

Research paper

The spatial configuration of greenspace affects semi-aquatic turtle occupancy and species richness in a suburban landscape

Jacquelyn C. Guzy^{a,*}, Steven J. Price^b, Michael E. Dorcas^a^a Department of Biology, Davidson College, Davidson, NC 28035-7118, United States^b Department of Forestry, University of Kentucky, Lexington, KY 40546-0073, United States

HIGHLIGHTS

- We sampled semi-aquatic turtles from 2010 to 2011 at 20 suburban ponds.
- We used a hierarchical Bayesian model to estimate species richness and occupancy.
- Species richness and occupancy increased with greater connectance of greenspaces.
- Richness was greater at golf ponds than rural or urban ponds indicating suitability.
- In suburban areas, maintaining connectivity of greenspaces should be a priority.

ARTICLE INFO

Article history:

Received 10 April 2012

Received in revised form 17 April 2013

Accepted 24 April 2013

Keywords:

Connectance metric

Connectivity

Terrestrial and aquatic habitat

Hierarchical Bayesian model

Golf course

Landscape composition

ABSTRACT

Within urbanized areas, the importance of greenspaces for wildlife has been widely investigated for some animal groups, but reptiles have generally been neglected. To assess the importance of the amount, spatial distribution, and configuration of greenspaces (comprised of terrestrial and aquatic areas), we examined semi-aquatic turtle species richness in urbanized areas. In this study, we sampled turtles from 2010 to 2011 at 20 ponds, including farm (rural) ponds, ponds in urbanized environments, and golf course ponds. We used a hierarchical Bayesian species-richness model to estimate species richness and species-specific occupancy responses to three pond types (rural, golf, or urban) and four landscape measurements of greenspace (i.e., Euclidean nearest neighbor, interspersion juxtaposition, percent of landscape, and connectance), generated in FRAGSTATS. We found that probability of occupancy of four species, *Kinosternon subrubrum*, *Trachemys scripta*, *Chelydra serpentina*, and *Pseudemys concinna* increased substantially with an increase in connectance of greenspace within 500 m of each pond. When the model examining the configuration of greenspaces was analyzed, estimated species richness was greater at golf ponds as compared to either rural or urban ponds, and richness increased with increasing connectivity of greenspaces. Our results indicate that in golf course ponds can potentially support a greater diversity of semi-aquatic turtle species than rural or urban ponds and thus may be considered superior habitat in suburban environments. In addition, we suggest that maintaining connectivity of greenspaces in suburban areas is important for semi-aquatic turtles and should be considered in urban planning.

© 2013 Elsevier B.V. All rights reserved.

1. Introduction

Protecting natural and semi-natural greenspaces is becoming a critical component of land-use management within urbanized areas. Greenspaces are defined as land, water and geological features which have been naturally colonized by plants and animals (Harrison, Burgess, Millward, & Dawe, 1995) and this includes

the continuum from intensely managed greenspace such as golf courses to wilderness areas. Examples of greenspaces include forests, shrublands, meadows, marshes, ponds, rivers, lakes, reservoirs, golf courses, suburban parks, and land alongside waterways with mixtures of forest and herbaceous plants.

Land managers are increasingly incorporating greenspace into development plans for both aesthetic reasons and in an effort to offset environmental impacts of urban expansion and intensification. Greenspace can reduce demands for natural resources (Grove, 1990; Jim & Chen, 2003; Little, 1990) via reduced cooling costs, windbreak effects, and reduced urban heat island effects (Meier, 1991; Rudie & Dewers, 1984; Simpson & McPherson, 1996; Solecki et al., 2005), and can counteract increased carbon dioxide levels as greenspaces are carbon sinks (Rowntree & Nowak,

* Corresponding author at: Davidson College, Department of Biology, Box 6935, Davidson, NC 28035-7118, United States. Tel.: +1 704 894 2768; fax: +1 704 894 2512.

E-mail addresses: jackieguzy@gmail.com (J.C. Guzy), steven.price@uky.edu (S.J. Price), midorcas@davidson.edu (M.E. Dorcas).

1991). These areas can also mitigate the impact of urban development by conserving water (McPherson, 1990), improving air quality (Smith, 1981), controlling rainfall, runoff and flooding (Sanders, 1986), and lowering noise levels (Cook, 1978). In addition, greenspaces in urbanized areas can also act as refuges for wildlife. The importance of urban greenspaces for wildlife has been widely investigated for some groups, including birds, mammals, and insects (e.g., Chamberlain, Gough, Vaughan, Vickery, & Appleton, 2007; Fabianek, Gagnon, & Delorme, 2011; Loram, Tratalos, Warren, & Gaston, 2007; McGeoch & Chown, 1997; Ong, 2003; VanDruff & Rowse, 1986), but for some taxonomic groups, such as semi-aquatic reptiles, studies are insufficient.

Urban greenspaces often include water bodies on golf courses and in remnant forests among housing developments and agricultural lands; these water bodies have been shown to support turtle populations (Eskew, Price, & Dorcas, 2010; Failey, McCoy, Price, & Dorcas, 2007; Harden, Price, & Dorcas, 2009; Price, Guzy, & Dorcas, in press; Roe, Rees, & Georges, 2011; Ryan, Conner, Douthitt, Sterrett, & Salsbury, 2008). More specifically, semi-aquatic turtle species regularly nest within residential lawns and road side banks (Joyal, McCollough, & Hunter, 2001; Klemens, 1993; Linck, DePari, Butler, & Graham, 1989) and ponds in developed landscapes may be more eutrophic, a condition benefiting some turtles (Marchand & Litvaitis, 2004). However, in urbanized regions, turtles are vulnerable to human-subsidized predators which frequently consume turtle eggs (Marchand & Litvaitis, 2004), and also to road mortality, particularly during nesting and dispersal events (Aresco, 2005; Steen et al., 2006). Urbanized aquatic habitats are likely to suffer increased channelization and siltation, a reduction in aquatic vegetation, and degradation of appropriate basking sites (Spinks, Pauly, Crayon, & Shaffer, 2003). Furthermore, the loss, degradation, and fragmentation of aquatic habitats from urban development can result in abnormal population structures and population declines or extinctions in aquatic turtles (Marchand & Litvaitis, 2004). Additionally, suitable terrestrial habitat for nesting and hibernating may be scarce or non-existent. As aquatic and terrestrial habitat is eliminated (or degraded), sites occupied by remaining turtles become isolated, reducing the ability of individuals to successfully disperse, which may eventually result in lower genetic variability among populations (e.g., Marchand & Litvaitis, 2004), reducing a population's long-term survival.

The semi-aquatic turtle assemblage at a given pond in a suburban location may be influenced by the surrounding landscape context. For example, Price et al. (in press) found that *Trachemys scripta* and *Chrysemys picta* abundances in ponds on golf courses were similar to abundances in farm ponds and both species had lowest abundances in ponds surrounded by residential development. Failey et al. (2007) found that relative abundance of semi-aquatic turtle species, size distributions for each sex, and sex ratios were not distinguishable between rural (farm) and golf course pond types. Further, body condition indices for *C. picta* from golf course ponds were higher than those from rural ponds, perhaps because of increased food availability (Failey et al., 2007). Marchand and Litvaitis (2004) found that in urban ponds, the number of injured turtles per pond was associated with increasing urban area within 100 m of ponds and suggest that semi-aquatic turtle population structure may be altered by human-associated effects (e.g., dense road networks and abundant predator populations). Finally, the amount, spatial distribution, and composition of greenspaces (terrestrial and aquatic habitats) within urbanized areas may also be important for semi-aquatic turtles. For example, Roe, Brinton, and Georges (2009) found that the probability of movement by a freshwater turtle species decreased with increasing distance between wetlands. Joyal et al. (2001) suggest that the overall size of a wetland complex, the juxtaposition of wetlands of different types, and wetland isolation influences habitat use

and movements of semi-aquatic turtles. Other studies have found that larger ponds often have greater semi-aquatic turtle abundance (Failey et al., 2007; Lindeman, 1990; Price et al., in press) and Cosentino, Schooley, and Phillips (2010) found that highly connected wetlands had high probabilities of being occupied by semi-aquatic turtles.

Given the importance of greenspaces in urbanized areas and the potential importance of the surrounding landscape context for semi-aquatic turtles our objectives were to examine the amount, spatial distribution, and configuration of greenspaces within suburban areas to assess their importance to semi-aquatic turtles. Our hypotheses were: (1) species richness will be higher in golf and rural ponds as compared to suburban ponds, (2) the probability of occupancy will be higher in golf course and rural ponds as compared to suburban ponds, and (3) the probability of occupancy will increase with greenspaces that are closer together, more interspersed (i.e., not clumped), larger, and more connected.

2. Methods

From 2010 to 2011 we sampled 20 suburban ponds for semi-aquatic turtles. Our study ponds were located in the Charlotte-Metropolitan area (Mecklenburg, Cabarrus, and Iredell counties) in North Carolina, USA (Fig. 1). This region is located in the Piedmont of North Carolina, which consists of gently rolling hills (elevations ~61–457 m) and mild climatic conditions (~5 °C in winter to ~32 °C in summer). Land-cover in this area is dominated by an urban/suburban landscape along with agriculture and pasture land, and second-growth forests (Price, Dorcas, Gallant, Klaver, & Willson, 2006). Over the past four decades the area has seen a large reduction of forest and agricultural lands by suburban development, and some counties within the region have lost up to 60% of undeveloped land to urban landcover (Price et al., 2006).

