Responses of riparian reptile communities to damming and urbanization

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ABSTRACT

Various anthropogenic pressures, including habitat loss, threaten reptile populations worldwide. Riparian zones are critical habitat for many reptile species, but these habitats are also frequently modified by anthropogenic activities. Our study investigated the effects of two riparian habitat modifications – damming and urbanization – on overall and species-specific reptile occupancy patterns. We used time-constrained search techniques to compile encounter histories for 28 reptile species at 21 different sites along the Broad and Pacolet Rivers of South Carolina. Using a hierarchical Bayesian analysis, we modeled reptile occupancy responses to a site's distance upstream from dam, distance downstream from dam, and percent urban land use. The mean occupancy response by the reptile community indicated that reptile occupancy and species richness were maximized when sites were farther upstream from dams. Species-specific occupancy estimates showed a similar trend of lower occupancy immediately upstream from dams. Although the mean occupancy response of the reptile community was positively related to distance downstream from dams, the occupancy response to distance downstream varied among species. Percent urban land use had little effect on the occupancy response of the reptile community or individual species. Our results indicate that the conditions of impoundments and subsequent degradation of the riparian zones upstream from dams may not provide suitable habitat for a number of reptile species.

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1. Introduction

Riparian zones, defined as transitional, semi-terrestrial areas regularly influenced by freshwater (Naiman et al., 2005), generally contain high levels of biodiversity (Naiman et al., 1993; Pollock et al., 1998). Riparian zones serve as dispersal corridors for many animal and plant species (Burbrink et al., 1998; Jansson et al., 2005) and are valuable reservoirs of biodiversity because they can support a distinct set of species relative to those found in non-riparian habitats (Sabo et al., 2005). Despite the importance of riparian zones for biodiversity, much of the riparian habitat in the United States has been affected by anthropogenic activities, such as damming, forest removal, grazing, water withdrawal, and urban development (Wissmar and Beschta, 1998).

Flow regulation through damming can be especially detrimental to riparian habitat. In the United States alone, over 75,000 large dams disrupt the flow of rivers (Poff and Hart, 2002). Damming changes the water quality of a river system by reducing the sediment load downstream (Allan and Castillo, 2008), increasing sediment load upstream (Baxter, 1977), and by lowering dissolved oxygen levels in impoundments (Clark et al., 2009). Damming has been linked to population declines of aquatic organisms including plants (Blanch et al., 2000), macroinvertebrates (Voelz and Ward, 1991), mussels (Vaughn and Taylor, 1999), and fish (Haxton and Findlay, 2008; Kinsolving and Bain, 1993; Liermann et al., 2012). Recent studies suggest that semi-aquatic species within riparian zone communities can also be negatively impacted by damming (Bateman et al., 2008; Eskew et al., 2012; Reese and Welsh, 1998a,b). Semi-aquatic species are sensitive to damming because flow regulation can fragment habitat by isolating the main river channel from adjacent riparian floodplains (Poff and Hart, 2002). Flow regulation through damming can also reduce periodic flooding, which can lead to population declines among organisms whose life histories are adapted to the river's natural flow regime (Bayley, 1995; Lytle and Poff, 2004; Townsend, 2001). Regulated rivers can provide suitable habitat for non-native organisms that would not thrive under naturally variable flow conditions, and these species may displace native species (Bunn and Arthington, 2002; Fuller et al., 2011; Lytle and Poff, 2004). Finally, high spate events caused by water releases from dams may displace individuals immediately downstream from dams (Lind et al., 1996).

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Urbanization can also have significant negative effects on riparian zones. Habitat loss as a result of urbanization threatens species across many taxonomic groups and is thought to be the leading cause of species endangerment in the United States (Czech et al., 2000). Adjacent to riparian zones, urbanization creates high levels of nitrification, limits denitrification, and lowers the water table (Groffman et al., 2003). Ecologists often advocate for the maintenance of forested buffer zones around river systems to minimize the detrimental effects of urbanization on the riparian zone and associated biota (Moore and Palmer, 2005). Conversely, some species can take advantage of anthropogenic changes and thrive in urbanized, riparian environments (Barrett and Guyer, 2008; Pattishall and Cundall, 2009).

