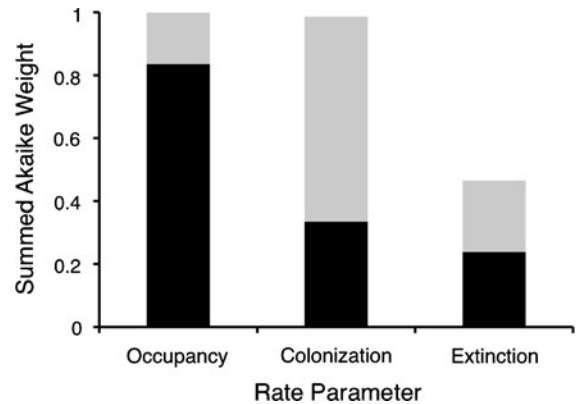
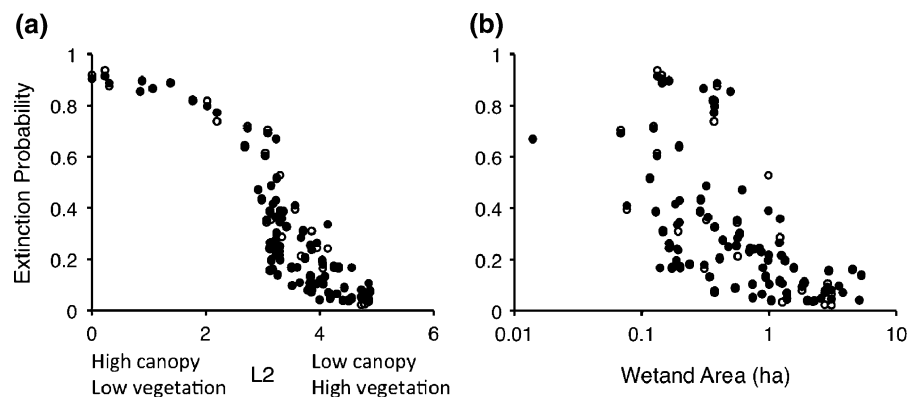


Fig. 4 Relative support of source quality connectivity (black bars) vs. connectivity (grey bars) based on summed Akaike weights for models of initial occupancy, colonization, and extinction probabilities of *Chrysemys picta*. Measures of source quality connectivity incorporated an effect of source-patch habitat quality on connectivity

among wetlands. Specifically, wetland connectivity had a positive effect on initial occupancy and colonization probabilities, whereas wetland area positively affected colonization probability, and negatively affected extinction probability. However, integration of habitat quality of both target and source wetlands was necessary to explain patterns of occupancy and turnover for *C. picta*.

Occupancy dynamics and local habitat quality

The initial distribution of *C. picta* was largely determined by spatial connectivity and local habitat quality. The relationship between initial occupancy and connectivity resembled a space-filling distribution (Cade and Noon 2003) in which connectivity set a lower bound on occupancy probability (Fig. 2).

Highly connected wetlands had high probabilities of being occupied by *C. picta*, whereas occupancy of isolated sites was likely driven by hydroperiod, emergent vegetation cover, and pH (representing PCA axis L1). The first year of our study marked the final year of drought conditions that persisted since 2005 (Illinois State Water Survey, www.isws.illinois.edu/data/climatedb), and low water and occasional dry periods occurred in many wetlands in early 2007. Given these conditions, we think wetland hydroperiod, reflecting the average time a given wetland held water, was an important driver of initial occupancy.