We studied turtles in three pond types, as defined by their surrounding landscape attributes. We classified study ponds as rural ($n=5$) if surrounded by pastureland/forest with limited suburban development within 500 m, as golf if occurring on golf courses ($n=10$), or as urban ($n=5$) if surrounded predominantly by suburban development within 500 m. Like the vast majority of ponds in the Piedmont, all of our study ponds were man-made, most created for agricultural purposes between 1930 and 1950, and others created between 1966 and 1997 as part of golf courses. Rural pond size averaged 0.68 hectares (range 0.15–1.54 ha), golf course ponds averaged 1.69 hectares (range 0.45–6.13 ha), and urban ponds averaged 0.65 hectares (0.4–1.0 ha).

In studying the potential importance of landscape characteristics surrounding suburban ponds, we selected a radius of 500 m surrounding the edge of each pond to attempt to include close to 100% of expected turtle movements from ponds. This distance was applicable for our study because outside of nesting forays, drying ponds, and dispersal events where turtles might travel considerable distances (Bennett, 1972; Ernst & Lovich, 2009; McAuliffe, 1978; Obbard & Brooks, 1980), in general, semi-aquatic turtles are associated with particular ponds or groups of ponds (e.g., Burke & Gibbons, 1995). Previous studies (Semlitsch & Bodie, 2003; Steen et al., 2012) examined migration data for aquatic-associated reptiles and determined the overall core terrestrial habitat to be from up to 289 m from the edge of the aquatic site, although Harden et al. (2009) found few linear terrestrial movements by a semi-aquatic turtle were as great as 581 m.

2.1. Turtle sampling

We sampled turtles at golf course ponds from 5 May through 28 August, at rural ponds from 6 May until 30 July, and at urban ponds

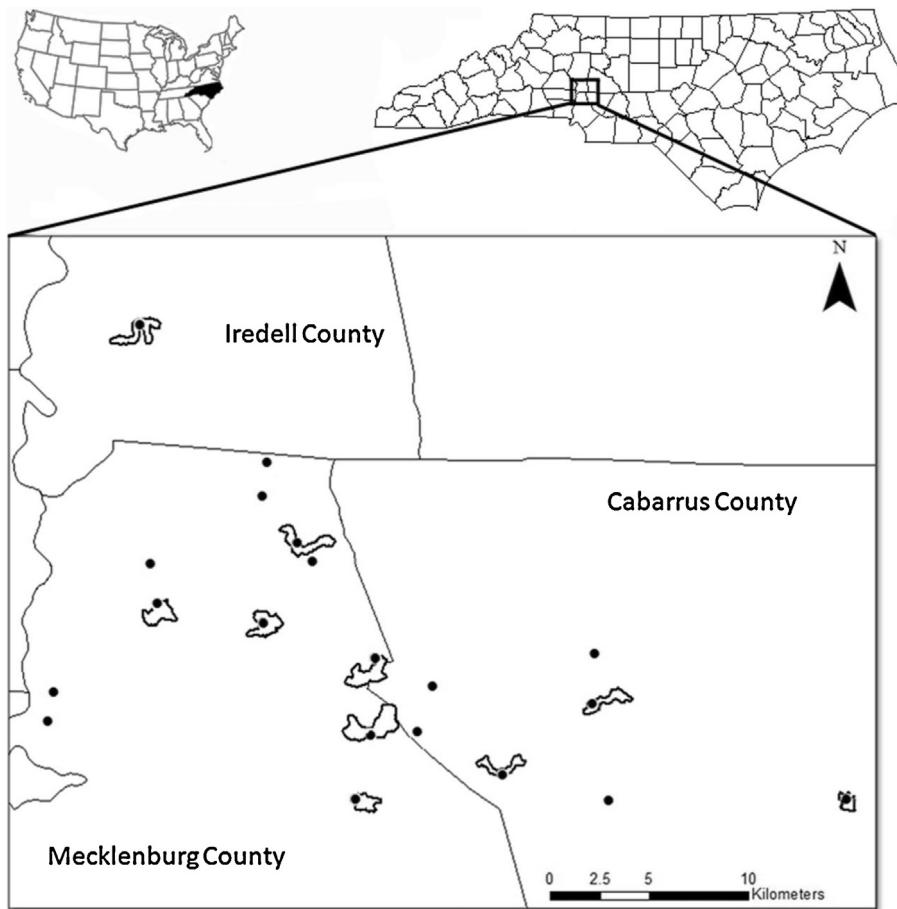


Fig. 1. Study area located in the western Piedmont (Iredell, Cabarrus, and Mecklenburg Counties) of NC, USA. Solid dots represent study ponds; those located on golf courses show course boundaries.

from 15 May until 23 July each year. In each pond, we placed 10 hoop net traps baited with sardines in shallow water around the pond perimeter. Bait (one can of sardines per trap) was replaced every 4 days. Traps were checked every other day for 10 days each year, and after capture, all turtles were identified to species, sexed using secondary sexual characters (Gibbons & Lovich, 1990) and individually marked by filing notches in the marginal scutes (Sexton, 1959). Turtles were released within a few hours after initial capture.

2.2. Quantification of habitat fragmentation

We measured a series of landscape variables associated with each pond using a geographical information system (ARCMAP, v 10.0; ESRI, 2010), based on georeferenced 1":200" digital Orthophotos for each county (NC OneMap, 2011). We classified land-cover within a 500m radius of each site into four non-exclusive categories: greenspace, aquatic, terrestrial, and urban. The greenspace category included all terrestrial and aquatic areas; examples of these are forests as well as ponds, streams, pasture, and golf courses (including golf greens, fairways, and the rough). The aquatic category was restricted to only aquatic habitats (ponds, lakes, streams, and creeks), and similarly, the terrestrial category was restricted only to terrestrial areas (forests, pastures, golf course greens, fairways, and the rough). Finally, the urban category was comprised of residential, recreational, commercial, and industrial land-cover including all buildings and associated lawns, pavement and roads. These four category designations allowed us to investigate the influence of greenspace configuration and also to

separately consider aquatic and terrestrial habitats and their configuration as potential influence on turtles because they use both aquatic and terrestrial areas (Gibbons, 2003).

For each study site, landscape metrics (see below) were calculated for the greenspace and aquatic habitats categories. We used FRAGSTATS 3.3 (McGarigal, Cushman, Neel, & Ene, 2002) to generate four metrics to explore landscape fragmentation: Euclidean nearest neighbor (ENN), interspersion juxtaposition index (IJI), percent land-cover (PLAND), and connectance (CONNECT). Previous research has identified these four metrics as important to characterizing landscape-patch configuration (Bierwagen, 2007; Cushman, McGarigal, & Neel, 2008; Griffith, Martinko, & Price, 2000). We define a landscape as an area of land containing a mosaic of habitat patches and define a 'patch' as each individual occurrence of a particular land cover type (e.g., greenspace, aquatic habitats, or urban areas) in the landscape. Patches were defined using the eight neighbor rule (McGarigal et al., 2002), which takes into account both orthogonal (i.e., cells share a side with focal cell) and diagonal cells as neighbors.

In our study, these metrics reflect the fragmentation of greenspace by urbanization and provide a comprehensive view of landscape structure including greenspace isolation and proximity, contagion/interspersion, area, and connectivity. In particular, based on turtle biology, we expect that the degree of greenspace isolation, aggregation, size, and connectedness influences turtle occupancy. More specifically, the ENN index has been used to quantify patch isolation (e.g., Kong, Yin, Nakagoshi, & Zong, 2010; Magle, Theobald, & Crooks, 2009; Moore, Van Niel, & Harvey, 2011) and reports the mean distance between like patches within a specified

radius. The IJI quantifies landscape configuration and approaches 0 when the patches are adjacent to only like patches (i.e., clumped) and increases to 100 percent when patches are maximally interspersed throughout the specified radius (McGarigal & Marks, 1995). The PLAND index is the percentage the landscape comprised of the patch type. Finally CONNECT is a percentage measure of the number of joinings between similar patches within a specified distance and assesses whether each patch is connected to any other matching patch in the landscape. More specifically, CONNECT equals the number of joinings between all like patches divided by the total number of possible joinings between like patches; those minimally connected have values closer to zero, and patches maximally connected have CONNECT values closer to 100%. Because collinearity between predictor variables can confound their independent effects, we calculated Spearman-rank correlation coefficients using Statistica v.7.1 (StatSoft, 2005) for all pairwise combinations of independent variables (Hair, Anderson, Tatham, & Black, 1998; Knapp, Matthews, Preisler, & Jellison, 2003) and verified that our metrics were uncorrelated (i.e., all p -values >0.05).

2.3. Statistical analyses

We used hierarchical Bayesian modeling to estimate turtle species richness and species-specific responses to pond type (rural, urban, golf) and also to four site-specific covariates (Euclidean nearest neighbor/ENN, interspersion juxtaposition index/IJI, percent of landscape/PLAND, and connectance/CONNECT). This hierarchical approach incorporated species-specific and assemblage-level (i.e., all turtle species together) attributes into the same modeling framework by providing separate estimates for species-specific occurrence and detection probabilities and reporting site-specific species richness estimates (Dorazio & Royle, 2005; Zipkin, Dewan, & Royle, 2009). Our analysis of species richness accounted for imperfect detection (avoids assuming all species are present at every site or that non-detection represents species absence; Dorazio & Royle, 2005; Dorazio, Royle, Soderstrom, & Glimskar, 2006; Kéry, Royle, Plattner, & Dorazio, 2009) and also improved individual parameter estimates by considering them in the context of the larger group (Sauer & Link, 2002; Zipkin et al., 2009).

Our species richness models (see Models 1–4 below) were similar to Zipkin et al. (2009) and estimated species and assemblage responses to site covariates of ponds and greenspace at each site. One level of our model assumes a “true” (but only partially observed) presence-absence matrix z_{ij} for species $i = 1, 2, \dots, N$ at site $j = 1, 2, \dots, J$ where $z_{ij} = 1$ if a species i occurs in site j , and $z_{ij} = 0$ if the species does not occur. Because z_{ij} is uncertain, we specify a model for occurrence, with a Bernoulli distribution, where $z_{ij} \sim Bern(\Psi_{ij})$, and Ψ_{ij} is the probability that a species i occurs in site j .