Although global reptile declines have received less attention than parallel declines among amphibians, reptile species may be in greater danger of global extinction due to threats including habitat loss, pollution, and unsustainable harvest (Gibbons et al., 2000). The southeastern United States is home to approximately 100 species and subspecies of aquatic and semi-aquatic reptiles, 62 of which are of significant conservation concern (Buhlmann and Gibbons, 1997). Riparian zones are critical habitat for many reptiles (Brode and Bury, 1984; Burbrink et al., 1998; Soares and Brito, 2007); however, relatively few studies have focused specifically on the effects of anthropogenic habitat disturbance on riparian zone reptile communities (but see Barrett and Guyer, 2008; Clark et al., 2009; Reese and Welsh, 1998a,b). Some reptile species may be sensitive to urbanization pressures (Hamer and McDonnell, 2010), but others may benefit from riparian urbanization because it decreases canopy cover and creates deeper, warmer waters which riverine turtles and snakes prefer (Barrett and Guyer, 2008). Decreases in habitat quality through flow regulation may also negatively affect certain reptile species (Clark et al., 2009; Reese and Welsh, 1998a,b). However, some turtle species do prefer lentic habitats (Bodie and Semlitsch, 2000), and might therefore favor impoundment habitats upstream from dams.

Because habitat alteration and loss affect a large number of reptile species (Gibbons et al., 2000), our study examined the effects of: (1) flow regulation through damming and (2) urbanization on reptile occupancy and species richness in riparian zones. Specifically, we used a multi-species hierarchical analysis which allowed us to simultaneously generate site-specific species richness estimates and examine habitat-dependent occupancy patterns for the reptile community despite low detectability for individual species (Zipkin et al., 2009).

2. Methods

2.1. Study sites

Active searches for reptiles and amphibians were conducted at 21 study sites in the upper Piedmont of South Carolina. The sites included floodplains, ephemeral ponds, and riverbanks along the Broad and Pacolet Rivers. At the outset of the selection process, we used a geographic information system (ArcGIS 9.1 ESRI, Redlands, CA), with layers from the National Wetland Inventory (NWI, http://www.fws.gov/wetlands/) and the National Land Cover Database (NLCD; available on the USGS seamless server (http://www.seamless.usgs.gov/index.php)) to identify approximately 200 riparian wetlands within our study area. After ground-truthing, we determined that 21 sites were sufficiently accessible for time-constrained active searches (Fig. 1; see Eskew et al., 2012 for more information on study site selection).

2.2. Data collection methods

We sampled for reptiles using time-constrained active search techniques consistent with recommendations for terrestrial reptile species inventories (McDiarmid et al., 2012). For each 30-min survey, two experienced investigators searched a site independently, lifting groundcover and visually scanning the area to detect and identify reptile species. Occasionally, one investigator searched alone for an hour at each site. Surveys were conducted during daylight hours and weather variables (i.e., air temperature, wind, degree of cloudiness, precipitation) were recorded after each survey. We conducted a total of thirteen surveys per site: three surveys were conducted at each site in June and early July of
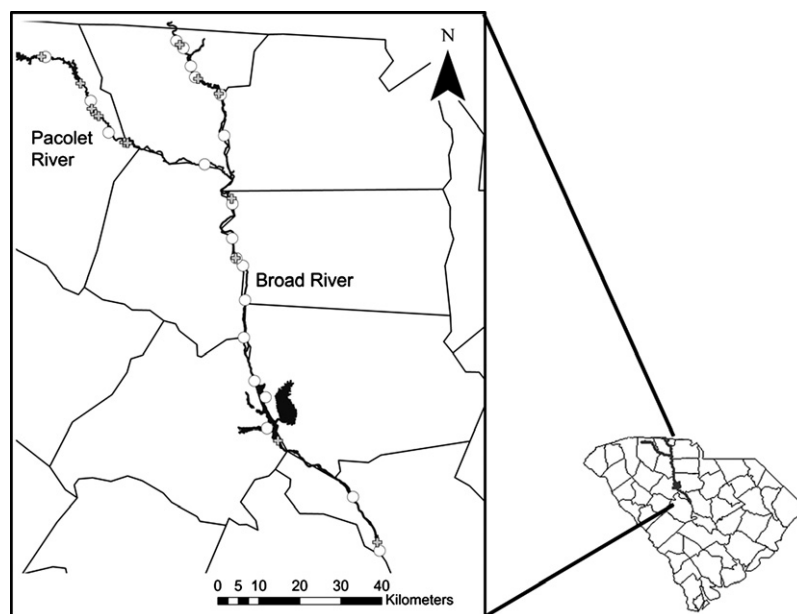

Fig. 1. Active search study sites along the Broad and Pacolet Rivers, South Carolina, USA. Study sites are shown as white circles and locations of dams are shown as gray crosses. Some of the crosses are obscured because of the proximity of the dams and the scale of the study area.

2010, two in September through early November of 2010, three in April and May of 2011, three in June and early July of 2011, and two in September and October of 2011. The temporal distribution of sampling occasions allowed us to detect species with diverse seasonal activity patterns. Our survey design, however, was insufficient to effectively document primarily nocturnal reptile species, including copperheads and corn snakes, which are present in the region.

