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Contributed Paper

Effects of River-Flow Regulation on Anuran Occupancy and Abundance in Riparian Zones

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Abstract: *The natural flow regimes of rivers worldwide have been heavily altered through anthropogenic activities, and dams in particular have a pervasive effect on riverine ecosystems. Flow-regulation effects of dams negatively affect species diversity and abundance of a variety of aquatic animals, including invertebrates and fishes. However, the effects on semiaquatic animals are relatively unknown. We conducted anuran calling surveys at 42 study locations along the Broad and Pacolet Rivers in South Carolina to address the potential effects of flow regulation by damming on anuran occupancy and abundance. We estimated occupancy and abundance with Program PRESENCE. Models incorporated distance upstream and downstream from the nearest dam as covariates and urbanization pressure as an alternative stressor. Distance from dam was associated with occupancy of 2 of the 9 anuran species in our analyses and with abundance of 6 species. In all cases, distance downstream from nearest dam was a better predictor of occupancy and abundance than distance upstream from nearest dam. For all but one species, distance downstream from nearest dam was positively correlated with both occupancy and abundance. Reduced occupancy and abundance of anurans likely resulted from downstream alterations in flow regime associated with damming, which can lead to reduced area of riparian wetlands that serve as anuran breeding habitat. Our results showed that damming has a strong negative effect on multiple anuran species across large spatial extents and suggest that flow regulation can affect semiaquatic animals occupying riparian zones.*

Keywords: amphibian, Broad River, damming, flow regime, rivers, South Carolina, urbanization

Efectos de la Regulación del Flujo de un Río sobre la Ocupación y Abundancia de Anuros en Zonas Ribereñas

Resumen: *Los regímenes naturales de flujo de ríos en todo el mundo han sido fuertemente alterados por actividades antropogénicas, y las presas en particular tienen un efecto dominante en los ecosistemas ribereños. Los efectos de la regulación de flujos por las presas afectan negativamente a la diversidad y abundancia de una variedad de animales acuáticos, incluyendo vertebrados y peces. Sin embargo, los efectos sobre animales semiacuáticos son relativamente desconocidos. Realizamos muestreos de vocalización de anuros en 42 localidades a lo largo de los Ríos Broad y Pacolet en Carolina del Sur para abordar los efectos potenciales de la regulación de flujo por represas sobre la ocupación y abundancia de anfibios. Estimamos la ocupación y abundancia con el Programa PRESENCE. Los modelos incorporaron la distancia río arriba y río debajo a la presa más cercana como covariables y la presión de urbanización como un factor estresante alternativo. La distancia a la presa fue asociada con la ocupación de 2 de 9 especies anuros en nuestros análisis y con la abundancia de 6 especies. En todos los casos, la distancia río abajo a la presa más cercana fue un mejor predictor de la ocupación o la abundancia que la distancia río arriba a la presa más cercana. Para todas menos una especie, la distancia río abajo a la presa más cercana se correlacionó positivamente tanto con la ocupación como con la abundancia. La ocupación y abundancia reducida de anuros probablemente*

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resultó de alteraciones río abajo en el régimen de flujo asociado con el represamiento, lo que puede llevar a la reducción de humedales ribereños que funcionan como hábitat reproductivo para los anuros. Nuestros resultados mostraron que el represamiento tiene un fuerte efecto negativos sobre múltiples especies de anuros en amplias extensiones espaciales y sugieren que la regulación de flujo puede afectar a animales semiacuáticos que ocupan zonas ribereñas.

Palabras Clave: anfibio, Carolina del Sur, régimen de flujo, represamientos, Río Broad, ríos, urbanización

Introduction

Natural riverine flow regimes are increasingly regulated and disrupted through anthropogenic activities (Poff et al. 1997; Revenga et al. 2000; Allan & Castillo 2008), and damming is a specific mechanism of flow regulation that is globally pervasive (McCully 1996; Nilsson et al. 2005). Dams negatively affect diversity and abundance of a number of organisms, including plants (Nilsson & Svedmark 2002; Naiman et al. 2005), macroinvertebrates (Voelz & Ward 1991), mussels (Vaughn & Taylor 1999), and fishes (Kinsolving & Bain 1993; Haxton & Findlay 2008). Typically, species diversity is positively associated with distance downstream from a dam, where flow regimes are similar to unregulated conditions due to tributary inflow (Voelz & Ward 1991; Kinsolving & Bain 1993; Vaughn & Taylor 1999).

