

DO OPEN SPACES WITHIN AN URBAN MATRIX INCREASE ANURAN ABUNDANCE?

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Abstract.—Urbanization is among the leading causes of amphibian declines worldwide. Urban open spaces, such as golf courses and parks, can potentially provide suitable habitat to amphibians within urbanized matrices. During the spring and summer of 2018, we conducted active call surveys to determine the relative abundance of anurans at 51 wetlands within the Piedmont ecoregion of South Carolina, USA. Approximately one third of these wetlands were located within urban open spaces, while the remainder were situated along a gradient of development. We evaluated species-specific relative abundances as a function of the presence or absence of urban open space, several within-wetland covariates, and two landscape-scale covariates. We also tested the hypothesis that open spaces mitigate the influence of high development, as measured by percent impervious surface around the wetland. Road length within a buffer around the wetland negatively affected all species, and this effect remained even for urban open space wetlands. Roads negatively impact anurans through direct mortality, dispersal limitations, and habitat fragmentation. Conservation efforts conducted within open spaces should attempt to focus on issues not only at an individual wetland scale, but also at scales outside of the open spaces themselves. Understanding how urbanization at various spatial scales affects anuran species can inform efforts to bolster amphibian conservation efforts in urban matrices.

Key Words.—frogs; Fowler’s Toad; Gray Treefrog; green space; impervious surface; N-mixture model; roads; Southern Leopard Frog

INTRODUCTION

Amphibian populations are declining worldwide, including in North America (Stuart et al. 2004; Adams et al. 2013; Miller et al. 2018). While there are multiple drivers of these declines, urbanization is a key process threatening amphibians (Hamer and McDonnell 2008; Marsh et al. 2017). Urbanization is widespread (Moore et al. 2003; Wang et al. 2012; Li et al. 2020) and leads to rapid replacement of natural habitat with urban infrastructure such as buildings, houses, roads, paved areas, and other impervious surfaces (McDonnell and Pickett 1990; Hamer and McDonnell 2010). Urbanization can negatively affect amphibian populations via outright habitat destruction (Rubbo and Kiesecker 2005), a reduction of habitat quality (Pope et al. 2000; McKinney 2002), an increase in vehicle-related mortality, and isolation of suitable habitats (Lehtinen et al. 1999; Elzanowski et al. 2009; Smallbone et al. 2011).

As the density of urbanization increases, the need to pinpoint areas that can be used for the conservation of species that would otherwise be negatively affected becomes apparent. Urban open spaces (also referred to as greenspaces) may act as important areas of biodiversity conservation (Goddard et al. 2009). Urban

open spaces are defined within this study as publicly accessible, managed outdoor spaces that are partially to completely covered by vegetation and exist primarily as semi-natural areas within an urbanized matrix (Jim and Chen 2003; Kong et al. 2010; U.S. Environmental Protection Agency. 2022. What is Open Space/Green Space. U.S. Environmental Protection Agency Available from <https://www3.epa.gov/region1/eco/uep/openspace.html> [Accessed 30 September 2022]). These open spaces include community gardens, public parks, sports recreation zones (e.g., golf courses), or cemeteries. Urban open spaces can help alleviate the negative effects that habitat loss, fragmentation, and isolation have on native biodiversity (Kong et al. 2010) and can sometimes create new habitat for wetland breeding amphibians (Birx-Raybuck et al. 2010; Brand and Snodgrass 2010; Marsh et al. 2017). On the other hand, urban open spaces may represent ecological traps for some species (Hale et al. 2015). Generating more information on the value of urban open space to wildlife can offer insights to urban planners and conservation initiatives.

Anurans represent a group of amphibians that may benefit from the proper management of urban open spaces and the wetlands within. At a higher risk of extinction than other taxa (Hamer and McDonnell 2008; Wake and

Vredenburg 2008), the relatively small home ranges and small body sizes of amphibians make them excellent candidates for studies focusing on localized effects of urbanization. Anurans in the USA are largely wetland-associated amphibian species that require ample space in and around aquatic and terrestrial habitats to carry out essential life-history processes such as reproduction, sheltering, and foraging. Urban research concerning anurans is heavily focused on assemblage-level response, and many species-specific responses to urbanization are poorly understood or unknown altogether (Scheffers and Paszkowski 2012). Different species of anurans are likely to be affected by urbanization in different ways as dispersal needs and capabilities, body size, and breeding strategies vary (Gagne and Fahrig 2010; Marsh et al. 2017). Overall, many anuran communities have been shown to respond negatively to urbanization (Hamer and McDonnell 2008; Scheffers and Paszkowski 2012) but assessing species-specific responses to urbanization can facilitate more efficient population management strategies (Cushman 2006).