2.3. Site landscape characteristics

We used aerial photos taken in 2006 to visually identify sixteen dams in the river reaches of our study sites (Fig. 1). On the Broad River we identified nine dams (seven used for hydroelectricity, one as a coal-plant cooling reservoir, and one a textile mill relic) and on the Pacolet River we identified seven dams (two for water reservoirs and five originally used in mills). Although the biophysical impacts of a dam vary in relation to its size and type, we considered the effects of all dams to be similar in our analyses because even small dams will affect flow regimes (Poff and Hart, 2002). We quantified the river distance (upstream and downstream) from each site to the nearest dams using the linear measurement tool in ArcGIS. We also quantified urbanization for each site using polygon tools in ArcGIS to determine percent urban land cover (e.g., residential housing and surrounding landscapes, buildings, industrial sites, major highways, etc.) in a 1-km buffer zone around each sampling location. Use of buffer zones resulted in quantification of urbanization not only in the riparian zone, but also in the nearby upland habitats, which are important for many reptile species (Burbrink et al., 1998).

2.4. Data analysis approach

Our data analysis used hierarchical (multi-level or state-space) Bayesian modeling to estimate community and species-specific responses to three site-specific covariates (distance downstream from dam, distance upstream from dam, and percent urbanization) and two survey-specific covariates (air temperature and day of year). Bayesian analyses use observed data to generate probability statements about the individual parameters being estimated (Link et al., 2002). More importantly, a hierarchical approach maintains separate estimates for species-specific occurrence and detection probabilities while relating these data to a broader analysis of species richness, thus combining species-level and community-level attributes into the same modeling framework (Dorazio and Royle, 2005; Zipkin et al., 2009). When applied to replicate samples, a hierarchical Bayesian analysis of species richness accounts for imperfect detection and avoids assuming either that every species is present at every site or that non-detection represents species absence at a site (Dorazio and Royle, 2005; Dorazio et al., 2006; Kéry et al., 2009). Furthermore, in a hierarchical analysis, individual parameter estimates, particularly for rare species, are improved (made more precise and less likely to be biased) by considering them in the context of the larger community (Sauer and Link, 2002; Zipkin et al., 2009).

We implemented a species richness model similar to that used by Zipkin et al. (2009) to estimate species and community responses to site covariates and survey covariates. One level of our model assumed a "true" (but only partially observed) presence–absence matrix z_{ij} for species $i = 1, 2,\ldots,N$ at site $j = 1, 2,\ldots,J$ where $z_{ij} = 1$ if a species i was present at site j, and $z_{ij} = 0$ if the species was absent. Because z_{ij} was uncertain, we specified a model for occurrence where $z_{ij} \sim Bern(\Psi_{ij})$, and Ψ_{ij} is the probability that a species i occurs in site j.

Based on the data collected, we generated species-specific observance matrices for thirteen sampling occasions at each site

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 kth 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 kth sampling occasion. This fulfills the condition that $x_{ijk} = 0$ if the species i is not present at site j, because in that case $z_{ij} = 0$.

We used the following equations to relate species-specific covariate parameters (α and β values) and occupancy and detection probabilities (Ψ_{ij} and Θ_{ijk} respectively) to the hierarchical models described above:

$$logit(\Psi_{ij}) = u_i + \alpha1_i downdistance_j + \alpha2_i updistance_j$$
$$+ \alpha3_i percenturban_j$$

$$logit(\Theta_{ijk}) = v_i + \beta1_i temperature_{jk} + \beta2_i dayofyear_{jk}$$
$$+ \beta3_i dayofyear_{jk}^2$$

The *downdistance* covariate was defined as the z-score of distance downstream from a dam to a particular study site as compared with distances for all sites. The *updistance* covariate was likewise defined as the z-score for a site's distance upstream from the nearest dam. The *percenturban* covariate was defined as the z-score of percent of the buffer zone containing urban land use. *Temperature* was defined as the z-score of temperature in degrees Celsius, *dayofyear* was defined as the z-score of Julian days since January 1st, and *dayofyear²* was defined as the squared z-score of Julian days since January 1st. Standardized covariates allowed us to estimate Ψ and Θ at mean site and survey covariates (where the z-scores equal zero) from model-generated estimates of u_i and v_i and also allowed direct comparison of model coefficients as effect sizes relative to variation in each covariate. Another benefit is efficiency of the MCMC algorithm. Our parameters u_i and v_i 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 and Royle, 2005).