Besides physically limiting dispersal (Poff & Hart 2002; Nilsson et al. 2005), dams may affect organisms by creating a stable downstream flow regime (Poff et al. 1997; Magilligan & Nislow 2005), which can negatively affect species adapted to naturally variable flow (Bunn & Arthington 2002; Lytle & Poff 2004). For example, the construction of dams can lead to less frequent natural flooding of rivers and surrounding riparian areas (Stevens et al. 2001), changing floodplain wetland hydroperiod (Nilsson & Berggren 2000; Hamer & McDonnell 2008). In contrast to these stabilizing effects, at some dams high-flow water discharges are aseasonal, which can reduce habitat quality (Freeman et al. 2001) or physically displace organisms (Lind et al. 1996).

Relatively little research has been conducted on the effects of flow regulation on amphibians (but see Lind et al. 1996; Bateman et al. 2008; Kupferberg et al. 2011). Because amphibians occupy both aquatic and terrestrial environments during different parts of their life cycle, their responses to alterations in flow likely differ from those of strictly aquatic species (e.g., fishes, mussels). The few studies of dam effects on amphibians show detrimental upstream flooding after dam construction (Brandão & Araújo 2008), reduced egg survival as a result of water releases from dams (Lind et al. 1996), and, conversely, the potential benefits of water releases from dams for restoration of downstream amphibian breeding habitats (Bateman et al. 2008). However, how dams affect the distribution and abundance of multiple amphibian species at a landscape extent has not been addressed. Additionally, relatively little work has been conducted on species that breed primarily within lentic habitats of the riparian zone (but see Bateman et al. 2008; Fuller et al. 2011), such as anurans (frogs and toads) in the southeastern United States (Dorcas & Gibbons 2008). These species use both permanent and seasonal riparian wetlands for reproduction and larval development. If these species are affected by dam flow regulation, it is likely they are most sensitive to changes in the frequency of overbank flooding that may ultimately reduce the area or quality or alter seasonal availability of breeding sites in the floodplain (Nilsson & Berggren 2000).

In addition to damming, riparian-zone amphibians are likely to be affected by other anthropogenic habitat changes (Gardner et al. 2007), including urbanization (Riley et al. 2005; Barrett & Guyer 2008; Hamer & McDonnell 2008). Urbanization may negatively affect amphibian populations in various ways including outright elimination of aquatic habitat (Nystrom et al. 2007) or alteration of upland habitat (e.g., construction of roads and other impervious surfaces). Changes in upland habitat can directly affect species that make substantial use of upland areas (Pillsbury & Miller 2008) or may trigger cascading effects into core aquatic habitats (Willson & Dorcas 2003; Simon et al. 2009).

We examined the effects of flow regulation by damming on anuran occupancy and abundance in riparian zones. We hypothesized that anuran populations are negatively influenced when in close proximity to dams and that the strongest effects occur downstream, as opposed to upstream, of dams. Additionally, we evaluated the potential effects of urbanization on anurans because it is a well-established amphibian stressor (Hamer & McDonnell 2008; Simon et al. 2009; Price et al. 2011). We also investigated the additive effects of flow regulation and urbanization because research results increasingly show that amphibians are affected by multiple, interacting stressors (Sih et al. 2004; Beebee & Griffiths 2005).

Methods

Study Sites

We used a geographic information system (ArcGIS, version 9.1, ESRI, Redlands, California) to identify potential study sites (i.e., calling-survey sampling points) along the Broad River and one of its major tributaries, the