Declines in anuran diversity may be reduced by managing and protecting existing habitat within otherwise developed areas to mitigate negative impacts on wildlife (Puglis and Boone 2012). Some man-made wetlands in urban open spaces are inhabited by anurans presumably because the created habitat is like wetlands in natural habitats (Brand and Snodgrass 2010). These spaces have the potential to provide habitat and offer habitat connectivity for anurans in an otherwise unsuitable, urbanized matrix (Hamer and Parris 2011; Puglis and Boone 2012). Several studies have examined variables affecting amphibians along a forested-to-urban gradient, with very few comparing forested or urban sites with open spaces such as golf courses (Scheffers and Paszkowski 2012).

We identified 51 wetlands along a rural-to-urban gradient in the upstate of South Carolina, USA, that vary in the amount of urbanization surrounding the wetland. Our literature review indicated that wetland-breeding amphibians require anywhere from 300–750 m of upland habitat surrounding the breeding site to complete necessary life-history processes (Semlitsch 2000; Semlitsch and Bodie 2003; Parris 2006; Bix-Raybuck et al. 2010). We assessed the amount of urbanization surrounding these wetlands by overlaying buffers of 300 m (core habitat) and 750 m (average maximum dispersal). We also defined sites based on the presence or absence of urban open space (as defined above) around the wetland. Our goal was to evaluate how urban open space, landscape covariates (e.g., urbanization and road length), and local attributes measured at the wetland affected the abundance of five anuran species. We used call survey data to estimate relative abundance of the focal species. We developed *a priori* hypotheses for

relationships we expected to find for each species based on habitat preferences described in the literature. We hypothesized that local covariates, such as hydroperiod, would be important for species previously demonstrated to be sensitive to fish (e.g., Spring Peepers, *Pseudacris crucifer*, and Gray Treefrogs, *Dryophytes versicolor*; Porej and Hetherington 2005). We predicted that species abundance would be negatively related to the landscape covariates road length and percent impervious surface. We also hypothesized an interaction between the presence of urban open space and impervious surface, for which we predicted that all species observed would have an increased probability of occupancy at wetlands within urban open space, especially when the percentage of impervious surface surrounding the wetland was high.

MATERIALS AND METHODS

Study area and wetland categorization.—We identified 73 potential wetlands using Google Earth Pro and a file of South Carolina wetlands provided by the National Wetlands Inventory (NWI; <https://www.fws.gov/wetlands/Data/State-Downloads.html>). Using this wetland geodatabase and county property assessor websites, we were able to obtain landowner information for privately owned wetlands. We narrowed the list of wetlands to 51 based on our ability to acquire permission to access the land. Study wetlands (Fig. 1) were in Anderson, Oconee, and Pickens counties, South Carolina, USA, and ranged from rural areas to areas of high urbanization (i.e., impervious surface within a 750-m buffer around the wetland ranged from 0–86%). We specifically selected a subset of wetlands that fell within urban open spaces (golf courses, parks, and public gardens) to address the primary research objective.

We delineated each wetland as a unique polygon in ArcMap (Esri, Redlands, California, USA) using a satellite imagery base map and knowledge of the actual wetland boundaries obtained from ground truthing. We added two buffers (300 and 750 m) around each wetland perimeter, representing the average core habitat and maximum average dispersal range from the wetland for the anuran species expected to be found within the study area (Semlitsch and Bodie 2003; Parris 2006; Bix-Raybuck et al. 2010). We also noted whether each wetland was within an urban open space, based on the definition provided in the Introduction. The distinct management strategies associated with wetlands and adjacent terrestrial habitat in open spaces create the impetus for assigning them to their own category (Hutto and Barrett 2021).

Wetland landscape and local characteristics.—We collected data on both landscape- and local-level factors hypothesized to influence the abundance (as measured