The model therefore contained eight species-specific parameters (u_i, $\alpha1_i$, $\alpha2_i$, $\alpha3_i$, v_i, $\beta1_i$, $\beta2_i$, and $\beta3_i$). A final component of the model estimated community summaries (designated with μ) assuming that the species-specific parameters were random effects, each governed by a community-level hyper-parameter. For instance, $\alpha1_i \sim N(\mu_{\alpha1}, \sigma_{\alpha1})$ where $\mu_{\alpha1}$ is the mean community response (across species) to the *downdistance* covariate, and $\sigma_{\alpha1}$ is the standard deviation in $\alpha1$ across species (Kéry et al., 2009). Because some sites were closer together relative to others, we tested for spatial autocorrelation in our model and found no effect of latitude or longitude on species richness or occupancy.

We used a Bayesian analysis of the model to estimate parameters and community summaries, implementing uninformative priors for the hyper-parameters (e.g., $U(0, 5)$ for all σ parameters and $U(-10$ to $10)$ for μ_{α} and μ_{β} parameters; species-specific model coefficients were truncated at ±5 from μ to avoid traps). The use of uninformative priors is well suited to ecological applications because it reflects a lack of prior knowledge of a parameter's true value (Link et al., 2002). 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 et al., 2000) using R2WinBUGS (Sturtz et al., 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. The 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 and Rubin, 1992).

3. Results

3.1. Site landscape characteristics

Our study sites were between 0.864 and 50.693 km upstream from the nearest dam (mean 17.451 km, SD 14.834 km) and 0.055–47.510 km downstream from the nearest dam (mean 14.103 km, SD 13.844 km). Urban land cover in the 1-km radius buffer surrounding sites ranged from 0% to 49.33% (mean 7.18%, SD 11.55%).

3.2. Active searches

We observed seven lizard species, eight turtle species, and thirteen snake species (Table 1). Although we observed three different *Eumeces* species (*E. laticeps*, *E. fasciatus*, and *E. inexpectatus*), all three were considered together in our analysis because species-specific identifications require scale counts, which were not possible for most observations. Raw counts of reptile species per site ranged from three to eleven species out of the total 28 detected among all sites. Our model-estimated number of species per site ranged from 12.00 species (95% symmetric credible interval [CI] 7–17; credible intervals are defined by quantiles of the posterior distribution) to 18.77 species (95% CI 14–23). Our model indicated highly variable occupancy among species, with mean estimated occupancy probabilities ranging from 14.9% (95% CI 2.02–66.8%) to 92.1% (95% CI 75.6–98.4%) (Table 1). Mean estimated species detection probabilities were low for all species and ranged from 1.1% (95% CI 0.2–7.2%) to 22.4% (95% CI 15.0–32.1%) (Table 1).

Table 1
Summary of species observed within riparian zones of the Broad and Pacolet Rivers, South Carolina, USA with model-estimated occupancy and detection probabilities and 95% credible intervals for each probability.

Species	Estimated occupancy	95% CI	Estimated detection	95% CI
Lizards				
Anolis carolinensis	0.921	0.756–0.984	0.101	0.054–0.173
Aspidoscelis sexlineatus	0.149	0.020–0.668	0.075	0.017–0.254
Eumeces[a]	0.874	0.660–0.975	0.224	0.150–0.321
Sceloporus undulatus	0.206	0.068–0.442	0.170	0.073–0.325
Scincella lateralis	0.733	0.452–0.929	0.092	0.047–0.163
Turtles				
Apalone spinifera	0.618	0.125–0.978	0.024	0.006–0.092
Chelydra serpentina	0.745	0.177–0.985	0.014	0.003–0.055
Chrysemys picta	0.652	0.188–0.977	0.040	0.013–0.118
Kinosternon subrubrum	0.445	0.108–0.937	0.042	0.011–0.131
Pseudemys concinna	0.902	0.690–0.985	0.133	0.080–0.206
Sternotherus odoratus	0.717	0.122–0.985	0.014	0.003–0.063
Terrapene carolina	0.888	0.626–0.986	0.139	0.082–0.224
Trachemys scripta	0.552	0.223–0.881	0.059	0.024–0.128
Snakes				
Agkistrodon piscivorus	0.558	0.047–0.982	0.012	0.002–0.077
Carphophis amoenus	0.868	0.446–0.988	0.034	0.013–0.082
Coluber constrictor	0.801	0.256–0.986	0.021	0.006–0.066
Diadophis punctatus	0.806	0.242–0.987	0.018	0.005–0.059
Elaphe obsoleta	0.902	0.554–0.990	0.033	0.013–0.075
Lampropeltis getula	0.671	0.099–0.984	0.016	0.003–0.074
Nerodia erythrogaster	0.561	0.047–0.982	0.012	0.002–0.075
Nerodia sipedon	0.444	0.143–0.849	0.072	0.029–0.157
Nerodia taxispilota	0.783	0.377–0.980	0.054	0.021–0.128
Opheodrys aestivus	0.563	0.066–0.980	0.015	0.003–0.073
Regina septemvittata	0.627	0.058–0.985	0.011	0.002–0.072
Storeria dekayi	0.618	0.077–0.983	0.015	0.003–0.074
Storeria occipitomaculata	0.679	0.098–0.984	0.014	0.003–0.066

[a] Includes three *Eumeces* species, *Eumeces laticeps*, *Eumeces fasciatus*, and *Eumeces inexpectatus*.

