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Anuran Community Occupancy Dynamics in Wayne National Forest in Southeast Ohio, USA

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Abstract.—**Amphibians are indicators of ecosystem health due to their high susceptibility to changing environmental conditions. Understanding how amphibian populations change in response to environmental pressures can be critical for successful land management strategies aimed at maintaining functioning ecosystems. Wayne National Forest (WNF) in Ohio, USA, harbors rich amphibian fauna, and wildlife managers monitored anuran (frog) species to determine the best forest management strategies for their protection. The goal of our study was to quantify pond-breeding amphibian community dynamics in WNF in relation to different land management strategies and environmental predictors using a hierarchical modeling framework. Using the North American Amphibian Monitoring Program protocol, we collected data at 30 sites monthly between March and June from 2005 to 2018. Thirteen species were detected, and we selected five with consistent detections (American Bullfrog, *Lithobates catesbeianus*, American Toad, *Anaxyrus americanus*, Gray Tree Frog, *Hyla versicolor*, Green Frog, *L. clamitans*, and Pickerel Frog, *L. palustris*) to evaluate extinction and colonization dynamics using multi-year (dynamic) occupancy models. We found most species had stable populations during the survey period. Distance to the nearest wetland was a positive predictor for occupancy for the American Bullfrog and Green Frog and negative for the other three. Detection for all was influenced by the month and air temperature during the survey. Our results suggest that pond-breeding amphibian occupancy in the WNF has remained stable during the survey period, and that surveys should keep pace with ongoing phenology shifts to fully evaluate the makeup and changes in the anuran communities.**

Key Words.—American Bullfrog; American Toad; amphibians; Gray Tree Frog; Green Frog; herpetology; Pickerel Frog

Introduction

Amphibians are among the most imperiled taxa and face a wide array of threats to their persistence, including climate change, habitat loss and alteration, disease, and pollution (Stuart et al. 2014). Their permeable skin and biphasic (aquatic and terrestrial) life cycles (Wilbur 1980) makes amphibians susceptible to many stressors that can act independently or in synergy across different life stages (Earl and Semlitsch 2013; Boes and Benard 2013; O'Regan et al. 2014; Thompson and Popescu 2021). Amphibians not only act as sentinels of environmental change in many systems (Collins and Storfer 2003), but also have significant contributions to ecosystem services and trophic webs. For example, annual breeding migrations move organic matter and nutrients between habitats and can affect biogeochemical cycles and ecosystem processes (Berven 2009; Capps et al. 2015; Earl et al. 2022). Thus, the loss of amphibian populations can have profound effects on the ecosystems they inhabit and can contribute to a host of other unknown effects. Additionally, anurans serve as prey for a host of terrestrial and aquatic species (Somers and Purves 1996; Corlett 2011; Costa et al. 2021), and their loss can have cascading effects up and down the trophic levels.

Monitoring trends in amphibian populations is a critical component of amphibian conservation. Populations of most amphibian species can fluctuate greatly both temporally and spatially (Berven 1990; Werner et al. 2009; Kupferberg et al. 2012; Earl et al. 2022). As such, there is a need for long-term data to analyze changes within amphibian communities, with calls for increased monitoring made across decades (Blaustein et al. 1994; Weir et al. 2005). Long-term data collected across larger geographic extents and temporal scales using powerful monitoring protocols can signal declines as well as recoveries in amphibian populations, which can trigger management and conservation actions. For example, when evaluating the effects of diseases caused by *Ranavirus* or chytrid fungus, long-term data provides important insights into what species are affected, and what pathogens disrupt communities the most (Bosch et al. 2018, 2021). Long-term data can also be useful in determining persistence of species and changes in diversity on the local level (Petranka et al. 2007), and programs such as the North American Amphibian Monitoring Program (NAAMP), a standardized data collection protocol, can be used to model detection and occurrence probability (MacKenzie et al. 2002; Weir et al. 2014; Ondei et al. 2018) and to compare data spatially and temporally.

The NAAMP was created to monitor trends in amphibian occupancy in the conterminous U.S., and to assess changes in local communities of calling amphibians using the unique calls of breeding amphibians (Weir et al. 2005). NAAMP was designed to be replicable, standardized, and easy to implement with little resource needs, and it is amenable to involving volunteer citizen scientists. NAAMP methods rely on repeated surveys of the same sites within a given year or anuran calling season. This repeated-visit approach allows for accounting for imperfect detection via Occupancy Modeling (MacKenzie et al. 2002). When monitoring the same sites across years, this statistical framework can be extended to dynamic occupancy models that concomitantly estimate population and metapopulation processes such as colonization and extinction where sampling is adequate (MacKenzie et al. 2003).