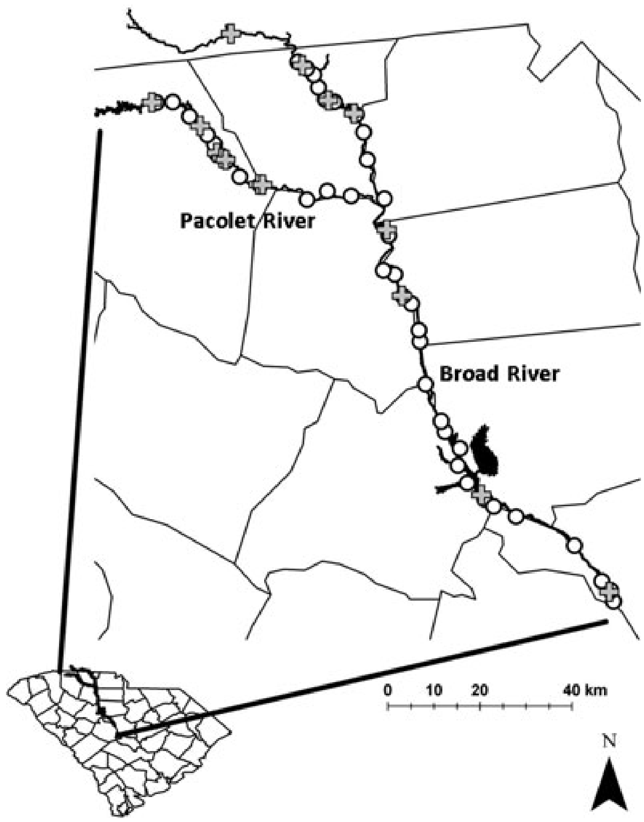

*Figure 1. Map of riparian-zone study sites (*n = *42) and dam locations (*n = *16) in the South Carolina Piedmont (U.S.A.) (dots, study sites; crosses, dams; one dam on a downstream portion of the Broad River is not shown). Inset shows the state of South Carolina (bold lines, reaches of the study rivers).*

Pacolet River, in the South Carolina Piedmont (U.S.A.), a plateau region characterized by low rolling hills (Gade et al. 1986). We used 30-m resolution data layers from the National Wetland Inventory and National Land Cover Data (Fry et al. 2011) to locate approximately 200 riparian areas. We defined riparian areas as semiterrestrial zones that regularly receive fresh water from a local water source (Naiman et al. 2005), in our case the Broad and Pacolet Rivers. Therefore we attempted to locate sites that were as close as possible to the river channel. After visiting sites to determine their accessibility, we identified approximately 80 potential study locations. We generated a circular buffer of 1-km radius around each site, a distance that encompasses a majority of the core terrestrial habitat used by most anuran species (Semlitsch & Bodie 2003). We chose final study sites on the basis of spatial independence (i.e., nonoverlapping 1-km radius circular buffers). This site-selection process yielded 42 suitable sampling points within riparian areas. Survey sites were an average of 125.1 m (SE 26.5) from the river channel (Fig. 1).

Data Collection

During manual calling surveys we recorded all species of anurans heard calling at each site. Such surveys are widely used as an efficient method to collect data on presence, absence, and abundance of anuran populations (Dorcas et al. 2010). Surveys lasted 5 min, a time of sufficient length to detect most anuran species that occur in the North Carolina Piedmont (Gooch et al. 2006). Surveys were conducted between 18:45 and 01:30. To maximize the probability of recording species with different phenology, we sampled during 3 seasons: spring (13 April to 8 May 2010), summer (8 to 24 June 2010), and winter (21 February to 24 March 2011). We surveyed each site 3 times within each calling period. Time lag between surveys within a calling period was 5–18 d.

Site Characteristics

We used ArcGIS to identify covariates for use in occupancy and abundance analyses. After georeferencing aerial photos of our entire study area taken in 2006, we visually identified every dam in the river reaches of our study sites (16 total) (Fig. 1). Of the 9 dams on the Broad River, 7 generated hydroelectric power, 1 sequestered water to cool factory equipment in a power-generation facility, and 1 was used historically to divert water to a textile mill. The 7 dams on the Pacolet River included 2 dams that held back human-made reservoirs used as local water sources and 5 that were built to power mill operations. Although the magnitude of ecological effects associated with damming vary according to dam size and operational type, even small dams may affect downstream water flow (Poff & Hart 2002), and dams have an overall homogenizing effect on hydrology despite differences in height and operational type (Poff et al. 2007). We therefore did not differentiate among dam types in our analyses.

We used river distance (recorded with the linear measurement tool in ArcGIS) from the nearest dam (upstream and downstream) as a measure of the level of flow regulation at each study site. To quantify the proportion of urbanization surrounding each study site, we used polygon tools in ArcGIS to measure total percent urban land cover (including residential housing and surrounding landscapes, buildings, industrial sites, and major highways) within each 1-km radius circular buffer.