During drought, freshwater turtles either migrate to permanent water sources to forage (Roe and Georges 2007) or aestivate on land (Bowne 2008). In 2007, *C. picta* typically occupied long-hydroperiod wetlands. Aestivation may have occurred near ephemeral wetlands during dry conditions, but the survival of aestivating individuals can be lower than individuals in aquatic refuges (Roe and Georges 2008). Landscape context likely influences the decision to move versus stay during drought. Roe and Georges (2008) found that movement of *Chelodina longicollis* individuals away from drying wetlands was common when permanent wetlands were spatially proximate, whereas aestivation was more likely in isolated sites. In a post-hoc analysis for *C. picta*, we found support for a model including a negative interaction between connectivity and L1 on initial occupancy ($L1 + C_{SQ} + L1 * C_{SQ}$, $\Delta AIC_C = 0.83$ compared to the top model for Occupancy₂₀₀₇ in Table 1). Thus, occupancy of ephemeral wetlands in 2007 (i.e., wetlands with high L1 scores) was greater in isolated than connected sites. While there may be fitness benefits associated with moving to permanent wetlands during dry conditions, the cost of movement from isolated, ephemeral wetlands may outweigh those benefits, resulting in continual occupancy of such sites during drought. If aestivation entails a survival cost for *C. picta*, then repeated bouts of aestivation may leave populations inhabiting isolated, ephemeral sites susceptible to local extinction during persistent droughts.

Extinction and colonization events at the wetland scale were common after 2007. Many colonizations in 2008 likely resulted from an increase in water levels among wetlands due to above-average precipitation compared to 2007. During drought conditions, high turtle densities in aquatic refugia can lead to low

growth rates and minimal reproductive activity (Kennett and Georges 1990). When water levels increase, emigration to newly inundated wetlands is thought to be a strategy to make use of the flush of primary productivity (Brinson et al. 1981). In our system, wetland inundation level and L2 scores positively affected colonization probability, suggesting that individuals actively selected sites (Stamps et al. 2005) with high water levels, abundant emergent vegetation, and minimal canopy cover. Net biomass production and food resources are likely greater in open marshes with abundant emergent vegetation than in closed canopy wetlands (Brinson et al. 1981). Local habitat quality, based on individual growth rates, influences settlement decisions of dispersing *C. picta* (Bowne et al. 2006).

Wetland connectivity and area had strong, positive effects on colonization probability. Whereas the relationship between connectivity and colonization indicates that *C. picta* is dispersal-limited, the effect of wetland area on colonization suggests a target effect. For animals searching for habitat at the landscape scale, Zollner and Lima (1999) showed that nearly straight-line movements are most effective for maximizing dispersal success when perceptual range is limited. With respect to wetland-finding ability of *C. picta*, movement experiments have shown that perceptual range is limited (≤ 100 m; Emlen 1969; Caldwell and Nams 2006), and that straight-line movement is a default searching strategy (Bowne and White 2004; Caldwell and Nams 2006). Because the probability of intercepting a habitat patch by a ground-dispersing animal moving in a straight line is proportional to the linear size of the patch (Bowman et al. 2002), the positive effect of wetland area on *C. picta* colonization probability suggests a target effect (Lomolino 1990). Thus, patch geometry influenced the probability of individuals encountering wetlands during transfer, whereas habitat quality affected likelihood of settlement.

Local extinctions depended on wetland area, emergent vegetation, and canopy cover. In metapopulations, negative area-extinction relationships are explained by a reduced threat of demographic stochasticity in large habitats supporting large populations. Although positive area-abundance relationships have been found in freshwater turtles (e.g., *Graptemys geographica*, Rizkalla and Swihart 2006), processes generating local extinctions in our system

may have been demographic or behavioral (Marsh 2001). For example, *C. picta* individuals hibernate underwater and tolerate hypoxic or anoxic conditions, but winterkills have been associated with pond drying and complete ice formation (Ultsch 2006), both of which are more likely in small wetlands with little water volume. In winter 2008–2009, temperatures in northern Illinois were below average, and complete ice formation was observed among wetlands (B. Towey, personal communication). Furthermore, the relationship between area and extinction probability was stronger in 2009 than in 2008 ($\beta_{2008} = -0.293 \pm 0.500$, $\beta_{2009} = -1.53 \pm 0.703$). Thus, cold winter conditions and ice formation may have caused direct mortality of hibernating individuals. Alternatively, individuals may have emigrated from small wetlands in the fall in search of better hibernacula (Sexton 1959). If individuals are not philopatric to summer foraging habitats among years, then the observed turnover may be more related to movement and habitat selection than demographic or environmental stochasticity.