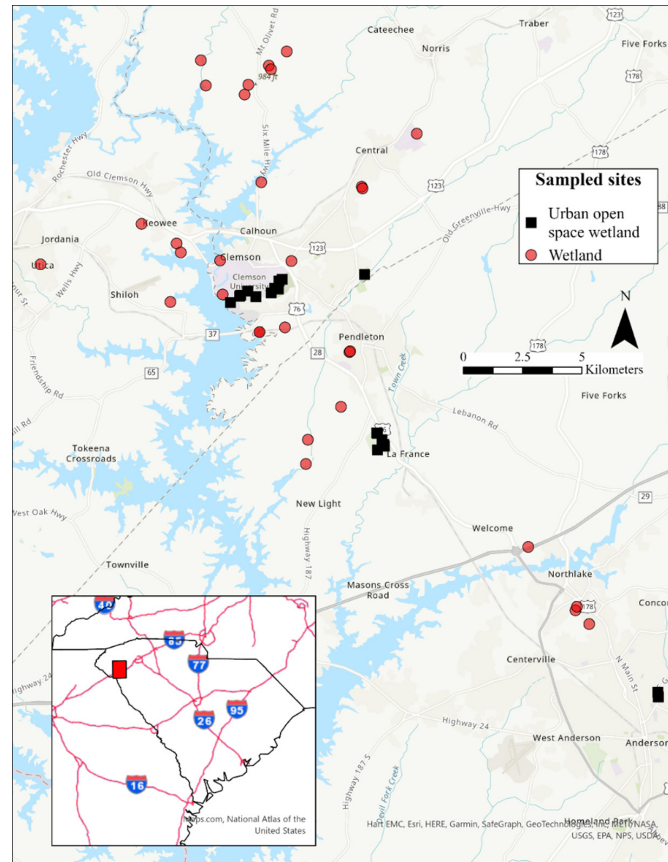


FIGURE 1. Distribution of wetlands surveyed for calling anurans within northwestern South Carolina, USA. The rectangle within the inset map represents the study region depicted within the primary map.

by calling index) of frogs (Table 1). We obtained data on developed land, impervious surface, and road length from the South Carolina Department of Transportation (<https://www.scdot.org/travel/travel-mappinggis.aspx>). Using these data, we were able to calculate levels of urbanization and road length within the radii of both buffer zones. We calculated road length as the total road length in meters within each buffer, whereas impervious surface and developed land were calculated as the percentage of coverage. We used the wetlands from the NWI that included all wetlands in South Carolina to determine the distance from the nearest body of water to the study wetlands. We then split this NWI wetlands layer into two separate categories: riverine bodies and freshwater wetlands (freshwater emergent, forested/shrub, and ponds), and calculated the straight-line distances from each of our focal wetlands to the nearest wetland feature in the each of the NWI wetland categories. To account for the possibility that study sites may be the closest neighbor of each other, we included the study sites when determining the distance to other freshwater wetlands, as several were not actually included in the NWI layer.

From March to July 2018, we recorded within-wetland habitat data during daytime dip net surveys that were

performed as part of a separate study (Hutto and Barrett 2021). We determined wetland size through ArcMap via a wetland delineation process by which we created polygons for each wetland individually. We measured depth (m) at what we presumed to be the deepest point using a meter stick, and we assigned a depth of > 1.2 m to wetlands deeper than the 1.2 m limit of the depth stick used. We obtained an average organic layer depth of the wetland by measuring the depth (cm) of the submerged organic layer at each dip net stop and then averaging them together for each wetland.

We measured canopy cover at each wetland after leaf-out (July) by taking photographs at each cardinal location using an iPhone 7 (Apple, Inc., Cupertino, California, USA) paired with a fisheye lens attachment (Amir, Shenzhen, Guangdong, China). We only took one photograph to obtain canopy cover at small (< 0.01 ha) wetlands where multiple photographs were unnecessary. We used the Gap Light Analyzer (Cary Institute of Ecosystem Studies, Millbrook, New York, USA) to attain a percentage of canopy cover for each photograph. We averaged canopy cover values across all photographs from a wetland to produce its canopy cover measurement. We measured aquatic vegetation cover

TABLE 1. Local- and landscape-scale call index covariates used in single-species N-mixture models for anurans along a rural-urban gradient in the South Carolina Piedmont ecoregion, USA.

Model covariate	Scale	Type	Description
Urban Open Space	Landscape	Categorical	Wetland type based on presence of open space around the wetland
Impervious surface	Landscape	Continuous	Percentage of impervious surface surrounding a wetland within 300 m
Road length	Landscape	Continuous	Road length (m) surrounding wetland (w/in 300 m)
River distance	Landscape	Continuous	Distance (m) from site to nearest riverine wetland
Freshwater distance	Landscape	Continuous	Distance (m) from site to nearest freshwater wetland (freshwater emergent, forested/ shrub, and ponds)
Aquatic vegetation	Local	Categorical	Mean aquatic vegetation percent cover at a site. Combined reeds, aquatic grass, and other aquatic vegetation. Categorized from 1 – 4 in equal intervals
Terrestrial vegetation	Local	Categorical	Presence/absence of a terrestrial buffer zone of vegetation at least 1-m wide and around at least 1/2 of the wetland edge
Hydroperiod	Local	Categorical	Binary variable indicating fluctuating or temporary wetland during survey period
Fish presence	Local	Categorical	Binary category indicating fish presence or absence
Canopy cover	Local	Continuous	Mean wetland canopy cover (%)
Organic depth	Local	Continuous	Mean depth of organic layer within a wetland (cm)
Area	Local	Continuous	Size of wetland (ha)
pH	Local	Continuous	Mean wetland pH
Conductivity	Local	Continuous	Mean wetland conductivity (mS ²)