Data Analyses

To obtain estimates of site occupancy (presence or absence of a particular species), we used single-season occupancy models in the computer program PRESENCE, which uses maximum-likelihood methods to estimate parameters (MacKenzie et al. 2002; MacKenzie et al. 2005). The number of surveys used in our analyses of occupancy and abundance varied among species because we based survey inclusion on whether a survey fell within a particular species' period of peak calling (Weir & Mossman 2005; Dorcas & Gibbons 2008; Dorcas et al. 2010). We generated model sets for each species that tested whether distance from nearest dam and percent urban land cover were associated with occupancy. Specifically, we compared models with 6 different sets of covariates: constant (null model with no covariates), percent urban land cover, distance downstream from the nearest dam, distance upstream from the nearest dam, distance downstream from the nearest dam and percent urban land cover, and distance upstream from the nearest dam and percent urban land cover. These 6 occupancy models were each paired with 2 different detection models, constant probability of detection or time-dependent probability of detection. Therefore, we analyzed 12 occupancy models total for each anuran species (model sets for all species are in the Supporting Information).

We standardized all covariates before analyses by calculating *z* scores (Donovan & Hines 2007). We distinguished between competing models with Akaike's Information Criterion (AIC) and used AIC values adjusted for small samples sizes (AIC_c) (lower values indicate greater parsimony) (Burnham & Anderson 2002). We used the MacKenzie-Bailey goodness-of-fit test to assess fit for each model set (MacKenzie & Bailey 2004). We ran the test for 1000 bootstrap iterations on the 2 models in each model set with the greatest number of parameters (those with 2 covariates and time-dependent detection) to generate estimates of the overdispersion factor, $\hat{c}$, and used the higher resultant $\hat{c}$ value to ensure a conservative estimation of goodness of fit. If $\hat{c}$ values were >1, which indicates overdispersion of data, we used AIC_c values adjusted for overdispersion ($QAIC_c$) (Burnham & Anderson 2002). We derived occupancy parameters from the top model (lowest AIC_c value) in each model set, whereas we calculated covariate parameters by averaging across all models within a given model set that included the covariate.

To estimate abundance, we implemented Royle-Nichols models in program PRESENCE. These models assume that heterogeneity in detection among sites is the result of underlying differences in abundance (Royle & Nichols 2003). Because we did not find strong support for occupancy models with 2 covariates, we considered only 4 models of abundance for each species: 1 with constant abundance and 3 with abundance varying according to 1 of the 3 covariates (distance downstream from nearest dam, distance upstream from nearest dam, and percent urban land cover) (all model sets shown in the Supporting Information). We used AIC_c to distinguish between competing models (Burnham & Anderson 2002).

Our data revealed that for a given set of occupancy or abundance models, only the covariate included in the top model was significant (i.e., the parameter estimate for the covariate did not overlap zero in the 95% CI). Therefore, we limited our attention to covariates included in the top model within a given model set.

Results

We detected 13 anuran species: northern cricket frog (*Acris creptians*), American toad (*Anaxyrus americanus*), Fowler's toad (*Anaxyrus fowleri*), southern toad (*Anaxyrus terrestris*), eastern narrow-mouthed toad (*Gastrophyrne carolinensis*), Cope's gray treefrog (*Hyla chrysoscelis*), green treefrog (*Hyla cinerea*), American bullfrog (*Lithobates catesbeianus*), green frog (*Lithobates clamitans*), pickerel frog (*Lithobates palustris*), southern leopard frog (*Lithobates sphenocephalus*), spring peeper (*Pseudacris crucifer*), and upland chorus frog (*Pseudacris feriarum*) (all names follow Frost et al. 2008). Data sets for all but 3 species (southern toad, eastern narrow-mouthed toad, and pickerel frog) proved sufficient for occupancy and abundance analyses (with extremely sparse data, PRESENCE may be unable to accurately estimate parameters of interest). We also excluded green treefrogs from analyses because they only recently expanded their range into the South Carolina Piedmont (Dorcas & Gibbons 2008), which introduces bias to our investigation of covariate effects. All species for which occupancy and abundance models were generated occur throughout our study area. The number of surveys used for analysis of each species ranged from 3 to 6 (Table 1). The proportion of sites at which a species was detected (i.e., naïve occupancy) ranged from 0.33 (southern leopard frog) to 0.95 (Fowler's toad) (Table 1). Because naïve occupancy of Fowler's toads was so high, it was not informative to examine the effects of covariates on their occupancy pattern. Thus, we excluded Fowler's toads from occupancy analyses.