We used a 14-y dataset (2005–2018) of repeated call surveys of pond-breeding anurans (Table 1) at 30 sites located on the Wayne National Forest in southeast Ohio, USA. This monitoring program began in 2005 to understand the effects of different land management strategies around sources of water on anurans in southeast Ohio, USA. We selected survey sites based on accessibility and water source availability, and Wayne National Forest (WNF) staff and volunteers monitored sites following NAAMP protocol from March through June of each year. The main objectives of this research were: (1) to characterize the composition of the pond-breeding anuran community in WNF; (2) to determine anuran occupancy trends in WNF; (3) to evaluate environmental predictors for occupancy and extinction rates; and (4) to evaluate survey specific covariates explaining detection and fine-tune future surveys. Overall, our research provides quantitative evidence for anuran population trends in southeast Ohio and produces baseline information for improving the survey methodology to meet other management and conservation objectives, such as changes in breeding phenology and detection.

Materials and Methods

Site selection.—Personnel of the Athens District of the Wayne National Forest (WNF), Ohio, USA, began surveys in 2005, using the NAAMP (Weir et

Table 1. Anuran species historically detected in southern Ohio, USA.

Common Name	Scientific Name	Prior Species Detection Records
American Toad	*Anaxyrus americanus*	Green 1948; Johnson 2003; Gooley 2013; Powell et al. 2016
American Bullfrog	*Lithobates catesbeianus*	Gooley 2013; Powell et al. 2016
Blanchard's Cricket Frog	*Acris blanchardi*	Lehtinen and Witter 2014
Cope's Gray Treefrog	*Hyla chrysoscelis*	Costanzo et al. 1992
Eastern Spadefoot Toad	*Scaphiopus holbrookii*	Green 1948; Smith et al. 1973; Johnson 2003; Gooley 2013
Fowler's Toad	*Anaxyrus fowleri*	Thornhill 1985; Smith and Green 2004; Powell et al. 2016
Gray Treefrog	*Hyla versicolor*	Gatz 1981; Little et al. 1989; Matson 1990
Green Frog	*Lithobates clamitans*	Gooley 2013; Powell et al. 2016
Leopard Frog	*Rana pipiens*	Powell et al. 2016
Mountain Chorus Frog	*Pseudacris brachyphona*	Hoffman 1980; Ospina et al. 2020
Pickerel Frog	*Lithobates palustris*	Schaff and Smith 1970; Gooley 2013; Powell et al. 2016
Spring Peeper	*Pseudacris crucifer*	Gooley 2013; Powell et al. 2016
Western (Midland) Chorus Frog	*Pseudacris triseriata*	Thomas 1951; Platz and Forester 1988, Powell et al. 2016
Wood Frog	*Lithobates sylvaticus*	Powell et al. 2016

al. 2009) as the basis for their site selection criteria. WNF personnel selected sites that were close to a permanent source of water, had public access, and occurred within the boundaries of WNF. Thirty sites were selected across Dover, Ward, and York townships in southeast Ohio, and they were divided into three groups of 10 sites (Fig. 1). York Route 91 sites were primarily located south of US-33 and the Hocking River and encompass regions of York Township and Nelsonville (Fig. 1). The survey sites included a mix of natural and man-made water sources and were located around the Hocking College Campus in Nelsonville. Dover Route 104 sites were located north of US-33 and the Hocking River and were primarily northeast of State Route 13 (Fig. 1). Sites were in and around Chauncey and Dover Township Ohio, as well as surrounding forested areas. Ward Route 119 sites were located north of US-33 and the Hocking River and encompassed regions of Carbon Hill-Buchtel and Ward townships (Fig. 1). Many of the sites were located close to developments such as homes, roads, and man-made culverts.

Data collection.—Volunteers and WNF staff conducted anuran call surveys once per month from March until June during the third week of each month, between 2005 and 2018. During this period, > 23,000 anuran call records were collected using methods outlined in the NAAMP protocol (Weir et al. 2005). The 14 species were surveyed at 30 sites, four times a year for 14 y. All surveys started 1 h after sunset and occurred only when air temperatures were > 10° C, during calm wind conditions, and not during heavy rainfall events, as high winds and rain interfere with the ability of surveyors to hear anuran vocalizations (Weir et al. 2009). In most years, the three routes were surveyed during the same night in any given month.