by making visual estimates of the amount of emergent and submerged aquatic vegetation. We placed our visual estimates into one of four categories (1 = 0–25%, 2 = 26–50%, 3 = 51–75%, 4 = 76–100%). We recorded the presence or absence of a buffer of herbaceous terrestrial vegetation surrounding wetlands and assigned wetland categories according to buffer presence (1 = vegetation present, 0 = vegetation absent). We required a buffer of terrestrial vegetation to be at least 1-m wide and extend around at least half of the wetland edge to label a buffer as present.

We visually noted fish presence at wetlands during survey visits and this was further assessed through dip net surveys (Hutto and Barrett 2021). We determined hydroperiod for a wetland during the study season (February–July 2018) by noting the presence or absence of water during each survey, call and dip net. We assigned a value = 0 (Fluctuating) to wetlands that were dry at any point during the study, whereas those that held water throughout the period of the study received a value = 1 (Stable). We measured water temperature, conductivity, and pH using an Oakton PCTSTestr™ (Cole Parmer, Vernon Hills, Illinois, USA) during each dip net visit. We used a Kestrel 2500 unit (Nielsen-Kellerman, Boothwyn, Pennsylvania, USA) to gather air temperature, relative humidity, and maximum wind speed.

We evaluated the Pearson Correlation Coefficients between all pairs of landscape and local variables and performed Variance Inflation Analysis (package usdm in Program R; Naimi et al. 2014) with the intention of eliminating multicollinearity in the modeling

process. We removed percentage developed land as it was highly correlated with impervious surface at both buffer sizes ($r \geq 0.85$, $P < 0.001$). We removed both impervious surface and road length at the 750-m scale as covariates because they were significantly correlated with impervious surface and road length at the core 300-m scale (Pearson's Product-moment Correlation, $r = 0.91$ and 0.78 ; $P < 0.001$ and < 0.001 , respectively). These variables also showed variance inflation factors > 2 , but when removed, all variance inflation factors were about 1.0. Given that hydroperiod and maximum depth are typically highly correlated (Babbitt et al. 2003), we removed wetland depth because hydroperiod may be more important for completion of anuran life cycles.

Anuran call surveys.—We conducted anuran call surveys once per month February–June 2018 for a total of five call surveys per wetland. We performed surveys during the evenings beginning approximately 30 min after sundown and ending no later than 1133 that evening. To maximize detection probability, we only conducted surveys when air temperatures were between 5.6° C and 30° C as recommended in the North American Amphibian Monitoring Protocol (NAAMP; Weir and Mossman 2005; Steelman and Dorcas 2010). We did not conduct surveys when wind speeds were consistently greater than 8–12 mph or when there was heavy rainfall, as either of those conditions may negatively affect detection of frog calls. We spent 5 min actively listening at each wetland and we recorded calls as an index of abundance per NAAMP protocol. The 5-min duration

has been demonstrated to be adequate for detecting species in our survey region (Gooch et al. 2006). The call index developed by NAAMP rates calling activity from one through three, with one representing lower activity and three representing the highest activity. Specifically, one indicates distinct individuals can be counted and calls are not overlapping, two means there may be overlapping calls, but individuals can be distinguished, and a three was assigned if there was a full chorus, and calls were constant, continuous, and overlapping. Studies that evaluated the effectiveness of this call index and its relation to actual abundance using mark-recapture methods found positive relationships between call index and abundance in Green Frogs (*Lithobates clamitans*; Nelson and Graves 2004) and Boreal Chorus Frogs (*Pseudacris maculata*; Corn et al. 2000). To account for ambient noise surrounding a wetland, we used the Massachusetts Noise Index (<https://www.usgs.gov/centers/eesc/science/north-american-amphibian-monitoring-program>) where 0 = no effect on sampling, 1 = slight effect on sampling, 2 = moderate effect on sampling, 3 = serious effect on sampling, 4 = profound effect on sampling. We also recorded Julian day as well as start and end times during each survey. Prior to analysis, we removed sampling periods in which anurans were not heard calling for each focal species, unless the focal species called at any wetland in a period prior to or following a period with an absence.