We generated species-specific observance matrices for ten sampling occasions at each of twenty sites where detection was represented as 1, and non-detection was represented as 0. Thus, the data provided a three dimensional matrix x_{ijk} for species i at site j for the k th sampling occasion. Another level of our model specified that $x_{ijk} \sim Bern(\Theta_{ijk} z_{ij})$ where z_{ij} is the true occurrence matrix described above, and the Θ_{ijk} is the detection probability for species i at site j for the k th sampling occasion. This fulfills the condition that $x_{ijk} = 0$ if the species i is not present at site j , because in that case $z_{ij} = 0$.

Each covariate was standardized (i.e., the mean was subtracted from each value and then divided by the SD) before analysis (except for pond type). We examined the effect of pond type on species-specific occupancy and species richness with the following equation:

$$\text{Model 1 (pond type)} : \text{logit}(\Psi_{ij}) = u_i + \alpha_1 RURAL_j + \alpha_2 URBAN_j + \alpha_3 GOLF_j$$

This model, investigating the influence of pond type, contained five species-specific parameters ($u_i, \alpha_1, \alpha_2, \alpha_3, v_i$). The parameters u_i (species-specific mean probability of occurrence) and v_i (species-specific mean probability of detection) for Model 1 (and Models 2–4, below) followed a joint normal distribution such that $[u_i, v_i | \Sigma] \sim N(0, \Sigma)$ (Dorazio et al., 2006). In this equation, Σ denotes a 2×2 symmetric matrix with diagonal elements σ_u^2 and σ_v^2 (respective variances in u_i and v_i) and with off-diagonal elements σ_{uv} equal to the covariance in u_i and v_i (Dorazio & Royle, 2005).

We examined the effect of landscape configuration of surrounding aquatic habitats on turtle occupancy and species richness of our 20 ponds using the following equation:

$$\text{Model 2 (aquatic habitats)} : \text{logit}(\Psi_{ij}) = u_i + \alpha_1 ENN_j + \alpha_2 IJI_j + \alpha_3 CONNECT_j + \alpha_4 PLAND_j$$

We examined the effect of landscape composition of surrounding terrestrial habitats on turtle occupancy and species richness of our 20 ponds with the following equation:

$$\text{Model 3 (terrestrial habitats)} : \text{logit}(\Psi_{ij}) = u_i + \alpha_1 ENN_j + \alpha_2 IJI_j + \alpha_3 CONNECT_j + \alpha_4 PLAND_j$$

We examined the effect of landscape composition of greenspace (i.e., all terrestrial and aquatic habitats) on turtle occupancy and species richness of our 20 ponds with the following equation:

$$\text{Model 4 (greenspace)} : \text{logit}(\Psi_{ij}) = u_i + \alpha_1 ENN_j + \alpha_2 IJI_j + \alpha_3 CONNECT_j + \alpha_4 PLAND_j$$

Finally, detection probabilities were modeled for each species, by using the following equation included within each of the models described above:

$$\text{logit}(\Theta_{ijk}) = v_i$$

The second, third, and fourth models discussed above (investigating the influence of aquatic, terrestrial, and greenspace habitats, respectively), contained six species-specific parameters ($u_i, \alpha_1, \alpha_2, \alpha_3, \alpha_4, v_i$). A final hierarchical component of the model estimated assemblage summaries (designated with μ) assuming that the species-specific parameters were random effects, each governed by an assemblage level hyper-parameter. For example, $\alpha_1 \sim N(\mu_{\alpha_1}, \sigma_{\alpha_1})$ where μ_{α_1} is the mean assemblage response (across species) to the ENN covariate (α_1), and σ_{α_1} is the standard deviation in α_1 across species (Kéry et al., 2009). This hierarchical analysis allowed us to estimate species-specific parameters even where species were rare (Zipkin et al., 2009).

Our four models used uninformative priors for the hyper-parameters (e.g., $U(0, 5)$ for all σ parameters and $U(-10 \text{ to } 10)$ for μ_{α} parameters; species-specific model coefficients were truncated at ± 5 from μ to avoid traps). The use of vague priors is well suited to an ecological application because it reflects a lack of prior knowledge of a parameter's true value (Link, Cam, Nichols, & Cooch, 2002). The mean and standard deviation of the model coefficients were calculated, along with the 2.5 and 97.5 percentiles of the distribution, which represent 95% Bayesian credible intervals. Species-specific occupancy and detection estimates were derived using the log transformation (i.e., $(\exp(\alpha))/(1 + \exp \alpha)$).

We organized our data in program R (2.14.0) (R Development Core Team 2010) and executed data analysis in the software program WinBUGS (Lunn, Thomas, Best, & Spiegelhalter, 2000) using R2WinBUGS (Sturtz, Ligges, & Gelman, 2005). The number of Markov chain Monte Carlo (MCMC) iterations was 300 000, and

we disregarded the first 30 000 as burn-in with a thinning rate of 3. Models were evaluated by examining history plots and the Gelman and Rubin statistic (Gelman & Rubin, 1992).

3. Results

During 2010 and 2011 we sampled 20 suburban ponds each for 100 trap-days per year (total 200 trap-days per site). We observed the following seven semi-aquatic turtle species: snapping turtle (*Chelydra serpentina*), painted turtle (*C. picta*), eastern mud turtle (*Kinosternon subrubrum*), eastern river cooter (*Pseudemys concinna*), eastern musk turtle (*Sternotherus odoratus*), spiny softshell (*Apalone spinifera*), and the pond slider (*T. scripta*). The spiny softshell was not used in analyses because we observed it only once (Table 1). While our models are good for rare species (Zipkin et al., 2009), the one occurrence of the spiny softshell was not attributed to low detection probability, but rather, this turtle was considered a transient from a third-order stream where they are common residents (Ernst & Lovich, 2009). Excluding the spiny softshell, the proportion of sites where each species was detected ranged from 20 to 100%, the number of captures ranged from 21 to 1288, and the number of individual turtles per species ranged from 5 to 770 (Table 1). Ponds had between 3 and 6 turtle species.

Measured landscape variables for each pond varied (Table 2); the average nearest greenspace (ENN) varied from 13.4 m to 40.6 m to 87.2 m at rural, golf, and urban ponds, respectively. Rural, golf, and urban sites were similar in the level of interspersion (IJI) of greenspace and averaged from 68.5, to 64.2, to 67.6%, respectively (Table 2). The percentage of area (PLAND) comprised of greenspace (within 500 m of each pond) varied by pond type and averaged 83.9, 56.7, and 50.9% for rural, golf, and urban sites, respectively. The percentage of area comprised of ponds (within 500 m of each pond), however, was very similar among pond types and averaged 1.8, 2.6, and 2.1 for rural, golf, and urban ponds respectively (Table 2). The average connectance (CONNECT) of both greenspace and aquatic habitats among rural, golf, and urban sites was similar and ranged from 70.1 to 88% (Table 2).

For each model, stationary distribution appeared to be achieved based upon well-mixed history plots and the Gelman and Rubin statistic (<1.01 for all monitored parameters; Gelman & Rubin, 1992). We report the results of each of our models below with respect to species occupancy (the estimated probability of occupancy for each individual species), group occupancy (the estimated probability of occupancy of the entire group or assemblage of species), and species richness (the number of turtle species).

Results of Model 1 (investigating the influence of rural, urban, or golf pond types) indicate no difference in turtle species occupancy by pond type as 95% symmetric credible intervals (CI) for each species and pond type contained zero. When all turtle species were considered together, as an assemblage, results of Model 1 indicate no difference in group occupancy by pond type [mean parameter estimates: $\mu_{\alpha 1}$ rural 1.08 (CI -1.96 to 3.85), $\mu_{\alpha 2}$ urban 1.54 (CI -1.35 to 4.12), and $\mu_{\alpha 3}$ golf 0.78 (CI -2.11 to 3.48)]. Regarding species richness, results of Model 1 indicate no difference between rural and urban ponds regarding the mean difference in number of species as credible intervals contained zero (Table 3). Similarly, there was no difference between golf and rural ponds regarding the mean difference in number of species (i.e., credible intervals contained zero; Table 3). Golf ponds, however, had greater species richness than urban ponds (mean difference of 0.62 [CI: 0.1–1.40] species; posterior probability golf > urban = 0.99; Table 3).

Results of Model 2 (investigating the influence of aquatic habitats) indicate no difference in individual turtle species occupancy regarding the configuration of surrounding aquatic habitats within 500 m of each pond as 95% CI's for each species contained zero. When all turtles were considered together, as an assemblage,

results of Model 2 indicate no difference in group occupancy [mean parameter estimates for the aquatic habitat covariates: $\mu_{\alpha 1}$ ENN 0.09 (CI -2.09 to 2.43), $\mu_{\alpha 2}$ IJI -0.25 (CI -1.74 to 1.16), $\mu_{\alpha 3}$ PLAND 0.01 (CI -1.16 to 1.12), and $\mu_{\alpha 4}$ CONNECT 0.15 (CI -1.44 to 1.83)]. Results of Model 2 indicate no difference between rural, urban, or golf ponds regarding the mean difference in species richness as credible intervals contained zero (Table 3).

Results of Model 3 (investigating the influence of terrestrial habitats) indicate no difference in individual turtle species occupancy regarding the configuration of surrounding aquatic habitats within 500 m of each pond as 95% CI's for each species contained zero. When all turtles were considered together, as an assemblage, results of Model 3 indicate no difference in group occupancy [mean parameter estimates for the terrestrial habitat covariates: $\mu_{\alpha 1}$ ENN 0.82 (CI -0.76 to 2.61), $\mu_{\alpha 2}$ IJI -0.09 (CI -1.08 to 0.84), $\mu_{\alpha 3}$ PLAND 0.07 (CI -1.97 to 2.23), and $\mu_{\alpha 4}$ CONNECT 0.36 (CI -1.45 to 2.30)]. Regarding species richness, results of Model 3 indicate no difference between rural, urban, or golf ponds regarding the mean difference in number of species as credible intervals contained zero (Table 3).