The role of wetland vegetation structure (emergent vegetation vs. canopy) in the extinction process is unclear. PCA axis L2 essentially separates wetlands into two categories: (1) forested wetlands with perennial woody plants, and (2) open marshes with herbaceous and emergent plants. Net biomass production is greater in open marshes than forested wetlands (Brinson et al. 1981), which suggests that food resources available to *C. picta* may be more abundant in marshes than forested wetlands. An alternative hypothesis is that predator activity is greater in forested than open sites, which can negatively affect population vital rates. Raccoons (*Procyon lotor*) are an important predator of *C. picta* (Marchand and Litvaitis 2004) and commonly forage in forest and wetland-edge habitats at RWF, as opposed to grassland and agricultural habitats surrounding many marshes in our system (Barding and Nelson 2008).

Quality of source patches

Our study adds to the increasing body of evidence showing that quality of focal habitat patches can affect occupancy dynamics in addition to measures of patch geometry characteristic of metapopulation studies (Hokit et al. 1999; Thomas et al. 2001;

Franken and Hik 2004; Armstrong 2005; Jaquière et al. 2008; Schooley and Branch 2009). However, our study is also instructive from the perspective of habitat quality of source patches. We used predicted patch occupancy probabilities as an index of habitat quality of sources in which probabilities were based on environmental covariates integrated via occupancy modeling. When explaining variation in initial occupancy probability, IFM connectivity metrics incorporating source-patch quality were more supported than simpler metrics using observed occupancy of sources. However, explicit inclusion of habitat quality in connectivity metrics did not help explain patterns of colonization probability.

The effect of source quality on initial occupancy is likely related to wetland hydrology. If local densities were high in long-hydroperiod wetlands in 2007, a common pattern for freshwater turtles during drought (e.g., Kennett and Georges 1990), then emigration potential was likely high from these sites as well. Because *C. picta* individuals emigrate from winter hibernacula during spring, summer occupancy may have depended on proximity of sites to high-quality refugia. We think the lack of an effect of source quality on colonization probability in 2008 was related to hydrology as well. Late summer rains recharged wetlands in 2007, resulting in more widespread distribution of suitable hibernacula during winter 2007–2008. Although colonization probability depended on connectivity, densities—and thus emigration potential—in the most permanent wetlands should decline as individuals use alternative wetlands for overwintering. Thus, long-hydroperiod wetlands appeared to function as major sources of emigration during drought. When short-hydroperiod wetlands refilled, emigration sources probably were more evenly distributed across the landscape, resulting in the sufficiency of a connectivity metric using observed occupancy of sources to explain patterns of colonization. Collectively, our results indicate that source-patch habitat quality can have an important impact on occupancy dynamics, but the effect can vary temporally due to environmental stochasticity.

Conclusions

In patchy populations in which habitat quality varies locally, population responses to temporal and spatial

variation can be the result of individual behavior or demography (Marsh 2001). Behavioral processes are clearly important for freshwater turtles as individuals track variable habitats and associate with multiple ponds (Bowne et al. 2006; Roe and Georges 2007; Roe et al. 2009). However, even in patchy systems such as our in which behavioral processes likely predominate, both metapopulation and habitat quality variables can be useful in explaining observed distributions and turnover. The effect of wetland area on *C. picta* extinction and colonization was particularly surprising in this regard, and further work is needed to tease apart the demographic and behavioral processes underlying those relationships.

Furthermore, our results underscore the importance of incorporating habitat quality of source patches as a predictor of occupancy dynamics, and that the effect of source quality can vary temporally. A recent review found that 43.2% of metapopulation studies incorporated focal habitat quality in their analyses, but only 11.4% of metapopulation studies incorporated habitat quality of source patches into connectivity measures (Schooley and Branch, unpublished manuscript). In systems where population size potentially scales with habitat quality, we stress the importance of evaluating source-patch quality as a predictor of occupancy and turnover, and we highlight occupancy modeling as a method to accomplish that goal.