Data analysis.—Using the index data from anuran call surveys, we developed N-mixture models to investigate species-specific relationships between call activity and environmental (local) covariates, while simultaneously accounting for factors that may have influenced detection probability related to frog calls (Royle 2004; Royle and Link 2005; Table 2). We developed all models using the p-count function within the unmarked package (Fiske and Chandler 2011) in Program R Version 3.4.1 (R Core Team 2017). These models assume population closure.

For the application described here, we assume the number of frogs capable of creating the maximum index observed were present throughout the modeled period.

We collected data on six detection probability covariates: (1) Julian day (modeled as a linear and quadratic effect); (2) time of day; (3) temperature; (4) humidity; (5) wind; and (6) noise. We never incorporated noise as a detection covariate as there were no sampling occasions where noise levels reached a point that would prevent surveyors from hearing calls. We recorded time of day as the start time of each 5-min survey. We logged temperature and humidity at the maximum value recorded during each survey. We measured wind as the maximum wind speed during a survey and then converted into a binary format where 1 corresponds to wind speed > 16 km/h and 0 for ≤ 16 km/h.

We began model evaluation by first examining the support for detection covariates modeled individually. We compared each of these univariate detection-only models and a null model using Akaike's Information Criterion (AIC; Burnham and Anderson 2002). We did not evaluate more complex structures for the detection process because only one detection covariate had strong model support for each species ($\Delta\text{AIC} < 2.0$; Table 3). Once we identified the detection covariate model with the most support ($\Delta\text{AIC} = 0.00$), we integrated that covariate in all further models assessing abundance and local covariates.

For each species we evaluated the influence of urban open space against five other hypothesized predictors of call index: (1) impervious surface; (2) road length; (3) a model with main effects of open space presence/absence, impervious surface, and an interaction between the two; (4) a global model containing all covariates except urban open space (Table 1); and (5) a null model. We compared the relative evidence for each of these hypotheses using AIC (Table 4). In the results we focus on relationships between call index and covariates for models with $\Delta\text{AIC} < 2.0$ and significant effect size for the parameter

TABLE 2. Covariates used in single-species N-mixture models to estimate detection probability for anurans along a rural-urban gradient in the South Carolina Piedmont ecoregion, USA.

Model covariate	Type	Description
Relative humidity	Continuous	Percent relative humidity recorded as maximum value during the 5-minute survey period using a Kestrel 2500.
Julian date	Continuous	Continuous count of days for the year, where Jan 1 is assigned 1 and Dec 31 is assigned 365 (non-Leap Year)
Julian date ²	Continuous	Julian date, but squared to assess they hypothesis that detection rates peak during the middle of a species calling window
Temperature	Continuous	Temperature in °C recorded as maximum value during the 5-minute survey period using a Kestrel 2500
Time of day	Continuous	Recorded in military time
Wind	Categorical	Recorded as maximum value during the 5-minute survey period using a Kestrel 2500, but transformed to a binary variable for the analysis; 0 if < 16km/hr, and 1 otherwise

estimate (standard error did not overlap with zero). We standardized all non-categorical variables to z-scores (mean = 0, standard deviation = 1). We evaluated null and global models for each species using each distribution option (Poisson, Negative Binomial, and Zero Inflated-Poisson) and then ranked by AIC to determine which distribution was best suited for each species. We focused on five species that represented a range of body sizes and life-history strategies such as clutch size and larval period: (1) American Bullfrogs (*L. catesbeianus*); (2) Fowler's Toads (*Anaxyrus fowleri*); (3) Gray Treefrogs (*Dryophytes versicolor*); (4) Northern Cricket Frogs (*Acris crepitans*); and (5) Southern Leopard Frogs (*L. sphenoccephalus*). We used the Poisson distribution to construct models for American Bullfrogs and Southern Leopard Frogs, whereas we used a Zero-Inflated Poisson distribution to construct models for Northern Cricket Frogs, Gray Treefrogs, and Fowler's Toads. For each species, we evaluated the role of spatial autocorrelation as a driver of results using Global Moran's I (ArcGIS Pro 3.0, Esri, Redlands, California, USA). We found no evidence to reject the null hypothesis of random spatial pattern for the American Bullfrog, Fowler's Toad, Gray Treefrog, and Northern Cricket Frog. We did reject the null hypothesis of random spatial patterning with respect to call index for Southern Leopard Frog ($P < 0.001$), so readers should interpret findings for that species with this limitation in mind.