Our study sites ranged between 48 and 47,510 m downstream from a dam (mean [SE] = 13,474 m [2,090]) and 298 and 50,693 m upstream from a dam (mean = 16,605 m [2,161]). Urban land cover ranged from 0% to 49.3% (mean = 10.0% [2.0]).

For northern cricket frogs and southern leopard frogs, the top occupancy model included downstream distance from nearest dam. The parameter estimate for this covariate did not overlap zero in the 95% CI after model averaging (Table 1). For these 2 species, distance downstream from nearest dam had a positive effect on occupancy (Fig. 2). Both spring peepers and upland chorus frogs were similarly affected, with strongest support for models that included distance downstream from dam, but in both cases the 95% CI for the parameter overlapped with zero after model averaging (Table 1). The top model for bullfrogs included a negative effect of percent urban land cover on occupancy, and model averaging affirmed

Table 1. Summary data for 9 anuran species recorded during calling surveys and covariate parameter estimates derived from occupancy and abundance model sets.

Species	*No. surveys used in final analysis*	*Naïve occupancy*[a]	*Covariate in top occupancy model*[b]	*Covariate parameter estimate (95% CI)*[c]	*Covariate in top abundance model*[b]	*Covariate parameter estimate (95% CI)*[d]
Northern cricket frog	4	0.43	down from dam	1.44 (0.43 to 2.46)[e]	down from dam	0.81 (0.43 to 1.19)[e]
American toad	3	0.52	urban	−0.90 (−2.12 to 0.32)	none	na
Fowler's toad	6	0.95	na	na	down from dam	−0.39 (−0.61 to −0.18)[e]
Cope's gray treefrog	5	0.79	none	na	none	na
Bullfrog	5	0.43	urban	−1.52 (−2.89 to −0.15)[e]	urban	−1.06 (−1.99 to −0.13)[e]
Green frog	5	0.43	none	na	down from dam	0.44 (0.07 to 0.82)[e]
Southern leopard frog	3	0.33	down from dam	0.94 (0.14 to 1.73)[e]	down from dam	0.72 (0.30 to 1.14)[e]
Spring peeper	6	0.76	down from dam	8.12 (−1.55 to 17.79)	down from dam	0.36 (0.12 to 0.60)[e]
Upland chorus frog	3	0.76	down from dam	4.59 (−5.90 to 15.08)	down from dam	0.35 (0.08 to 0.61)[e]

[a] *Proportion of sites at which the species was detected.*
[b] *Top models are those with the lowest AIC_c scores in a model set. Covariates are proportion of urban land cover within a 1-km radius circular buffer around each study site (urban) or distance of the site downstream from the nearest dam as measured along the river channel (down from dam).*
[c] *Size and direction of the relation between the covariate and occupancy. Parameter estimates derived by averaging across all occupancy models that included the covariate.*
[d] *Parameter estimates derived from the top abundance model.*
[e] *Significant directional trend (i.e., does not overlap with zero in the 95% CI).*

this trend (Table 1 & Fig. 3). Occupancy of American toads was similarly associated with percent urban land cover, although the 95% CI overlapped with zero (Table 1). Covariates did not have a strong effect on occupancy of either Cope's gray treefrogs or green frogs (Table 1).

The abundance of northern cricket frogs, Fowler's toads, green frogs, southern leopard frogs, spring peepers, and upland chorus frogs was significantly affected by distance downstream from nearest dam (Table 1). Abundances of all species except Fowler's toad increased as downstream distance from nearest dam increased (Fig. 4). Abundance of American toads and Cope's gray treefrogs was not affected by any covariates, but bullfrogs were more abundant in sites with lower percent urban land cover (Table 1 & Fig. 5).

Discussion

Both occupancy and abundance of anurans were affected by distance from nearest dam, our measure of flow regulation. For all model sets that indicated a significant effect of distance from nearest dam, downstream distance was a better predictor of occupancy and abundance than upstream distance, which suggests downstream habitat changes resulting from flow regulation had a much stronger effect on anuran occupancy and abundance than upstream changes (e.g., fragmentation and habitat changes due to reservoir creation). Distance downstream from the nearest dam was positively correlated with both occupancy and abundance of all species except Fowler's toad, which had lower abundance at sites farther downstream from dams. We found strong evidence that for many species occupying riverine habitats in our study system, flow regulation had greater effects on occupancy and abundance than percent urban land cover, which has often been cited as a factor that influences amphibian populations across landscapes (Hamer & McDonnell 2008; Simon et al. 2009). These results establish flow regulation as an important amphibian population stressor.