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References

- Armstrong DP (2005) Integrating the metapopulation and habitat paradigms for understanding broad-scale declines of species. *Conserv Biol* 19:1402–1410
- Baguette M (2004) The classical metapopulation theory and the real, natural world: a critical appraisal. *Basic Appl Ecol* 5:213–224
- Barding EE, Nelson TA (2008) Raccoons use habitat edges in northern Illinois. *Am Midl Nat* 159:394–402
- Bélisle M (2005) Measuring landscape connectivity: the challenge of behavioral landscape ecology. *Ecology* 86: 1988–1995
- Bowman J, Cappuccino N, Fahrig L (2002) Patch size and population density: the effect of immigration behavior. *Conserv Ecol* 6:9. <http://www.consecol.org/vol6/iss1/art9>. Accessed Feb 2010
- Bowne D (2008) Terrestrial activity of *Chrysemys picta* in northern Virginia. *Copeia* 2008:306–310
- Bowne DR, White HR (2004) Searching strategy of the painted turtle *Chrysemys picta* across spatial scales. *Anim Behav* 68:1401–1409
- Bowne DR, Bowers MA, Hines J (2006) Connectivity in an agricultural landscape as reflected by interpond movements of a freshwater turtle. *Conserv Biol* 20:780–791
- Brinson MM, Lugo AE, Brown S (1981) Primary productivity, decomposition and consumer activity in freshwater wetlands. *Annu Rev Ecol Syst* 12:123–161
- Brown JH, Kodric-Brown A (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58:445–449
- Burnham KP, Anderson DR (2002) Model selection and multi-model inference: a practical information-theoretic approach, 2nd edn. Springer, New York
- Cade BS, Noon BR (2003) A gentle introduction to quantile regression for ecologists. *Front Ecol Environ* 1:412–420
- Caldwell IR, Nams VO (2006) A compass without a map: tortuosity and orientation of eastern painted turtles (*Chrysemys picta picta*) released in unfamiliar territory. *Can J Zool* 84:1129–1137
- Emlen ST (1969) Homing ability and orientation in the painted turtle *Chrysemys picta marginata*. *Behaviour* 33:58–76
- Ernst CH, Barbour RW, Lovich JE (1994) Turtles of the United States and Canada. Smithsonian Books, Washington, D.C
- Fleishman E, Ray C, Sjögren-Gulve P, Boggs CL, Murphy DD (2002) Assessing the roles of patch quality, area, and isolation in predicting metapopulation dynamics. *Conserv Biol* 16:706–716
- Franken RJ, Hik DS (2004) Influence of habitat quality, patch size and connectivity on colonization and extinction dynamics of collared pikas *Ochotona collaris*. *J Anim Ecol* 73:889–896
- Hanski I (1994) A practical model of metapopulation dynamics. *J Anim Ecol* 63:151–162
- Hanski I, Gaggiotti OE (eds) (2004) Ecology, evolution, and genetics of metapopulations. Academic Press, San Diego
- Harrison S (1991) Local extinction in a metapopulation context: an empirical evaluation. *Biol J Linn Soc* 42:73–88
- Hokit DG, Stith BM, Branch LC (1999) Effects of landscape structure in Florida scrub: a population perspective. *Ecol Appl* 9:124–134
- Jaquière J, Guélat J, Broquet T, Berset-Brändli L, Pellegrini E, Moresi R, Hirzel AH, Perrin N (2008) Habitat-quality effects on metapopulation dynamics in greater white-toothed shrews, *Crocidura russula*. *Ecology* 89: 2777–2785