RESULTS

During the 5-mo sampling period, we collected 255 nights of call surveys resulting in 508 detections of 12 anuran species. Of the 12 species detected, three are listed under the Wildlife Action Plan of the South Carolina Department of Natural Resources (2015) as priority species (Pickerel Frogs, *L. palustris*, Northern Cricket Frogs, *A. crepitans*, and Upland Chorus Frogs, *P. feriarum*). Detections for these 12 species ranged from 10–92 (mean detections = 42.3 ± 25.04 standard deviation).

Temperature or time of year had an influence on detection probability for all species (Table 3). Detection probability increased for Fowler's Toads as temperature increased. Detections were higher later in the season for Northern Cricket Frogs. For American Bullfrogs, Gray Treefrogs, and Southern Leopard Frogs, detection probability was low in early samples, increased during middle samples, then decreased again.

We found evidence that development, as measured by road length or impervious surface, within a 300-m buffer around the wetland negatively influenced calling index (hereafter, relative abundance) for all species (Table 4). Road length was included in the top-supported model for American Bullfrogs, Gray Treefrogs, and Southern

Leopard Frogs (Fig. 2), and it was a factor among the top models ($\Delta AIC < 2$) for Northern Cricket Frogs and Fowler's Toad; however, the standard error included zero for both species, suggesting the effect was not significant. There was support for a model where increased impervious surface negatively impacted the relative abundance of Northern Cricket Frogs and Fowler's Toads.

We did not find support for our hypothesis that urban open spaces would ameliorate the influence of development on the focal species (i.e., the model with an interaction between urban open space and impervious surface was never among the top models). Models with only urban open space as a covariate of relative abundance did receive support for three of the five focal species: American Bullfrogs, Northern Cricket Frogs, and Fowler's Toad. In all cases, models predicted lower abundance for open space wetlands relative to wetlands outside of open space. In the open space model for Fowler's Toads, the standard error around the open space coefficient included zero. The model that included local covariates did not receive support for any species, which was contrary to our hypothesis that hydroperiod may be an important predictor of abundance for some species, such as Gray Treefrogs, known to be sensitive to

TABLE 3. The most supported ($\Delta AIC < 2.0$) models based on Akaike's Information Criterion and model weights (w) for variables hypothesized to influence detection probability among amphibian species breeding in wetlands in northwestern South Carolina, USA. Detection covariates were selected without site-level covariates of abundance in the model [$\lambda(\cdot)$]. Once the most supported detection covariates were identified, they were then incorporated into the site-level covariate model selection step. The variable k is the number of model parameters. Species are Northern Cricket Frog (*Acris crepitans*), Fowler's Toad, (*Anaxyrus fowleri*), Gray Treefrog (*Dryophytes versicolor*), American Bullfrog (*Lithobates catesbeianus*), and Southern Leopard Frog (*L. sphenoccephalus*).

Model, by species	ΔAIC	w	k	Effect size of detection covariate (SE)
Northern Cricket Frog				
$\lambda(\cdot)p(\text{Julian day})$	0	0.72	4	1.65 (0.20)
$\lambda(\cdot)p(\text{Julian date}^2)$	1.93	0.28	5	JD: 1.63 (0.22); JD ² : 0.06 (0.24)
Fowler's Toad				
$\lambda(\cdot)p(\text{temp})$	0	1	4	1.04 (0.20)
Gray Treefrog				
$\lambda(\cdot)p(\text{Julian date}^2)$	0	1	5	JD: 1.07 (0.27); JD ² : -2.51 (0.39)
American Bullfrog				
$\lambda(\cdot)p(\text{Julian date}^2)$	0	1	5	JD: 0.86 (0.43); JD ² : -1.47 (0.36)
Southern Leopard Frog				
$\lambda(\cdot)p(\text{Julian date}^2)$	0	1	5	JD: -1.44 (0.34); JD ² : -1.36 (0.32)