When all turtle species were considered together, as an assemblage, results of Model 4 (investigating the influence greenspace [terrestrial plus aquatic habitats]) indicate a significant response in turtle occupancy regarding greenspace configuration. Mean responses to all four occupancy covariates for Model 4 varied (Table 4; greenspace mean parameter estimates [$\mu_{\alpha 1}$ ENN -0.78 (CI -0.48 to 2.46), $\mu_{\alpha 2}$ IJI -0.35 (CI -1.54 to 0.78), $\mu_{\alpha 3}$ PLAND, 0.08 (CI -2.04 to 1.92), and $\mu_{\alpha 4}$ CONNECT 0.92 (CI 0.12–2.15)]) suggesting that turtles occurred more frequently when greenspace patches were closer together, less interspersed/more aggregated, larger in area, and more physically connected (Table 4). However, three occupancy covariates (ENN, IJI, PLAND) contained positive and negative values in the 95% credible intervals listed above, reflecting uncertainty in the mean response of the assemblage, independent of among-species variation. Thus, only a strong relationship between increasing occupancy with increasing connectance of greenspaces is inferred. When examining the absolute value of the coefficient of variation (CV; $[\sigma \div |\mu|]$) we found that across-species standard deviation (σ) for the ENN, IJI, and PLAND covariate effects were greater than the corresponding mean (μ) covariate estimates (i.e., greater than one, Table 4; $CV_{\alpha 1} = 1.14$, $CV_{\alpha 2} = 2.29$, and $CV_{\alpha 3} = 22.3$), however, the standard deviation across species for the CONNECT covariate effect was less than the mean estimate ($CV_{\alpha 4} = 0.85$). The CV ratio is used to compare standard deviations between different means and summarizes the degree of uncertainty relative to the mean. Thus, our model indicated that the occupancy response to greenspace connectance (CONNECT) was consistent across species, while the responses to greenspace nearest neighbor (ENN), aggregation (IJI), and percent of landscape (PLAND) were not. Regarding species richness, results of Model 4 indicate no difference between rural and urban ponds regarding the mean difference in number of species as credible intervals contained zero (Table 3). Golf ponds, however, had greater species richness than rural ponds (mean difference of 0.40 [CI: 0.0–1.0] species; posterior probability golf > urban = 0.98; Table 3). Likewise, golf ponds had greater species richness than urban ponds (mean difference of 0.53 [CI: 0.10–1.00] species; posterior probability golf > urban = 0.99; Table 3).

We found that occupancy of four species (eastern mud turtle, pond slider, snapping turtle, and eastern river cooter) increased substantially with greater than 40% connectance in greenspace (terrestrial and aquatic habitats) within 500 m of each pond (Table 4, Fig. 2; parameter estimates: eastern mud turtle 0.88: (CI 0.22–2.02), pond slider 0.95 (CI 0.50–2.19), snapping turtle 1.09 (CI 0.55–2.69), and eastern river cooter 1.46: (CI 0.17–4.04). Once greenspace connectance reaches above 80%, occupancy estimates for the snapping turtle and pond slider are 95%, eastern mud turtle is 80%;

Table 1

Proportion of sites where each species was detected, total number of captures, and total number of unique turtles observed.

		Proportion of sites (%)	Number of captures	Number of unique turtles
Snapping turtle	<i>Chelydra serpentina</i>	0.90	84	73
Painted turtle	<i>Chrysemys picta</i>	1.00	1288	770
Eastern mud turtle	<i>Kinosternon subrubrum</i>	0.70	66	52
Eastern river cooter	<i>Pseudemys concinna</i>	0.20	21	5
Eastern musk turtle	<i>Sternotherus odoratus</i>	0.45	85	72
Pond slider	<i>Trachemys scripta</i>	0.90	652	486
Spiny softshell	<i>Apalone spinifera</i>	0.05	1	1

Table 2

Quantification of land-cover surrounding suburban study ponds within the Piedmont of North Carolina, USA.

Pond type	Landcover type	Mean Metric values (range)			
		ENN (m) ^a	IJI (%) ^b	PLAND (%) ^c	CONNECT (%) ^d
Rural (500 m radius)	Greenspace	13.4 (0.5–23.3)	68.5 (44.7–97.8)	83.9 (68.1–98)	73.3 (0–100)
	Aquatic areas	253.3 (71.6–452.6)	17.7 (0–88.6)	1.8 (0.7–4.2)	90.7 (66.7–100)
Golf (500 m radius)	Greenspace	40.6 (13–86.6)	64.2 (27.3–98.3)	56.7 (36.9–82.5)	76.2 (48.9–100)
	Aquatic areas	53.4 (17.4–109.5)	48.7 (0–85.1)	2.6 (0.3–8.2)	87.7 (70.7–100)
Urban (500 m radius)	Greenspace	87.2 (26.9–239.1)	67.6 (41.9–96.9)	50.9 (31.1–63.2)	88 (71.4–100)
	Aquatic areas	216 (91.1–374)	65.3 (0–99.4)	2.1 (1.1–3.2)	70.1 (57.1–100)
Entire golf course	Greenspace	11.2 (0.01–25.8)	75.7 (31.6–99.2)	75.2 (45.1–98.3)	38.5 (0–100)
	Aquatic areas	181.8 (10.8–470.7)	7.2 (0–33)	4.2 (0.9–8.1)	48.4 (16.7–90)

^a ENN (Euclidean nearest neighbor)= mean distance (m) to nearest neighboring patch of same type, based on shortest edge-to-edge distance.

^b IJI (interspersion juxtaposition index)= quantifies landscape configuration and approaches 0 when the patches (e.g., greenspace or aquatic habitats) are adjacent to only like patches (i.e., clumped) and increases to 100% when patches are maximally interspersed throughout the specified radius.

^c PLAND (% land cover)= sum of class area divided by total landscape area.

^d CONNECT (connectance)= a % measure that assesses how each patch is connected to matching patches in the landscape. Based on the number of joinings between matching patch types, divided by the total number of possible joinings between matching patch types.

and eastern river cooter occupancy estimates increased from 0 to 25%. For the remaining two species (Fig. 2), 95% CI for this variable contained zero (eastern musk turtle: 0.59, 95% CI –0.45 to 1.52; painted turtle: 0.54, 95% CI –1.29 to 1.71; Table 4), indicating that greenspace connectance within 500 m likely has an uncertain effect on their occupancy. Just as we observed consistent, positive estimates of species-specific responses to increasing connectivity of greenspaces (Fig. 2), this pattern was further reflected in model-generated estimates (i.e., Model 4) of species richness at hypothetical sites for variable increases in percentage of connectivity. Specifically, species richness estimates increased with increasing percentage of connectance of greenspaces within 500 m of ponds and varied from a mean of 2.58 species at greenspaces that are 10% connected (95% CI 0.45–4.78) to 4.8 species at greenspaces that are 100% connected (95% CI 3.25–6.0; Fig. 3).

4. Discussion

We identified four turtle species (eastern mud turtle, pond slider, snapping turtle, and eastern river cooter) which strongly respond to increasing connectance of greenspace within a 500 m radius of suburban ponds. We also found estimates of species richness were greater for ponds located on golf courses as compared to ponds in urbanized areas. When we examined the effects of greenspace configuration, we found that estimated species richness was greater at golf ponds than either rural or urban ponds. Further, these trends in species richness were driven by increasing connectivity of greenspaces. Finally, we examined the configuration of terrestrial and aquatic habitats together, and also separately, and found that for semi-aquatic turtles, it is important to consider both of these habitat types collectively, as “greenspace”.

Table 3

Summary of mean difference in species richness between pond types and the posterior probability that the average species richness for one pond type is greater than another pond type. The mean difference in number of species is derived from calculations at each iteration of respective models. In the “Pond Type” column, the habitat with the greater species richness is listed first. Bold values indicate statistical significance.

Pond type	Mean difference in No. of species	Credible interval		Posterior probability
		2.50%	97.50%	
Model 1: pond type				
Rural vs. urban	0.30	–0.20	0.80	0.85
Golf vs. rural	0.32	–1.00	0.40	0.90
Golf vs. urban	0.62	0.10	1.40	0.99
Model 2: Configuration of aquatic habitats				
Rural vs. urban	0.14	–0.50	0.70	0.65
Golf vs. rural	0.16	–0.80	0.40	0.75
Golf vs. urban	0.30	–0.20	0.80	0.91
Model 3: Configuration of terrestrial habitats				
Rural vs. urban	0.17	–0.30	0.60	0.71
Golf vs. rural	0.27	–0.80	0.20	0.95
Golf vs. urban	0.36	–0.10	0.80	0.96
Model 4: Configuration of greenspace habitats				
Rural vs. urban	0.14	–0.30	0.50	0.71
Golf vs. rural	0.40	0.00	1.00	0.98
Golf vs. urban	0.53	0.10	1.00	0.99

Table 4

Summary of Model 4 hyper-parameters for occupancy covariates for semi-aquatic turtles in suburban ponds within the Piedmont of North Carolina, USA. The symbol μ indicates a mean assemblage response (i.e., all species together) while σ indicates the standard deviation in the response to the covariate across species. Bold values indicate statistical significance. Refer to Table 2 for definitions of "Metric Type".