3.3. Community-level summary

When all reptiles were considered together, mean responses to all three occupancy covariates ($\mu_{\alpha 1}$ – distance downstream from dam, $\mu_{\alpha 2}$ – distance upstream from dam, and $\mu_{\alpha 3}$ – percent urbanization) were positive (mean parameter estimates: 0.47 (95% CI −0.35 to 1.37), 0.44 (95% CI −0.02 to 0.94), and 0.13 (95% CI −0.19 to 0.50) respectively; Table 2) suggesting that reptiles occurred more frequently farther away from dams (in both directions) and also more frequently at more urbanized locations. All three occupancy covariates contained positive and negative values in the 95% credible interval, reflecting uncertainty in the mean community responses; however, the lower 95% credible limit for distance upstream was very close to zero indicating strong support for reptile communities to be more species rich farther upstream from dams. Furthermore, while across-species standard deviation (σ) for the downstream and urbanization covariate effects were greater than the corresponding mean (μ) covariate estimates (CV$_{\alpha 1}$ = 2.64 and CV$_{\alpha 3}$ = 1.69; Table 2), the standard deviation across species for the upstream covariate effect was less than the mean estimate (CV$_{\alpha 2}$ = 0.61; Table 2). The highest mean covariate effect was observed for distance downstream ($\mu_{\alpha 1}$ = 0.47, Table 2) but the standard deviation across species was much greater for this covariate than for the other site-specific effects ($\sigma_{\alpha 1}$ (1.24) $\gg \sigma_{\alpha 2}$ (0.28) and $\sigma_{\alpha 1}$ (1.24) $\gg \sigma_{\alpha 3}$ (0.22); Table 2). Standard deviation across species was similar for upstream and urbanization effects ($\sigma_{\alpha 2}$ = 0.28 and $\sigma_{\alpha 3}$ = 0.22, Table 2), but the mean urbanization effect was not as great as the mean upstream distance effect ($\mu_{\alpha 3}$ (0.13) < $\mu_{\alpha 2}$ (0.44); Table 2). Thus, our model indicated that the mean occupancy response to upstream distance from nearest dam was consistently positive for each species, while the distance downstream and percent urbanization responses were not.

The community response to detection covariates ($\mu_{\beta 1}$ – temperature, $\mu_{\beta 2}$ – day of year linear term, and $\mu_{\beta 3}$ – day of year squared term) indicated greater detection probability at lower temperatures and a weakly optimal sampling time (mean parameter estimates: −0.19 (95% CI, −0.48 to 0.08), 0.11 (95% CI −0.23 to 0.38), and 0.24 (95% CI 0.01 to 0.46), respectively; Table 2). For these covariates we observed relatively high variation among species responses (CV$_{\beta 1}$ = 2.53, CV$_{\beta 2}$ = 4.00, CV$_{\beta 3}$ = 1.29; Table 2).

3.4. Responses to upstream distance from dam

We observed a positive mean occupancy response across reptile species to increased distance upstream from nearest dam, assuming average urbanization and average distance downstream from a dam (Fig. 2). We likewise observed consistent, positive estimates of species-specific responses to the distance upstream covariate, assuming average urbanization and average distance downstream from a dam (Fig. 3). This pattern was further reflected in model-generated estimates of species richness at hypothetical sites for variable distances upstream from a dam. Assuming average urbanization and average distance downstream from a dam, species richness estimates increased farther upstream from dams varying from a mean of 14.24 species at a distance of 2.55 km upstream from a dam (95% CI 9–20) to 19.60 species 51 km upstream from a dam (95% CI 13–25; Fig. 4).