Dams result in a number of downstream flow regime changes that may ultimately account for the occupancy and abundance trends we observed. In general, river reaches downstream from dams have reduced peak flows and flooding frequency that result in a lowered water table and reduced lateral water flows (Nilsson & Berggren 2000; Naiman et al. 2005). Such changes may result in a reduction of area or elimination of riparian-zone wetlands that provide critical lentic breeding habitat for anurans. For example, Bateman et al. (2008) observed relatively low toad abundance along a regulated river during a 7-year study, except during the year a flood pulse was released from a local dam and restored water to the toads' riparian-zone breeding habitats. Flooding events are also responsible for delivering nutrients and detritus to riparian zones (Bayley 1995) that tadpoles depend on for growth and development; thus, dams that reduce the frequency or extent of flooding events likely have negative effects on tadpole survival. Additionally, reduced flows downstream from dams can result in succession of riparian areas to woodlands (Nilsson & Svedmark 2002) or expansion of riparian vegetation into the river

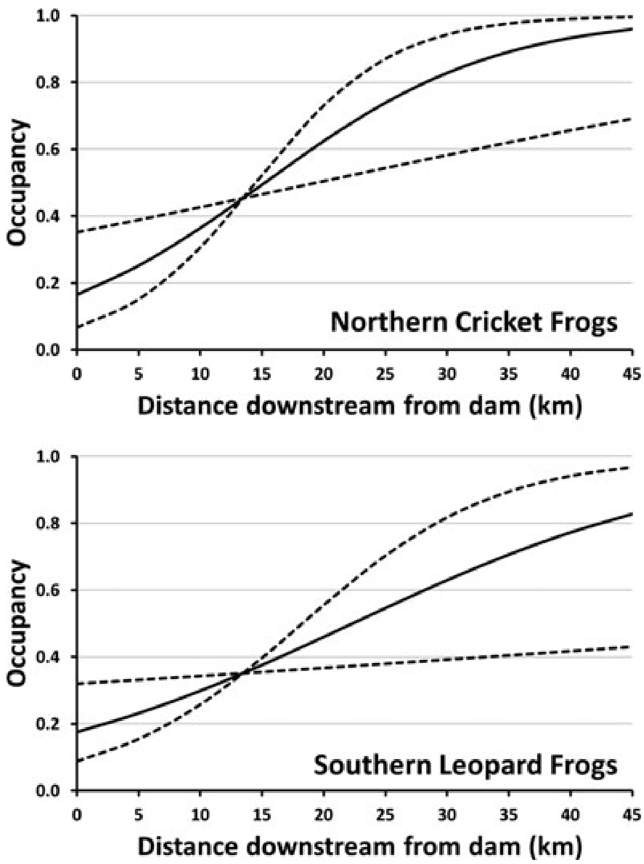

Figure 2. Effect of downstream distance from nearest dam on probability of occupancy of 2 anuran species along the Broad and Pacolet Rivers, South Carolina (U.S.A.) (solid lines, relation between downstream distance from nearest dam and occupancy; dashed lines, 95% CIs for model-averaged estimates of the covariate effect).

channel, which can alter channel shape and result in further reduction of anuran breeding habitat (Lind et al. 1996).

Downstream effects of dams may negatively affect the quality of anuran habitat, especially with respect to extent of breeding habitats within the floodplain, and the species-specific trends we observed suggest these effects are substantial stressors within our study system. The species for which we detected no negative effect of distance from dam on occupancy or abundance (American toads, Fowler's toads, Cope's gray treefrogs, and bullfrogs) are species that are arguably less reliant on the types of floodplains supported by a natural flow regime. The 2 toad species are both extremely terrestrial relative to the rest of our anuran assemblage, and Cope's gray treefrog is an arboreal, primarily woodland, species that frequently breeds in marginal habitats (i.e., roadside ditches, retention ponds) (Dorcas & Gibbons 2008). Additionally, flow regulation may not negatively affect bull-