Species	Parameter	Metric type	Parameter estimate	Occupancy estimate (%)	Standard deviation	Credible intervals	
						2.5%	97.5%
<i>Chelydra serpentina</i>	α_1	ENN	0.73	0.67	0.94	-0.88	3.01
	α_2	IJI	0.01	0.50	0.73	-1.20	1.74
	α_3	PLAND	-0.79	0.31	0.99	-2.86	1.12
	α_4	CONNECT	1.09	0.75	0.70	0.55	2.69
<i>Chrysemys picta</i>	α_1	ENN	0.69	0.67	0.87	-0.90	2.70
	α_2	IJI	-0.38	0.41	0.69	-1.82	1.04
	α_3	PLAND	0.06	0.51	1.03	-1.95	2.16
	α_4	CONNECT	0.54	0.63	0.73	-1.29	1.71
<i>Kinosternon subrubrum</i>	α_1	ENN	0.67	0.66	0.66	-0.49	2.15
	α_2	IJI	-0.72	0.33	0.65	-2.25	0.35
	α_3	PLAND	1.66	0.84	1.03	-0.14	3.96
	α_4	CONNECT	0.88	0.71	0.53	0.22	2.02
<i>Pseudemys concinna</i>	α_1	ENN	0.42	0.60	0.90	-1.45	2.31
	α_2	IJI	-0.78	0.31	0.84	-2.88	0.49
	α_3	PLAND	0.30	0.57	1.11	-1.71	2.99
	α_4	CONNECT	1.46	0.81	0.96	0.17	4.04
<i>Sternotherus odoratus</i>	α_1	ENN	0.93	0.72	0.74	-0.20	2.74
	α_2	IJI	-0.19	0.45	0.51	-1.16	0.85
	α_3	PLAND	-0.38	0.41	0.59	-1.61	0.74
	α_4	CONNECT	0.59	0.64	0.50	-0.45	1.52
<i>Trachemys scripta</i>	α_1	ENN	1.25	0.78	1.10	-0.34	4.07
	α_2	IJI	-0.06	0.49	0.66	-1.21	1.43
	α_3	PLAND	-1.34	0.21	0.97	-3.41	0.35
	α_4	CONNECT	0.95	0.72	0.56	0.50	2.19
Mean assemblage response	$\mu_{\alpha 1}$	ENN	-0.78	0.31	0.75	-0.48	2.46
	$\sigma_{\alpha 1}$	ENN	0.89	—	0.87	0.03	3.16
	$\mu_{\alpha 2}$	IJI	-0.35	0.41	0.59	-1.54	0.78
	$\sigma_{\alpha 2}$	IJI	0.80	—	0.76	0.03	2.74
	$\mu_{\alpha 3}$	PLAND	0.08	0.52	0.98	-2.04	1.92
	$\sigma_{\alpha 3}$	PLAND	1.78	—	1.14	0.29	4.76
	$\mu_{\alpha 4}$	CONNECT	0.92	0.72	0.57	0.12	2.15
	$\sigma_{\alpha 4}$	CONNECT	0.79	—	0.78	0.02	2.82

4.1. Influence of pond type and greenspace connectance on occupancy and richness

We found no effect of pond type (rural, urban, or golf) on turtle occupancy, either for individual species or when considering the response of the turtle assemblage as a whole, perhaps indicating that, although the land-use surrounding our study ponds was different, overall, they are similarly suburbanized. However, a

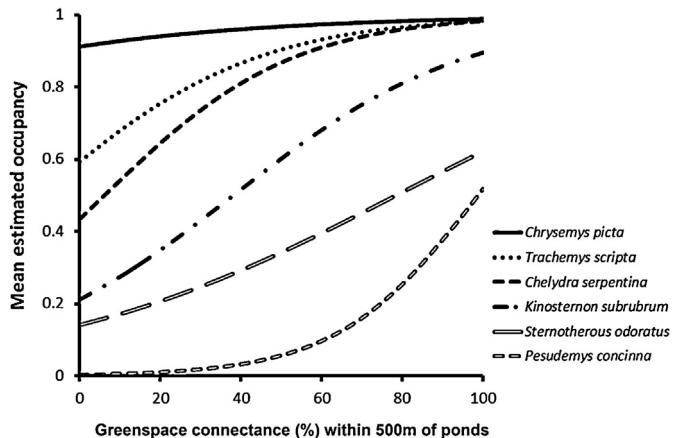


Fig. 2. Relationship between estimated probability of occupancy of six semi-aquatic turtle species versus greenspace connectance (%) within a 500 m radius of 20 ponds in the western Piedmont of NC, USA.

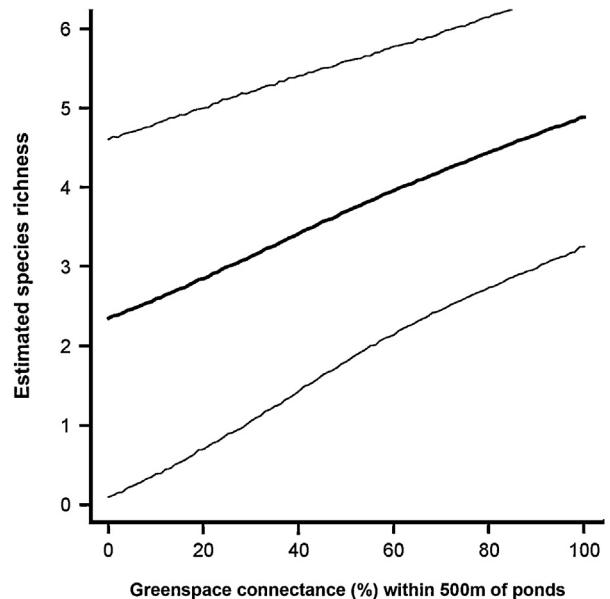


Fig. 3. Estimated semi-aquatic turtle species richness at suburban ponds within the Piedmont of North Carolina, USA in relation to increasing connectivity of greenspaces within a 500 m radius. Bold line represents the posterior mean and dashed thin lines represent a 95% credible interval of the posterior mean.

larger number of sample sites, particularly rural and urban, would likely improve our ability to interpret any patterns. In addition, as mentioned previously, finer-scale differences in pond-type such as density of roads, nutrient and food availability, or structural difference in ponds may exist which also may drive un-observed patterns of turtle occupancy.

We did, however, find that estimated species richness was higher in ponds located on golf courses compared to those in urbanized areas. This may be because nearly all golf courses in our study had several ponds. In our study, golf courses contained an average of 13 water bodies (range 4–25) and 6 out of ten contained lakes or streams in addition to ponds; one contained a large marsh in addition to ponds and streams. Because some semi-aquatic turtles prefer lentic water bodies, such as *C. picta*, *C. serpentina*, *T. scripta*, and *K. subrubrum*, and others prefer lotic water bodies such as *P. concinna* and *A. spinifera* (Ernst & Lovich, 2009), the tendency for golf courses to have somewhat diverse aquatic habitat types may explain our finding of increased species richness at golf courses. Further, the potentially diverse array of aquatic habitats on golf courses likely also includes a range of physical characteristics that suit more species of turtle. For example, larger ponds may provide turtles with more resources, such as food and basking sites, and a reduction in aggressive interactions (e.g., for *C. serpentina*; Galbraith, Chandler, & Brooks, 1987) but small ponds are critical for semi-aquatic turtle persistence in a landscape (Gibbs, 1993) where species, such as *C. picta* may increase in abundance with the presence of organic substrate and abundant shoreline vegetation (Marchand & Litvaitis, 2004). Other factors may include the tendency for golf courses to have large expanses of open-canopy habitat which is preferential for nesting turtles (Bodie & Semlitsch, 2000; Congdon & Gatten, 1989). As discussed by Price et al. (in press), urbanized areas are expected to have high abundances of human-subsidized predators, which frequently consume turtle eggs (Marchand & Litvaitis, 2004), but some studies (i.e., Foley, Price, & Dorcas, 2012) found depredation rates on simulated turtle nests to be similar between golf, farm and residential ponds and instead, they suggest a greater threat is road mortality incurred during nesting and dispersal events (Aresco, 2005; Steen et al., 2006). In addition, some golf courses may be more species rich because of increased nutrient levels from fertilizers which result in greater aquatic plant growth (a turtle food source; Gibbons, 2008; Knight & Gibbons, 1968); however, although we did not measure nutrient loads, all of the ponds in our study were likely enriched through fertilization of residential lawns, golf course fairways, or from agriculture and cattle.

When examining the model accommodating potential differences in greenspace configuration, we found that estimates of species richness were higher on golf courses than either rural or urban ponds and that this relationship was likely driven by the connectance of greenspaces. Galat et al. (1998) found higher turtle species richness in connected wetlands and suggest that these habitats and their interaction with the Missouri River may contribute key processes that are important to overall turtle biodiversity, specifically, connectivity of habitat patches which may lead to successful dispersal among ponds (Bowne, Bowers, & Hines, 2006). Although golf courses may provide more connectance of greenspace, it is critical to note that development trends indicate a significant proportion of golf courses constructed in recent years are associated with real estate projects (Mulvihill, 2001). Indeed, several of the golf course ponds in our study had significant amount of residential development (>30%) within the course boundaries and Price et al. (in press) found that this negatively affected abundances of semi-aquatic turtles. They suggest that residential development within golf courses (and thus likely a decrease in greenspace connectance) may significantly influence

the potential a golf courses holds as wildlife habitat. In our case, residential development in golf courses may likely influence the course's potential to maintain higher levels of semi-aquatic turtle species richness.