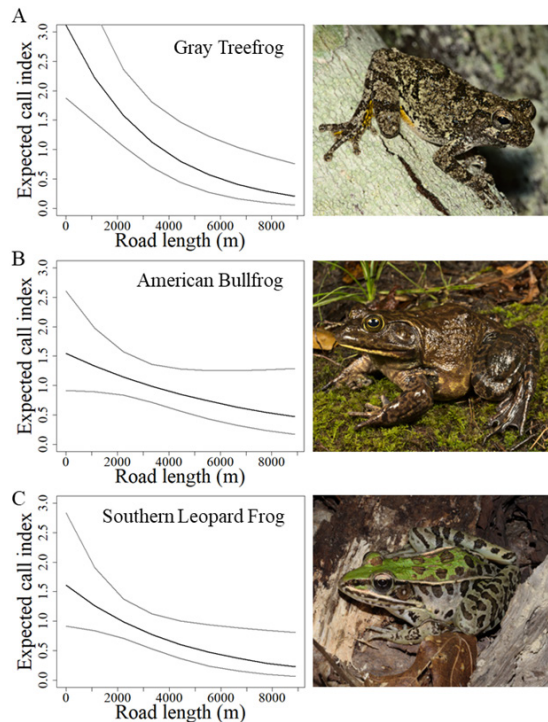


FIGURE 2. Expected call index of anurans from surveyed wetlands in the South Carolina Piedmont ecoregion, USA. (A) Gray Treefrogs (*Dryophytes versicolor*), (B) American Bullfrogs (*Lithobates catesbeianus*), and (C) Southern Leopard Frogs (*L. sphenoccephalus*) showed decreasing call index as a function of road length within a 300-m wetland buffer. (Photographed by Ben Stegenga: Gray Treefrog and American Bullfrog; and Scott Bolick: Southern Leopard Frog).

fish. The null model was present in top ranked models for Fowler's Toads, American Bullfrogs, and Northern Cricket Frogs.

DISCUSSION

As predicted, we found support for the hypothesis that impervious surface and road length influenced relative abundance for the wetland-breeding anurans we evaluated. We did not find evidence that the urban open spaces we surveyed provided a buffer to protect against these effects. Impervious surface or road length appeared among the top models for all five focal species, and in all cases the relationship with these variables was negative (Table 4; Fig. 2). Negative effects of roads and impervious surfaces on species richness and abundance are well documented (Fahrig et al. 1995; Findlay and Houlihan 1997; Knutson et al. 1999; Findlay et al. 2001; Marsh et al. 2017). Anurans traveling among breeding wetlands and upland habitats experience relatively high rates of mortality while crossing roads (Ashley and Robinson 1996; Mazerolle 2004; Consentino et al. 2014), which could affect the ability of a species to colonize a

wetland due to adult mortality prior to breeding as well as adult and juvenile mortality during dispersal. Aside from effects of direct mortality, roads produce behavioral and physical obstacles to movement (Bouchard et al. 2009). These obstacles can negatively affect the ability of a species to make seasonal migrations and disrupt dispersal within metapopulations (Gibbs 1998; Hels and Nachman 2002; Consentino et al. 2014).

Evidence from this study and others suggests the scale of inference and species-specific responses both contribute to variation in estimates of road effects on anurans. Marsh et al. (2017) showed that at smaller scales (about 300 m, the same scale tested in our study), road density negatively affected American Bullfrogs as well as Gray Treefrogs, while Southern Leopard Frogs showed no relationship at any scale. Consentino et al. (2014) found that roads negatively affected Southern Leopard Frogs, though the relationship was not highly significant as standard error estimates for effect size crossed zero. The negative effect of roads on these anuran species may be the result of higher densities of smaller, secondary roads surrounding wetlands acting as dispersal barriers, fragmenting habitat, and causing direct mortality. At the 300-m scale, road densities may affect different species of anurans in similar manners, regardless of body size or movement ability (Consentino et al. 2014).

The absence of an interaction between impervious surface and our urban open space covariate from the list of well-supported, species-specific models suggests that the urban open spaces that were part of our study did not provide a meaningful buffer from the effects of development. The diversity of uses present within our urban open space category yielded a wide range of wetland environments and surrounding buffers so that not all the greenspace wetlands functioned similarly to one another (Hutto and Barrett 2021). Terrestrial vegetation surrounding wetlands in urban open spaces may provide a more suitable habitat structure for anurans, offering shelter for adults and metamorphs and acting as calling and amplexus sites (Parris 2006; Puglis and Boone 2012). Buffer zones such as these can also help alleviate the effects that applied chemicals can have on a wetland (Puglis and Boone 2012).

Many urban open spaces are constructed in association with real estate projects and are therefore deep within the urbanization matrix (Mulvihill 2001). Open spaces that are isolated within a large surrounding urban matrix may function like the urban areas around them and not offer the same benefits to wildlife seen in open spaces with low surrounding development (Price et al. 2013). One study found that higher amounts of residential development within and around the boundaries of golf courses had a negative effect on the abundance of semi-aquatic turtles, whereas wetlands within golf courses surrounded by

TABLE 4. Most supported single species N-mixture models based on Akaike's Information Criterion ($\Delta AIC < 2.0$) and model weight (w) that evaluated univariate landscape scale habitat covariates of anuran abundance (l) along with a null and global model and the top species-specific detection covariate. The variable k is the number of model parameters. Models were applied separately to five anuran species with encounter histories sufficient for parameter estimation. The final column represents the β -estimate (effect size) and standard error associated with the covariate of relative abundance. These estimates are on a logit scale and based on covariates that were centered and scaled. For models that include the Open Space covariate, the effect size is relative to sites that were not within urban open spaces. Species are Northern Cricket Frog (*Acris crepitans*), Fowler's Toad, (*Anaxyrus fowleri*), Gray Treefrog (*Dryophytes versicolor*), American Bullfrog (*Lithobates catesbeianus*), and Southern Leopard Frog (*L. spehnocephalus*). The abbreviation SE = standard error.