4. Discussion

Our surveys documented 28 reptile species in the Broad River Basin, a number comparable to reptile species richness assessments conducted in three national parks in the Piedmont region of Georgia (Tuberville et al., 2005). Based on our analyses, reptile occupancy responded variably to distance downstream from dams

Table 2
Summary of hyper-parameters for occupancy and detection covariates for reptiles within riparian zones of the Broad and Pacolet Rivers, South Carolina, USA. The symbol μ indicates a mean community response, while σ indicates the standard deviation in the response to the covariate across species.

| Community level hyper-parameter		Mean	Standard deviation	95% Credible intervals	
$\mu_{\alpha1}$	Distance downstream	0.47	0.43	−0.35	1.37
$\sigma_{\alpha1}$	Distance downstream	1.24	0.50	0.36	2.32
$\mu_{\alpha2}$	Distance upstream	0.44	0.25	−0.02	0.94
$\sigma_{\alpha2}$	Distance upstream	0.28	0.22	0.01	0.83
$\mu_{\alpha3}$	Percent urban	0.13	0.17	−0.19	0.50
$\sigma_{\alpha3}$	Percent urban	0.22	0.19	0.01	0.70
$\mu_{\beta1}$	Temperature	−0.19	0.14	−0.48	0.08
$\sigma_{\beta1}$	Temperature	0.48	0.13	0.27	0.79
$\mu_{\beta2}$	Day of year (linear term)	0.11	0.16	−0.23	0.38
$\sigma_{\beta2}$	Day of year (linear term)	0.44	0.15	0.18	0.78
$\mu_{\beta3}$	Day of year (squared term)	0.24	0.12	0.01	0.46
$\sigma_{\beta3}$	Day of year (squared term)	0.31	0.13	0.07	0.58
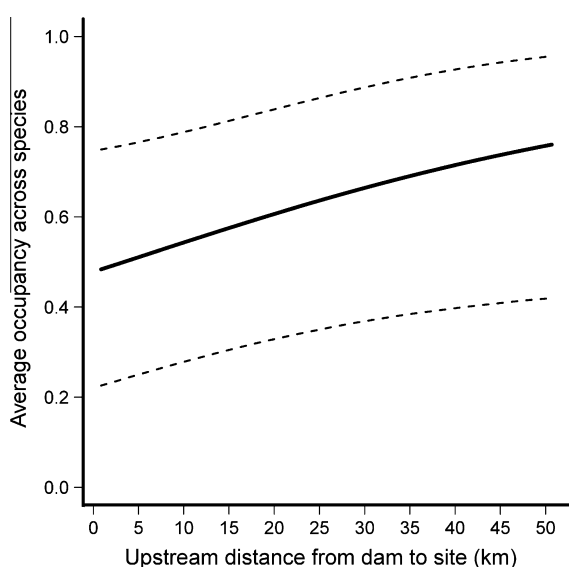
Fig. 2. Mean reptile occupancy probability increases with greater distance upstream from a dam in the Broad and Pacolet Rivers, South Carolina, USA. Solid line represents the posterior mean community response and dashed lines represent a 95% credible interval of the posterior mean. Occupancy probabilities were calculated at mean values of downstream distance from dam and percent urbanization.

and urbanization. Conversely, we observed a consistent preference across a diverse number of reptile species for sites farther upstream from dams. Because reptile responses to this covariate were largely consistent, we also observed decreased reptile species richness immediately upstream from dams. Increased species richness farther upstream from dams suggests that river stretches immediately upstream of dams may not provide suitable habitat for some reptile species.

Studies on various riparian animals including fish (Haxton and Findlay, 2008; Kinsolving and Bain, 1993), anurans (Barrett and Guyer, 2008; Eskew et al., 2012), and mussels (Vaughn and Taylor, 1999) have pointed to the negative downstream ecological effects of dams. Studies have attributed negative downstream impacts to reduced flow (Eskew et al., 2012; Haxton and Findlay, 2008), deceased water temperature due to hypolimnetic draws (Haxton and Findlay, 2008; Vaughn and Taylor, 1999), and reduced seasonal flooding (Barrett and Guyer, 2008; Eskew et al., 2012). However, we did not observe a distinct trend in reptile occupancy responses downstream from dams. Reptiles may not show consistent responses to downstream impacts because, unlike anurans, fish, and mussels, most reptile species are not restricted to aquatic habitats for any part of their life cycle. Aquatic turtles, however, are

more dependent on the river channel. Reese and Welsh (1998a,b) indicated that habitat for the turtle *Clemmys marmorata* is degraded downstream from dams. A comparative study of the turtle in one dammed and one free flowing tributary of a river showed an unstable adult-dominated age structure in the dammed tributary (Reese and Welsh, 1998a). The dammed tributary also had less suitable habitat for *C. marmorata* with lower water temperatures and a higher water velocity than the undammed fork (Reese and Welsh, 1998b). Conversely, low flow below dams can expose rocks and thus increase basking areas, which are important for thermoregulation in turtle and water snake species. Certain lizard species including the six-lined racerunner and the southeastern five-lined skink also prefer drier habitats (Gibbons et al., 2009), and may therefore be unaffected or benefitted by drier conditions in riparian zones downstream from dams. Reptile species occupancy may have responded variably or insignificantly to distance downstream from a dam, and thus we did not observe a consistent reptile occupancy response to this variable.