4.2. Importance of greenspace connectance

The reasons for the relationship between higher occupancy probability and species richness with increasing connectance may be due to several factors, including a fostering of metapopulation dynamics, and in our study these results are likely directly related to turtle movements through terrestrial environments. Even though patterns of terrestrial movement are unique for each species, the importance of terrestrial activity to the population ecology of aquatic turtles is well documented, especially for the eastern mud turtle, but also for the pond slider, snapping turtle, and painted turtle (Bennett, Gibbons, & Franson, 1970; Buhlmann, 1995; Buhlmann & Gibbons, 2001; Burke & Gibbons, 1995; Ernst & Lovich, 2009; Gibbons, 1970, 1983; Harden & Dorcas, 2008; Harden et al., 2009), although the eastern river cooter has also been documented utilizing terrestrial areas (Marchand, 1942; Minton, 1972). Many turtles, including all species we observed in this study, are equally as dependent on terrestrial habitats as they are on the aquatic habitats surrounding or connecting wetlands. Such terrestrial areas are critical for nesting, hibernating, aestivating, foraging, adult residency, and terrestrial dispersal; and while these terrestrial activities vary from species to species, they are each dependent on terrestrial connections between neighboring wetlands (Buhlmann & Gibbons, 2001; Gibbons, 2003). In our study, greenspaces are comprised of natural/semi-natural terrestrial land-cover linked by neighboring aquatic habitats and thus serve as travel routes which maintain metapopulation processes by facilitating immigration and gene exchange among populations (e.g., Howeth, McGaugh, & Hendrickson, 2008); this movement between populations is critical for species persistence across landscapes (Bowne et al., 2006). Given the long distance some turtles travel, these greenspaces also may facilitate colonization, which might otherwise be impossible without accessible terrestrial corridors (Tuberville, Gibbons, & Greene, 1996).

Bowne et al. (2006) found that regarding turtle movement, connectivity of ponds was influenced by the quality of those ponds which leads to active selection or avoidance of habitat by turtles. Similarly, Cosentino et al. (2010) found that highly connected wetlands had high probabilities of being occupied by painted turtles, whereas occupancy of isolated sites was likely driven by hydroperiod, emergent vegetation cover, and pH; thus integration of habitat quality of wetlands was necessary to better explain patterns of occupancy and turnover. Roe et al. (2009) investigated wetland connectivity via movements of a freshwater turtle (*Chelodina longicollis*) and found that the probability of movement decreased with increasing distance between wetlands and suggest that groups of wetlands should be considered the minimum habitat units harboring local populations (Haig, Mehlman, & Oring, 1998; Petranka, Smith, & Scott, 2004; Roe & Georges, 2007). Joyal et al. (2001) found that spotted turtles (*Clemmys guttata*) and Blanding's turtles (*Emydoidea blandingii*) used several wetlands and suggest that important features of wetland complexes include the overall size of the complex, the juxtaposition of wetlands of different types, and wetland isolation. Findings such as these underscore the importance of pond connectivity in our study, particularly in urban areas, where road mortality is a major threat to nesting and dispersing turtles (Aresco, 2005; Steen et al., 2006). Among our 20 study ponds, the number of other ponds within 500 m ranged between 2 and 7 and averaged 4.6 and we have observed inter-pond movement among this study's marked turtles. Maintaining greenspace connectivity between these terrestrial semi-natural areas and adjoining aquatic

habitats is important for the various life-stages of semi-aquatic turtles (e.g., Bowne et al., 2006).

The importance of maintaining connectivity of greenspace (i.e., terrestrial plus aquatic areas) is perhaps greatest in terms of larger-scale movements. We found that increased connectance of greenspace resulted in increased turtle occupancy probability and increased species richness. Each of our 20 study ponds is man-made and ages of ponds average 36.7 years (range: at least 12–67 years). The degree of connectance of greenspace surrounding each pond likely facilitated turtle movement, and the resultant occupancy of these ponds. In general, there are four categories of long-range movement in turtles (Gibbons, 1986) which include excursions by females to suitable nesting sites (Gibbons, 1968; Obbard & Brooks, 1980), seasonal migrations to and from overwintering sites (Converse, Iverson, & Savidge, 2002; Steen, Sterrett, Miller, & Smith, 2007), departure from an unsuitable habitat such as those experiencing drought (Gibbons, Greene, & Congdon, 1983) or flooding (McAuliffe, 1978), and movements by males in search of mating opportunities (Berry & Shine, 1980). In urban areas, where effects of increasing human development have been shown to negatively affect turtles via road mortality (Steen & Gibbs, 2004), increased predation (Baldwin, Marchand, & Litvaitis, 2004), and habitat loss (Klemens, 2000), maintaining connectivity of greenspaces is likely to be very important, especially because semi-aquatic turtles can be affected by alterations to either their aquatic habitats or the surrounding landscape (Marchand & Litvaitis, 2004).

Interestingly, we did not observe any effects of greenspace connectance for the eastern musk turtle or painted turtle; for the eastern musk turtle this is not particularly surprising because home ranges are generally confined to one body of water, they hibernate underwater, and overland movements are likely seasonal or forced (e.g., drought) (Ernst & Lovich, 2009; Semlitsch & Bodie, 2003; Williams, 1952). Conversely, the painted turtle does use terrestrial areas (Baldwin et al., 2004; Ernst & Lovich, 2009), and was observed at every study pond on several occasions. This, in conjunction with using occupancy data, can make distinguishing a relationship to various land-cover patterns very difficult and probability of occupancy of this species in suburban ponds may be affected by variables we did not measure. Examples of other variables that may influence turtles include organic substrates and abundant coverage by shoreline vegetation (Marchand & Litvaitis, 2004) which is a food source (Sexton, 1959), hydroperiod, pH, and canopy coverage (Cosentino et al., 2010), and also availability of plentiful basking sites in deep water (Cadi & Joly, 2003). In addition, while our buffer of 500 m is likely large enough to incorporate all turtle movements around ponds, most movements are likely to be less (Steen et al., 2012), and for some species a smaller buffer may be more effective at characterizing trends in occupancy and landscape configuration. Alternatively, we may not have observed any effects of greenspace connectance for musk turtles and painted turtles because of their biology (i.e., differences among terrestrial use patterns) rather than unmeasured pond or landscape features. Both species have extremely different terrestrial use patterns; musk turtles being strongly tied to one water body and painted turtles exhibiting an enhanced propensity and ability to travel overland between aquatic habitats. Compared to some turtle species in our study, terrestrial migration distances by painted turtles can be quite large (Semlitsch & Bodie, 2003) and males have been shown to demonstrate a remarkable ability to disperse between very distant aquatic habitats over time (Tuberville et al., 1996), perhaps explaining their presence at 100% of our study sites.

4.3. Value of population viability analyses

Although a positive relationship between occupancy and greenspace connectance was found within this study, viability

analyses must be conducted to determine whether the populations are stable and whether greenspaces actually represent a long-term management strategy for sustaining turtle populations. Increased connectivity of greenspaces may allow individuals to successfully disperse and increase a population's long-term survival; however occupancy is not the appropriate metric for examining long-term population viability. For example, ponds can become sinks (Howes et al., 2009) where turtles survive but may not reproduce at rates that sustain their population, and it may take decades for this to be evident if occupancy is the only measure. Additionally, while we focus on the importance of greenspaces and their connectivity, we point out that all greenspaces in our study may not support turtles to the same degree (e.g., a pond bordered by an undisturbed forest vs. a woodlot fragment) and also that certain important characteristics of urban areas are more detrimental for turtles (e.g., roads; Aresco, 2005; Steen et al., 2006) and our general characterization of urban landcover does not account for this.

5. Conclusions

Our study suggests that golf courses had higher estimates of species richness than urban ponds and when considering landscape configuration, the trend for increased turtle richness at golf courses surpassed both rural and urban ponds. This trend is driven by increasing connectance of greenspaces. Our study also shows that semi-aquatic turtle occupancy increased with increased connectance of greenspaces, which, in our study, were composed of both terrestrial and aquatic areas together. These greenspace areas are critical in terms of nesting, hibernating, foraging, and dispersal which are activities dependent on terrestrial connections with water bodies (Buhlmann & Gibbons, 2001; Gibbons, 2003). Therefore, maintaining connectivity of greenspaces is important for turtle persistence in urban areas and should be considered when planning urban areas. Preserving or establishing a maximally connected combination of forested, wetland, and other natural habitats, along with some open areas for nesting (with limited high-impact development; Marchand & Litvaitis, 2004) may provide the best long term strategy for turtles in suburban landscapes.

Acknowledgments

We thank B. Halstead for his extensive assistance developing our statistical model. We thank M. Kern, C. Oldham, R. Bauer, S. Foley, E. Eskew, S. Hunt, and C. Williams for assisting in fieldwork. For help in locating study ponds, we thank D. Testerman. We thank the participating landowners for the use of their property during this project. Funding for this project was provided by Davidson College Biology Department, Duke Energy, the Duke Endowment through the Davidson Research Initiative, and the National Fish and Wildlife Foundation Wildlife Links Program. In addition, we thank three anonymous reviewers for their comments and suggestions which improved the manuscript.

References

- Aresco, M. J. (2005). The effect of sex-specific terrestrial movements and roads on the sex ratio of freshwater turtles. *Biological Conservation*, 123, 37–44.
- Baldwin, E. A., Marchand, M. N., & Litvaitis, J. A. (2004). Terrestrial habitat use by nesting painted turtles in landscapes with different levels of fragmentation. *Northeastern Naturalist*, 11, 41–48.
- Bennett, D. H. (1972). Notes on the terrestrial wintering of mud turtles (*Kinosternon subrubrum*). *Herpetologica*, 28, 245–247.
- Bennett, D. H., Gibbons, J. W., & Franson, J. C. (1970). Terrestrial activity in aquatic turtles. *Ecology*, 51, 738–740.
- Berry, J. F., & Shine, R. (1980). Sexual size dimorphism, and sexual selection in turtles (Order Testudines). *Oecologia*, 44, 185–191.
- Bierwagen, B. (2007). Connectivity in urbanizing landscapes: The importance of habitat configuration, urban area size, and dispersal. *Urban Ecosystems*, 10, 29–42.