- Kennett RM, Georges A (1990) Habitat utilization and its relationship to growth and reproduction of the eastern long-necked turtle, *Chelodina longicollis* (Testudinata: Chelidae), from Australia. *Herpetologica* 46:22–33
- Levins R (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull Entomol Soc Am* 15:237–240
- Lima SL, Zollner PA (1996) Towards a behavioral ecology of ecological landscapes. *Trends Ecol Evol* 11:131–135
- Lomolino MV (1990) The target area hypothesis: the influence of island area on immigration rates of nonvolant mammals. *Oikos* 57:297–300
- MacKenzie D, Nichols J, Royle JA, Pollock KH, Bailey LL, Hines JE (2006) Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, Burlington
- Marchand M, Litvaitis J (2004) Effects of habitat features and landscape composition on the population structure of a common aquatic turtle in a region undergoing rapid development. *Conserv Biol* 18:758–767
- Marsh DM (2001) Behavioral and demographic responses of túngara frogs to variation in pond density. *Ecology* 82:1283–1292
- McAuliffe JR (1978) Seasonal migrational movements of a population of western painted turtle, *Chrysemys picta bellii* (Reptilia, Testudines, Testudinidae). *J Herpetol* 12:143–149
- McCullough DR (ed) (1996) Metapopulations and wildlife conservation. Island Press, Washington, D.C
- Moilanen A, Nieminen M (2002) Simple connectivity measures in spatial ecology. *Ecology* 83:1131–1145
- Pellet J, Fleishman E, Dobkin DS, Gander A, Murphy DD (2007) An empirical evaluation of the area and isolation paradigm of metapopulation dynamics. *Biol Conserv* 136:483–495
- Phillips CA, Brandon RA, Moll EO (1999) Field guide to amphibians and reptiles of Illinois. Illinois Natural History Survey Manual 8, Champaign
- Prugh LR (2009) An evaluation of patch connectivity measures. *Ecol Appl* 19:1300–1310
- Prugh LR, Hodges KE, Sinclair ARE, Brashares JS (2008) Effect of habitat area and isolation on fragmented animal populations. *P Natl Acad Sci USA* 105:20770–20775
- R Development Core Team (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Ray N (2005) PATHMATRIX: a geographical information system tool to compute effective distances among samples. *Mol Ecol Notes* 5:177–180
- Rizkalla CE, Swihart RK (2006) Community structure and differential responses of aquatic turtles to agriculturally induced habitat fragmentation. *Landscape Ecol* 21:1361–1375
- Roe JH, Georges A (2007) Heterogeneous wetland complexes, buffer zones, and travel corridors: landscape management for freshwater reptiles. *Biol Conserv* 135:67–76
- Roe JH, Georges A (2008) Maintenance of variable responses for coping with wetland drying in freshwater turtles. *Ecology* 89:485–494
- Roe JH, Brinton AC, Georges A (2009) Temporal and spatial variation in landscape connectivity for a freshwater turtle in a temporally dynamic wetland system. *Ecol Appl* 19:1288–1299
- Schooley RL, Branch LC (2007) Spatial heterogeneity in habitat quality and cross-scale interactions in metapopulations. *Ecosystems* 10:846–853
- Schooley RL, Branch LC (2009) Enhancing the area-isolation paradigm: habitat heterogeneity and metapopulation dynamics of a rare wetland mammal. *Ecol Appl* 19:1708–1722
- Sergio F, Newton I (2003) Occupancy as a measure of territory quality. *J Anim Ecol* 72:857–865
- Sexton OJ (1959) Spatial and temporal movements of a population of the painted turtle *Chrysemys picta marginata* (Agassiz). *Ecol Monogr* 29:113–140
- Stamps JA, Krishnan VV, Reid ML (2005) Search costs and habitat selection by dispersers. *Ecology* 86:510–518
- Thomas CD (1994) Extinction, colonization, and metapopulations: environmental tracking by rare species. *Conserv Biol* 8:373–378
- Thomas CD, Hanski I (2004) Metapopulation dynamics in changing environments: butterfly responses to habitat and climate change. In: Hanski I, Gaggiotti OE (eds) *Ecology, genetics, and evolution of metapopulations*. Academic Press, San Diego, pp 489–514
- Thomas JA, Bourn N, Clarke RT, Stewart KE, Simcox DJ, Pearman GS, Curtis R, Goodger B (2001) The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. *P Roy Soc Lond B Bio* 268:1791–1796
- Ultsch GR (2006) The ecology of overwintering among turtles: where turtles overwinter and its consequences. *Biol Rev* 81:339–367
- Zollner PA, Lima SL (1999) Search strategies for landscape-level interpatch movements. *Ecology* 80:1019–1030