We show that upstream distance from a dam is a more consistent indicator of reptile species occupancy than either of the other variables investigated. Reptile preference for habitats farther upstream from dams may be attributed to various elements of a reservoir ecosystem. Anoxia in deep zones of a reservoir (Baxter, 1977) may influence reptile occupancy and has been indicated as a conservation concern for river turtles in potential dam locations (Tucker et al., 2001). A physiological investigation of *Elusor macrurus* indicates that the turtle does not acclimate to long-term hypoxia while diving, and thus large reservoirs may not provide suitable habitat for this and other bimodally respiring turtle species including *Apalone spinifera*, *Sternotherus odoratus* and *Kinosternon subrubrum* (Clark et al., 2009). Furthermore, since river turtles must often be well adapted to deep water with strong currents (Moll and Moll, 2004), lentic-adapted turtles could displace river-adapted turtles in reservoirs, thus threatening species richness immediately upstream from dams.

Damming permanently inundates a river's riparian zone, which would normally provide unique flood-adapted vegetation and microhabitats for reptile species (Bayley, 1995). Although new floodplain areas may be established, reservoir drawdowns are very different from typical flood pulses in that the eulittoral zone between high and low water levels is primarily submerged and only occasionally exposed; this new eulittoral zone typically remains barren in temperate reservoirs (Baxter, 1977). Rivers support greater turtle species richness than lakes or ponds due to the complex habitat structure of rivers and floodplains (Dreslik and Phillips, 2005), and much of this riparian complexity is eliminated when reservoirs are formed. Absence of seasonal flooding also reduces the frequency of fish consumption by certain semi-aquatic snakes, and has thus been implicated in increased intraspecific competition among snakes (Hampton and Ford, 2007).
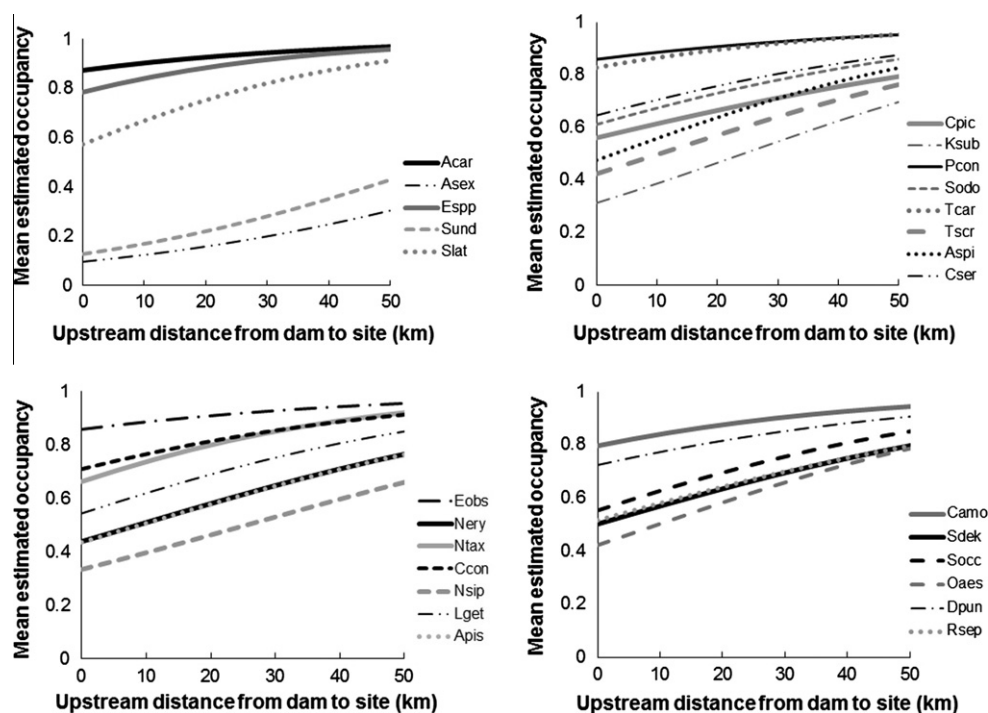
Fig. 3. Species-specific mean probabilities of occurrence increase with greater distance upstream from a dam. Upper left, lizards: green anole (Acar), six-lined racerunner (Asex), *Eumeces* species (Espp), eastern fence lizard (Sund), and ground skink (Slat). Upper right, turtles: painted turtle (Cpic), mud turtle (Ksub), river cooter (Pcon), musk turtle (Sodo), box turtle (Tcar), yellowbelly slider (Tscr), spiny softshell (Aspi), and snapping turtle (Cser). Bottom left and right, snakes: rat snake (Eobs), redbelly watersnake (Nery), brown watersnake (Ntax), racer (Ccon), northern watersnake (Nsip), king snake (Lget), cottonmouth (Apis), worm snake (Camo), brown snake (Sdek), redbelly snake (Socc), rough green snake (Oaes), ringneck snake (Dpun), and queen snake (Rsep). Credible intervals are omitted for clarity. These curves are intended to depict general trends rather than exact relationships.
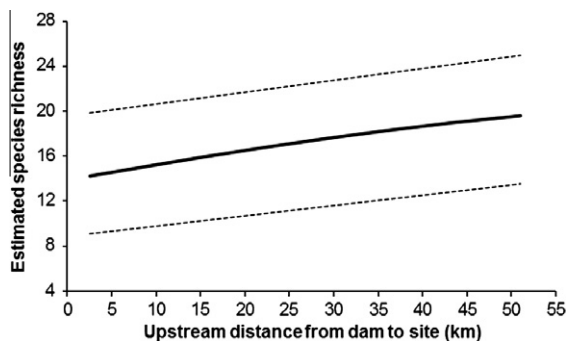