Model, by species	ΔAIC	w	k	Effect size of covariate estimate (SE)
Northern Cricket Frog				
$\lambda(.)$ p(Julian date)	0	0.33	4	—
$\lambda(\text{Open space})$ p(Julian date)	0.83	0.22	5	-0.41 (± 0.39)
$\lambda(\text{Impervious surface})$ p(Julian date)	1.05	0.20	5	-0.24 (± 0.23)
$\lambda(\text{Road length})$ p(Julian date)	1.69	0.14	5	-0.11 (± 0.21)
Fowler's Toad				
$\lambda(.)$ p(Temperature)	0	0.42	4	—
$\lambda(\text{Impervious surface})$ p(Temperature)	1.54	0.19	5	-0.14 (± 0.20)
$\lambda(\text{Open space})$ p(Temperature)	1.62	0.19	5	-0.23 (± 0.38)
$\lambda(\text{Road length})$ p(Temperature)	1.97	0.16	5	-0.03 (± 0.15)
Gray Treefrog				
$\lambda(\text{Road length})$ p(Julian date ²)	0	0.82	6	-0.68 (± 0.20)
American Bullfrog				
$\lambda(\text{Road length})$ p(Julian date ²)	0	0.34	5	-0.30 (± 0.16)
$\lambda(\text{Open space})$ p(Julian date ²)	0.19	0.31	5	-0.56 (± 0.33)
$\lambda(.)$ p(Julian date ²)	1.19	0.19	3	—
Southern Leopard Frog				
$\lambda(\text{Road length})$ p(Julian date ²)	0	0.61	5	-0.49 (± 0.22)

lower amounts of residential development supported turtle abundances equal to those in more natural ponds (Price et al. 2013). Similarly, land alterations within an open space can lead to homogenization of the landscape and a reduction in habitat quality (Puglis and Boone 2012), a process not considered by our wetland categories. It has been suggested that urban open spaces, particularly golf courses, should be included in residential designs in a manner that promotes higher levels of biodiversity (Colding et al. 2006).

Observing anuran occupancy and abundance across one field season may be insufficient, as multi-seasonal colonization and extinction patterns can offer insights not described here (Randall et al. 2015). Further, the presence of calling males at a wetland does not necessarily indicate successful reproduction, only the presence of adult males. Future research may benefit from exploring reproductive success and variables not addressed in this study. The presence of the null model among the top-ranked models for American Bullfrogs, Fowler's Toads, and Northern Cricket Frogs either suggests the species disperse so widely that presence is essentially equal across wetlands in a given year, or that unmeasured variables influenced the distribution. Long-term studies would allow for a better description of the species-environment relationship, characterization of

reproductive success, and evaluation of metapopulation dynamics among wetlands. Such efforts are necessary to determine if wetlands in urban open spaces and the open spaces themselves can serve as source populations for amphibians, or if they largely function as sinks instead (Puglis and Boone 2012).

Conclusions.—Development-related variables consistently predicted call index, although the well-supported models were variable across species. Multiple factors are known to shape anuran occupancy or abundance at wetlands (Pillsbury and Miller 2008; Hamer and Parris 2011; Birx-Raybuck et al. 2010). Other researchers have concluded that landscape variables alone explained < 35% of the variation within their datasets (Bonin et al. 1997; Hecnar 1997; Knutson et al. 1999); however, Beebe (1985) found that landscape variables are better predictors than individual wetland characteristics in determining amphibian diversity, although the scale at which species respond to landscape variables can differ (Hermann et al. 2005). Additional work should be performed to more clearly quantify whether urban open space wetlands provide habitat that is distinct from other wetlands, and if there are subsets of open space that offer more suitable breeding and adjacent upland habitat. Further work should also explore if the size or

management of the urban open space helps to mitigate the influence of roads and other forms of impervious surfaces. The success of amphibian conservation relies on a continued effort to understand the specific mechanisms that drive community structure and distribution within an urbanized environment. Long-term monitoring along multiple spatial scales at a variety of wetland types will only add to our knowledge of these species and the factors that influence them, helping to more effectively conserve and reestablish amphibian populations and the habitat they require.

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