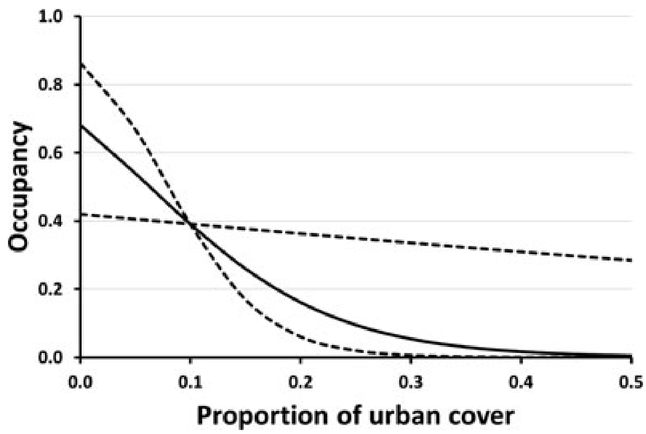

Figure 3. Effect of proportion of urban land cover within the 1-km radius circular buffer on probability of occupancy of bullfrogs along the Broad and Pacolet Rivers, South Carolina (U.S.A.) (solid line, relation between urban land cover and occupancy; dashed lines, 95% CI for model-averaged estimate of the covariate effect).

frogs as strongly as other species because they tend to use permanent breeding pools that are relatively unaffected by flow alteration (Lind et al. 1996). Bullfrogs may in fact prefer such areas over habitat located in the hydrodynamic floodplain (Fuller et al. 2011). In contrast, some of the species affected by flow regulation (northern cricket frogs, spring peepers, and upland chorus frogs) prefer ephemeral, relatively shallow breeding sites that hold enough water to host emergent aquatic vegetation but do not support fish (Butterfield et al. 2005; Gray et al. 2005; Moriarty & Lannoo 2005). These specific requirements are likely not met in riparian zones subject to decreases in the frequency of flooding events.

Dams also alter the temporal pattern of flow events. Magilligan and Nislow (2005) analyzed the hydrological effects of 21 large dams throughout the United States and found that in the months of April and May flows downstream from dams are lower compared with unregulated river stretches. These temporal changes in flow patterns may be especially important for anurans because each species breeds during a specific season. Temporal alterations to flow regime may therefore render some riparian areas unsuitable for breeding (e.g., no standing water for egg deposition) when particular species are reproductively active. In fact, some of the species we found to be affected by dams (northern cricket frogs and green frogs) generally begin breeding in April or May and conclude by mid-July (Gray et al. 2005; Pauley & Lannoo 2005; Dorcas & Gibbons 2008). It is possible that reduced downstream flows during this time of the year as a result of dams cause reduced breeding success for these species.

Large, aseasonal water discharge events may be especially detrimental to anuran populations. Such discharges