- Bodie, J. R., & Semlitsch, R. D. (2000). Spatial and temporal use of floodplain habitats by lentic and lotic species of aquatic turtles. *Oecologia*, 122, 138–146.
- Bowne, D. R., Bowers, M. A., & Hines, J. E. (2006). Connectivity in an agricultural landscape as reflected by interpond movements of a freshwater turtle. *Conservation Biology*, 20, 780–791.
- Buhlmann, K. A. (1995). Habitat use, terrestrial movements, and conservation of the turtle, *Dicrochelys reticularia* in Virginia. *Journal of Herpetology*, 29, 173–181.
- Buhlmann, K., & Gibbons, J. W. (2001). Terrestrial habitat use by aquatic turtles from a seasonally fluctuating wetland: Implications for wetland conservation boundaries. *Chelonian Conservation and Biology*, 4, 115–127.
- Burke, V. J., & Gibbons, J. W. (1995). Terrestrial buffer zones and wetland conservation: A case study on freshwater turtles in a Carolina bay. *Conservation Biology*, 9, 1365–1369.
- Cadi, A., & Joly, P. (2003). Competition for basking places between the endangered European pond turtle (*Emys orbicularis galloitalica*) and the introduced red-eared turtle (*Trachemys scripta elegans*). *Canadian Journal of Zoology*, 81, 1392–1398.
- Chamberlain, D. E., Gough, S., Vaughan, H., Vickery, J. A., & Appleton, G. F. (2007). Determinants of bird species richness in public green spaces. *Bird Study*, 54, 87–97.
- Cook, D. I. (1978). Trees, solid barriers, and combinations: Alternatives for noise control. In G. Hopkins (Ed.), *Proceedings of the National Urban Forestry Conference* (pp. 330–339). Syracuse, NY: USDA Forest Service, SUNY College of Environmental and Forestry.
- Congdon, J. D., & Gatten, R. E. (1989). Movements and energetics of nesting *Chrysemys picta*. *Herpetologica*, 45, 94–100.
- Converse, S. J., Iverson, J. B., & Savidge, J. A. (2002). Activity, reproduction and overwintering behavior of ornate box turtles (*Terrapene ornata ornata*) in the Nebraska Sandhills. *American Midland Naturalist*, 148, 416–422.
- Cosentino, B. J., Schooley, R. L., & Phillips, C. A. (2010). Wetland hydrology, area, and isolation influence occupancy and spatial turnover of the painted turtle, *Chrysemys picta*. *Landscape Ecology*, 25, 1589–1600.
- Cushman, S. A., McGarigal, K., & Neel, M. C. (2008). Parsimony in landscape metrics: Strength, universality, and consistency. *Ecological Indicators*, 8, 691–703.
- Dorazio, R. M., & Royle, J. A. (2005). Estimating size and composition of biological communities by modeling the occurrence of species. *Journal of the American Statistical Association*, 100, 389–398.
- Dorazio, R. M., Royle, J. A., Soderstrom, B., & Glimskar, A. (2006). Estimating species richness and accumulation by modeling species occurrence and detectability. *Ecology*, 87, 842–854.
- Ernst, C. H., & Lovich, J. E. (2009). *Turtles of the United States and Canada* (2nd ed., pp.). Washington, DC, USA: Smithsonian Institution.
- Eskew, E. A., Price, S. J., & Dorcas, M. E. (2010). Survival and recruitment of semi-aquatic turtles in an urbanized region. *Urban Ecosystems*, 13, 365–374.
- ESRI Inc. (2010). *Arc Info User's Manual, Version 9.3.1*. Redlands, CA: Environmental Systems Research Institute Inc.
- Fabianek, F., Gagnon, D., & Delorme, M. (2011). Bat distribution and activity in Montréal Island green spaces: Responses to multi-scale habitat effects in a densely urbanized area. *Ecoscience*, 18(1), 9–17.
- Failey, E. L., McCoy, J. C., Price, S. J., & Dorcas, M. E. (2007). Ecology of turtles inhabiting golf course and farm ponds in the western Piedmont of North Carolina. *Journal of the North Carolina Academy of Science*, 123, 221–232.
- Foley, S. M., Price, S. J., & Dorcas, M. E. (2012). Nest-site selection and nest depredation of semi-aquatic turtles on golf courses. *Urban Ecosystems*, 15, 489–497.
- Galat, D. L., Fredrickson, L. H., Humborg, D. D., Bataille, K. J., Bodie, J. R., Dohrenwend, J., et al. (1998). Flooding to restore connectivity of regulated, large-river wetlands. *BioScience*, 48, 721–733.
- Galbraith, D. A., Chandler, M. W., & Brooks, R. J. (1987). The fine structure of home ranges of male *Cheydrea serpentina*: Are Snapping Turtles territorial? *Canadian Journal of Zoology*, 65, 2623–2629.
- Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, 7, 457–472.
- Gibbons, J. W. (1968). Population structure and survivorship in the painted turtle, *Chrysemys picta*. *Copeia*, 1968, 260–268.
- Gibbons, J. W. (1970). The influence of terrestrial activities and the population dynamics of aquatic turtles. *American Midland Naturalist*, 83, 404–415.
- Gibbons, J. W. (1983). Reproductive characteristics and ecology of the mud turtle, *Kinosternon subrubrum* (Lacepede). *Herpetologica*, 39, 254–271.
- Gibbons, J. W. (1986). Movement patterns among turtle populations: Applicability to management of the desert tortoise. *Herpetologica*, 42, 104–113.
- Gibbons, J. W. (2003). Terrestrial habitat: A vital component for herpetofauna of isolated wetlands. *Wetlands*, 23(3), 630–635.
- Gibbons, J. W. (2008). Pond Slider (*Trachemys scripta*). In J. Jensen, C. D. Camp, J. W. Gibbons, & M. Elliot (Eds.), *Amphibians and reptiles of Georgia* (pp. 500–502). Athens, GA: University of Georgia Press.
- Gibbons, J. W., Greene, J. L., & Congdon, J. D. (1983). Drought-related responses of aquatic turtle populations. *Journal of Herpetology*, 17, 242–246.
- Gibbons, J. W., & Lovich, J. (1990). Sexual dimorphism in turtles with emphasis on the slider turtle (*Trachemys scripta*). *Herpetological Monographs*, 4, 1–29.
- Gibbs, J. P. (1993). Importance of small wetlands for the persistence of local populations of wetland-associated animals. *Wetlands*, 13, 25–31.
- Griffith, J. A., Martinko, E. A., & Price, K. P. (2000). Landscape structure analysis of Kansas at three scales. *Landscape and Urban Planning*, 52, 45–61.
- Grove, N. (1990). Greenways: Paths to the future. *National Geographic*, 177(6), 77–99.
- Haig, S. M., Mehlman, D. W., & Oring, L. W. (1998). Avian movements and wetland connectivity in landscape conservation. *Conservation Biology*, 12, 749–758.
- Hair, J. F., Anderson, J. E., Tatham, R. L., & Black, W. C. (1998). *Multivariate data analysis* (5th ed., pp.). Upper Saddle River, NJ: Prentice Hall.
- Harden, L. A., & Dorcas, M. E. (2008). Using thermal biology to investigate habitat use and activity of eastern mud turtles (*Kinosternon subrubrum subrubrum*) on a golf course. In R. E. Jung, & J. C. Mitchell (Eds.), *Herpetological conservation (Vol. 3) Urban herpetology*. Salt Lake City, UT: Society for the Study of Amphibians and Reptiles.
- Harden, L. A., Price, S. J., & Dorcas, M. E. (2009). Terrestrial activity and habitat selection of eastern mud turtles (*Kinosternon subrubrum*) in a fragmented landscape: Implications for habitat management of golf courses and other suburban environments. *Copeia*, 2009, 78–84.
- Harrison, C., Burgess, J., Millward, A., & Dawe, G. (1995). Accessible natural greenspace in towns and cities: A review of appropriate size and distance criteria. English Nature Research Report No. 153, English Nature, Peterborough.
- Howes, B. J., Brown, J. W., Gibbs, H. L., Herman, T. B., Mockford, S. W., Prior, K. A., et al. (2009). Directional gene flow patterns in disjunct populations of the black ratsnake (*Pantherophis obsoletus*) and Blanding's turtle (*Emydoidea blandingii*). *Conservation Genetics*, 10, 407L 417.
- Howeth, J. G., McGaugh, S. E., & Hendrickson, D. A. (2008). Contrasting demographic and genetic estimates of dispersal in the endangered Coahuilan box turtle: A contemporary approach to conservation. *Molecular Ecology*, 17, 4209–4221.
- Jim, C. Y., & Chen, S. S. (2003). Comprehensive greenspace planning based on landscape ecology principals in compact Nanjing City, China. *Landscape and Urban Planning*, 65(3), 95–116.
- Joyal, L. A., McCollough, M., & Hunter, M. L. (2001). Landscape ecology approaches to wetland species conservation: A case study of two turtle species in southern Maine. *Conservation Biology*, 15, 1755–1762.
- Kéry, M., Royle, J. A., Plattner, M., & Dorazio, R. M. (2009). Species richness and occupancy estimation in communities subject to temporary emigration. *Ecology*, 90, 1279–1290.
- Klemens, M. W. (1993). *Amphibians and reptiles of Connecticut and adjacent regions*. Hartford, Connecticut: State Geological and Natural History Survey of Connecticut.
- Klemens, M. W. (Ed.). (2000). *Turtle Conservation*. Washington: Smithsonian Institution Press.
- Knapp, R. A., Matthews, K. R., Preisler, H. K., & Jellison, R. (2003). Developing probabilistic models to predict amphibian site occupancy in a patchy landscape. *Ecological Applications*, 13, 1069–1082.
- Knight, A. W., & Gibbons, J. W. (1968). Food of the painted turtle, *Chrysemys picta*, in a polluted river. *American Midland Naturalist*, 80(2), 559–562.
- Kong, F., Yin, Y., Nakagoshi, N., & Zong, Y. (2010). Urban green space network development for biodiversity conservation: Identification based on graph theory and gravity modeling. *Landscape and Urban Planning*, 95, 16–27.
- Linck, M. H., DePari, J. A., Butler, B. O., & Graham, T. E. (1989). Nesting behavior of the turtle, *Emydoidea blandingii*, in Massachusetts. *Journal of Herpetology*, 23, 442–444.
- Lindeman, P. V. (1990). Closed and open model estimates of abundance and test of model assumption for two populations of the turtle, *Chrysemys picta*. *Journal of Herpetology*, 24, 78–81.
- Link, W. A., Cam, E., Nichols, J. D., & Cooch, E. G. (2002). Of BUGS and birds: Markov Chain Monte Carlo for hierarchical modeling in wildlife research. *Journal of Wildlife Management*, 66, 277–291.
- Little, C. (1990). *Greenways for America*. Baltimore, MD: Johns Hopkins University Press.
- Loram, A., Tratalos, J., Warren, P. H., & Gaston, K. J. (2007). Urban domestic gardens (X): The extent and structure of the resource in five major cities. *Landscape Ecology*, 22, 601–615.
- Lunn, D. J., Thomas, A., Best, N., & Spiegelhalter, D. (2000). WinBUGS – A Bayesian modelling framework: Concepts, structure, and extensibility. *Statistics and Computing*, 10, 325–337.
- Magle, S. B., Theobald, D. M., & Crooks, K. R. (2009). A comparison of metrics predicting landscape connectivity for a highly interactive species along an urban gradient in Colorado, USA. *Landscape Ecology*, 24, 267–280.
- Marchand, L. J. (1942). A contribution to a knowledge of the natural history of certain freshwater turtles. M.A. Thesis. University of Florida, Gainesville, Florida.
- Marchand, M. N., & Litvaitis, J. A. (2004). Effects of habitat features and landscape composition on the population structure of a common aquatic turtle in a region undergoing rapid development. *Conservation Biology*, 18, 758–767.
- McAuliffe, J. R. (1978). Seasonal migrational movements of a population of the western painted turtle, *Chrysemys picta bellii* (Reptilia, Testudinidae). *Journal of Herpetology*, 12, 143–149.
- McGarigal, K., Cushman, S. A., Neel, M. C., & Ene, E. (2002). FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available from: <http://www.umass.edu/landeco/research/fragstats/fragstats.html>
- McGarigal, K., & Marks, B. J. (1995). *FRAGSTATS: Spatial pattern analysis program for quantifying landscape structure*. Portland, Oregon: USDA.
- McGeoch, M. A., & Chown, S. L. (1997). Impact of urbanization on a gall-inhabiting Lepidoptera assemblage: The importance of reserves in urban areas. *Biodiversity and Conservation*, 6, 979–993.
- McPherson, E. G. (1990). Modeling residential landscape water and energy use to evaluate water conservation policies. *Landscape Journal*, 9(2), 122–134.
- Meier, A. K. (1991). Measured cooling savings from vegetative landscapes. In E. Vine, D. Crawley, & P. Centolella (Eds.), *Energy efficiency and the environment*:

- Forging the link* (pp. 321–334). Washington, DC: American Council for an Energy-Efficient Economy.
- Minton, S. A. (1972). *Amphibians and reptiles of Indiana*. Indianapolis: Indiana University Press.
- Moore, C. H., Van Niel, K., & Harvey, E. S. (2011). The effect of landscape composition and configuration on the spatial distribution of temperate demersal fish. *Ecography*, 34, 425–435.
- Mulvihill, D. A. (2001). *Golfcourse development in residential communities*. Washington, DC, USA: The Urban Land Institute.
- NC OneMap. (2011). *Geospatial portal downloads*. <http://data.nconemap.com/geoportal/catalog/search/search.page>. Accessed 20.08.11
- Obbard, M. E., & Brooks, R. J. (1980). Nesting migrations of the snapping turtle (*Chelydra serpentina*). *Herpetologica*, 36, 158–162.
- Ong, B. L. (2003). Green plot ratio: An ecological measure for architecture and urban planning. *Landscape and Urban Planning*, 63, 197–211.
- Petraska, J. W., Smith, C. K., & Scott, A. F. (2004). Identifying the minimal demographic unit for monitoring pond-breeding amphibians. *Ecological Applications*, 14, 1065–1078.
- Price, S. J., Dorcas, M. E., Gallant, A. L., Klaver, R. W., & Willson, J. D. (2006). Three decades of urbanization: Estimating the impact of land cover change on stream salamander populations. *Biological Conservation*, 133, 436–441.
- Price, S. J., Guzy, J. C., & Dorcas, M. E. Do ponds on golf courses provide suitable habitat for wetland-dependent animals in suburban areas? An assessment of turtle abundances. *Journal of Herpetology*, in press
- R Development Core Team. (2005). *R: A language and environment for statistical computing, reference index version 2.14.0*. Vienna, Austria: R Foundation for Statistical Computing. ISBN: 3-900051-07-0, URL: <http://www.R-project.org>
- Roe, J. H., Brinton, A. C., & Georges, A. (2009). Temporal and spatial variation in landscape connectivity for a freshwater turtle in a temporally dynamic wetland system. *Ecological Applications*, 19, 1288–1299.
- Roe, J. H., & Georges, A. (2007). Heterogeneous wetland complexes, buffer zones, and travel corridors: Landscape management for freshwater reptiles. *Biological Conservation*, 135, 67–76.
- Roe, J. H., Rees, M., & Georges, A. (2011). Suburbs: Dangers or drought refugia for freshwater turtle populations? *Journal of Wildlife Management*, 75, 1544–1552.
- Rowntree, R. A., & Nowak, D. J. (1991). Quantifying the role of urban forests in removing atmospheric carbon dioxide. *Journal of Arboriculture*, 17(10), 269–275.
- Rudie, R. J., & Dewers, R. S. (1984). Effects of tree shade on home cooling requirements. *Journal of Arboriculture*, 10(12), 320–322.
- Ryan, T. J., Conner, C. A., Douthitt, B. A., Sterrett, S. C., & Salsbury, C. M. (2008). Movement and habitat use of two aquatic turtles (*Graptemys geographica* and *Trachemys scripta*) in an urban landscape. *Urban Ecosystems*, 11, 213–225.
- Sanders, R. A. (1986). Urban vegetation impacts on the hydrology of Dayton, Ohio. *Urban Ecology*, 9, 361–376.
- Sauer, J. R., & Link, W. A. (2002). Hierarchical modeling of population stability and species group attributes from survey data. *Ecology*, 86, 1743–1751.
- Semlitsch, R. D., & Bodie, J. R. (2003). Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. *Conservation Biology*, 17, 1219–1228.
- Sexton, O. J. (1959). Spatial and temporal movements of a population of the painted turtles, *Chrysemys picta marginata* (Agassiz). *Ecological Monographs*, 29, 113–140.
- Simpson, J. R., & McPherson, E. G. (1996). Potential of tree shade for reducing residential energy use in California. *Journal of Arboriculture*, 22, 10–18.
- Smith, W. H. (1981). *Air pollution and forests*. New York: Springer.
- Solecki, W. D., Rosenzweig, C., Parshall, L., Popec, G., Clark, M., Cox, J., et al. (2005). Mitigation of the heat island effect in urban New Jersey. *Environmental Hazards*, 6, 39–49.
- Spinks, P. Q., Pauly, G. B., Crayon, J. J., & Shaffer, H. B. (2003). Survival of the western pond turtle (*Emys marmorata*) in an urban California environment. *Biological Conservation*, 113, 257–267.
- StatSoft, Inc. (2005). *STATISTICA data analysis software system, version 7.1*. Tulsa, OK, USA: Statsoft Inc.
- Steen, D. A., Areseco, M. J., Beilke, S. G., Compton, B. W., Congdon, E. P., Dodd, C. K., et al. (2006). Relative vulnerability of female turtles to road mortality. *Animal Conservation*, 9, 269–273.
- Steen, D. A., & Gibbs, J. P. (2004). Effects of roads on the structure of freshwater turtle populations. *Conservation Biology*, 18, 1143–1148.
- Steen, D. A., Gibbs, J. P., Buhlmann, K. A., Carr, J. L., Compton, B. W., Congdon, J. D., et al. (2012). Terrestrial habitat requirements of nesting freshwater turtles. *Biological Conservation*, 150(1), 121–128.
- Steen, D. A., Sterrett, S. C., Miller, S. A., & Smith, L. L. (2007). Terrestrial movements and microhabitat selection of overwintering subadult eastern mud turtles (*Kinosternon subrubrum*) in southwest Georgia. *Journal of Herpetology*, 41, 532–535.
- Sturtz, S., Ligges, U., & Gelman, A. (2005). *R2WinBUGS: A package for running WinBUGS from R*. *Journal of Statistical Software*, 12, 1–16.
- Tuberville, T. D., Gibbons, J. W., & Greene, J. L. (1996). Invasion of new habitats by male freshwater turtles. *Copeia*, 3, 713–715.
- VanDruff, L. W., & Rowse, R. N. (1986). Habitat association of mammals in Syracuse, New York. *Urban Ecology*, 9, 413–434.
- Williams, J. E. (1952). Homing behavior of the painted turtle and musk turtle in a lake. *Copeia*, 2, 76–82.
- Zipkin, E. F., Dewan, A., & Royle, J. A. (2009). Impacts of forest fragmentation on species richness: A hierarchical approach to community modeling. *Journal of Applied Ecology*, 46, 815–822.