Fig. 4. Estimated reptile species richness in riparian zones of the Broad and Pacolet Rivers, South Carolina, USA in relation to distance upstream from dams. Solid line represents the posterior mean and dashed lines represent a 95% credible interval of the posterior mean.

Another potential stressor of reptiles in reservoir ecosystems is dam-induced sedimentation, which may extend for miles upstream depending on the steepness of a river gradient (Baxter, 1977). As soil and other particles settle to the benthos, microhabitats become embedded and riverine habitat complexity is reduced (Brannon and Purvis, 2008). Sedimentation and river turbidity have been associated with population declines and reduced species diversity for a number of animals including fish (Walters et al., 2003), salamanders (Brannon and Purvis, 2008), and mollusks (Henley et al., 2000). Sediment accumulation also negatively affects benthic macroinvertebrate populations, which serve as an important food source for other riverine species including fish and turtles (Harrison et al., 2007). Riverine macroinvertebrates also subsidize the diets of terrestrial lizards; in watersheds, lizard growth rates are positively correlated with abundance of this food source (Sabo and Power, 2002). Sedimentation and turbidity can also inhibit aquatic plant growth, thus reducing primary productivity in a river system (Henley et al., 2000) and the habitat used by semi-aquatic reptiles. Similar to reservoir anoxia, dam-related turbidity may limit cloacal respiration in bimodally respiring turtles (Tucker et al., 2001).

Urbanization is one of many sources of habitat degradation known to threaten reptile species (Gibbons et al., 2000; Hamer and McDonnell, 2010). Nonetheless, reptile species associated with riparian zones often persist even in urbanized areas if natural habitat buffers are present (Hamer and McDonnell, 2010). Furthermore, riverine snakes and turtles may prefer urbanized riparian habitats for their deeper, warmer waters with more basking habitat (Barrett and Guyer, 2008). Meanwhile, urbanization can favor introduced over native aquatic turtle species (Bury, 2008). These conflicting observations imply that different reptile species respond differently to urbanization. In our study, variable reptile occupancy trends could have diluted the community response to urbanization. Furthermore, the urbanization response may have appeared weak relative to dam effects because the reptile communities have had less time to be impacted by urbanization pressure. Many of the old mill dams date from the 1800s, while a number of the larger hydroelectric dams were constructed in early 1900s. It is also notable that some of our study sites are located along a State Scenic River and our most urbanized study site only contained 49.3% urban land use, so our findings may not apply to instances where urbanization pressure is greater.

Our study extends observed negative effects of damming to include various semi-aquatic and terrestrial reptile species, indicating that impoundments can have far-reaching ecological effects which extend beyond the river channel itself. The decreased reptile occupancy observed immediately upstream from dams may be linked to various direct and indirect effects of reservoirs and damming. Diminished reptile species richness upstream from dams

underlines the interconnectedness of river and floodplain communities. While substantial research has demonstrated that land-use patterns affect organisms inhabiting river channels (Brannon and Purvis, 2008; Gibbons et al., 2000), our research emphasizes that modifications to the river channel itself can affect occupancy and species richness for terrestrial and semi-aquatic species. Future research on damming and reptile populations should attempt to quantify dam-induced habitat alterations at study sites by measuring variables such as sedimentation and turbidity or vegetation patterns in eulittoral zones.

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