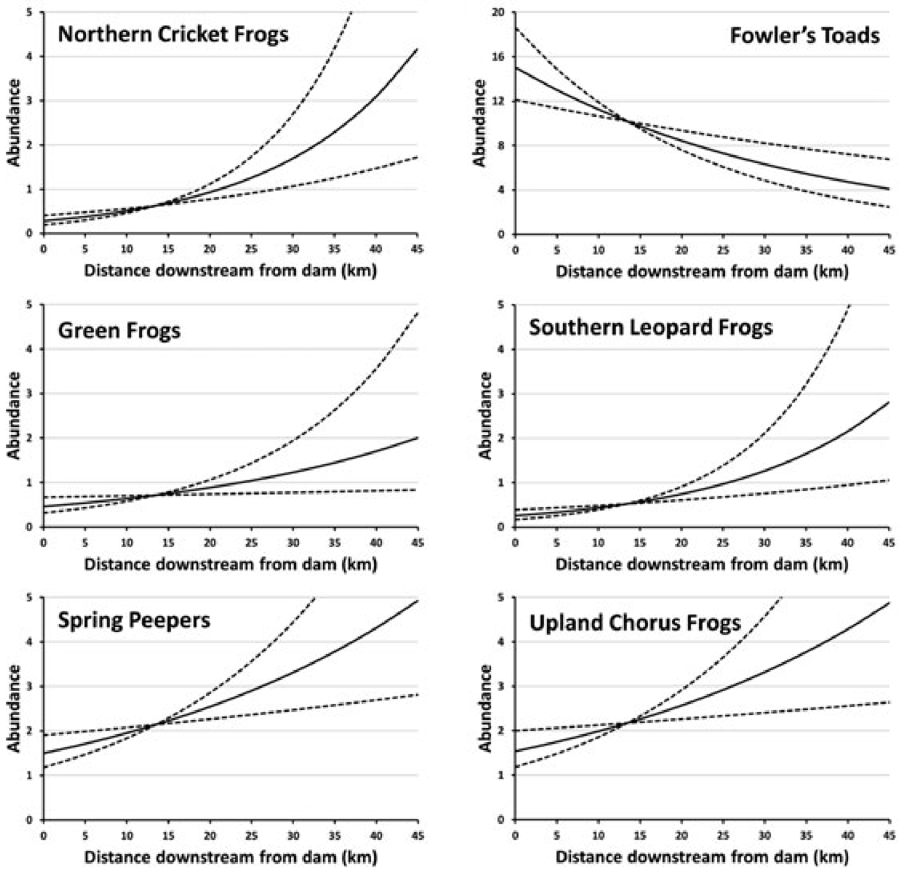

Figure 4. Effect of downstream distance from nearest dam on abundance of 6 anuran species along the Broad and Pacolet Rivers, South Carolina (U.S.A.) (solid lines, relation between downstream distance from nearest dam and abundance, estimated from Royle-Nichols models; dashed lines, 95% CIs for estimates of the covariate effect).

are typical of hydroelectric dam operation. For example, in a study of the foothill yellow-legged frog (*Rana boylii*), Lind et al. (1996) found that in some cases all egg masses laid in downstream river stretches are lost due to high-flow events. Results of a recent study show that high-velocity pulsed flows may physically displace foothill yellow-legged frog tadpoles and negatively affect their growth and survival (Kupferberg et al. 2011). In our study region, aseasonal high-velocity water releases may have similar negative effects on egg and tadpole survival, particularly those in riparian zones close to the water channel where they are most likely to be affected by scouring flows.

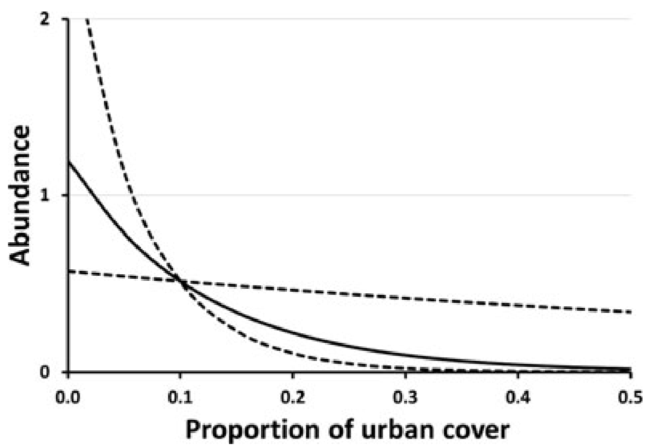

Figure 5. Effect of proportion of urban land cover on abundance of bullfrogs along the Broad and Pacolet Rivers, South Carolina (U.S.A.) (solid line, relation between urban land cover and abundance, estimated from Royle-Nichols models; dotted lines, 95% CI for estimate of the covariate effect).

Our results provide evidence that semiaquatic organisms, such as anurans, may be strongly affected by the same downstream effects of dams that have been previously demonstrated to influence strictly aquatic animals such as fishes and freshwater mussels (Kinsolving & Bain 1993; Vaughn & Taylor 1999). Although results of prior studies show negative effects of flow regulation on the foothill yellow-legged frog, a primarily lotic amphibian (Lind et al. 1996; Kupferberg et al. 2011), our results suggest that altered river flows also affect anuran species that breed in lentic habitats located in riparian zones. These findings and those of previous studies (Lind et al. 1996; Bateman et al. 2008) suggest dam management strategies that may benefit anuran populations. In cases where dam removal and subsequent riverine habitat restoration is infeasible, anuran assemblages would likely benefit from flow regulation that is as similar to natural flows as possible (Poff et al. 1997). Watersheds within eastern and western regions of the United States are largely regulated by rainfall and snowmelt events, respectively (Poff et al. 2007). Water releases in the form of pulsed flows (to mimic natural flooding events as in Bateman et al. [2008]) that are conducted on the basis of such environmental cues are likely to provide anurans with riparian zone aquatic habitats during appropriate seasons.

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Supporting Information

Occupancy and abundance model sets for all species (Appendix S1) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of material) should be directed to the corresponding author.

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