The start of the route was random across surveys, and the completion of any 10-site route took 2–3 h. At each site, air and water temperature, as well as sky and wind conditions, were recorded following the NAAMP protocol. Surveys occurred when wind speeds were less than a 4 on the Beaufort wind scale, or 20.9 km/h (Weir et al. 2009). Sky conditions were recorded as clear, partly cloudy, cloudy, or raining. Upon arrival at the sites, observers turned on electronic recorders and listened to vocalizations for 3 min in silence, noting which species they heard and their relative call abundance. Call abundance was ranked on a scale of 0 to 3 based on the NAAMP protocol (Weir et al. 2009) with 0 = no individuals of a given species recorded, 1 = no overlapping calls and the exact number of individuals was recorded, 2 = some overlapping calls and the number of individuals was estimated, and 3 = a continuous chorus that made it impossible to discern the exact number of individuals present.

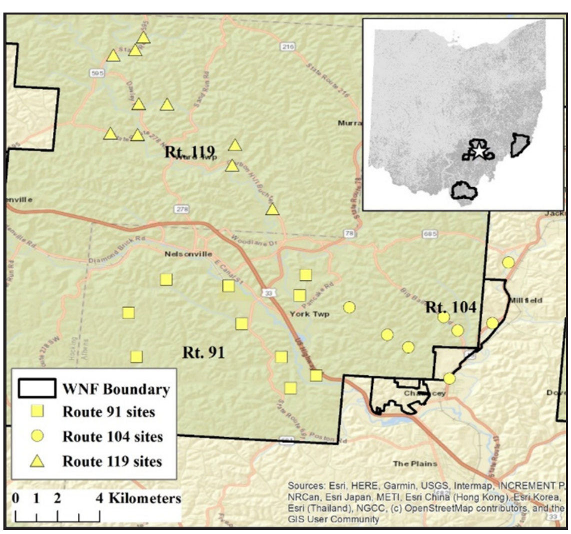

Figure 1. Survey sites located in the Athens Unit of Wayne National Forest in and around the Hocking River area, southeastern Ohio, USA. Sites contain a mix of natural and man-made water sources, and contain a patchwork of primarily forested, open, and developed land.

Site specific variables.—We extracted site specific variables from the National Land Cover Database (Homer et al. 2020) to determine local landcover composition within 100, 250, and 500 m circular neighborhoods using ArcGIS 10.8 (Esri, Redlands, California, USA) as land cover is known to influence spatial patterns of anuran occupancy (Mazerolle et al. 2005). We aggregated types of land cover due to low or non-existent coverage and due to the low importance of some landcover types on anuran occupancy (Table 2). Because beaver modification of lotic and lentic systems is known to increase amphibian diversity at local and landscape scales (Russell et al. 1999; Stevens et al. 2007; Cunningham et al. 2007; Karraker and Gibbs 2009; Popescu and Gibbs 2009), we also extracted information on the presence or absence of beaver disturbance. We also considered the number and type of water sources based on site surveys conducted by WNF staff. Water sources were classified as natural creek, pond and wetland, manmade, ephemeral pond, and unknown. Additionally, using Google Earth Pro (Google Earth Pro 2021), we measured the distance from each site to the nearest wetland (from the National Wetland

Table 2. Survey and site-specific variables used for modeling detection probability (*p*) and occupancy (**Ψ) of** anurans in Wayne National Forest, Ohio, USA. Data source codes are NLCD = National Land Cover Dataset (Jin et al. 2019), GE = Google Earth, and WNF = Wayne National Forest.

Variable	Description	Range	Data
Detection (*p*) variables			
MONTH	Survey Month (Mar. = 1, Apr. = 2…)	1–4 (categorical)	Surveys
TIME	Minutes After Sunset	0–273 min	Surveys
TEMP	Air Temperature	1.66°–26.66° C	Surveys
SKY	Sky Conditions (Clear, Cloudy, Partly Cloudy, Rain)	1–4 (categorical)	Surveys
Occupancy (Ψ) variables			
100.dev	Low developed in 100-meter buffer	Proportion	NLCD
100.devhigh	High developed in 100-meter buffer	Proportion	NLCD
100.for	Forested land in 100-meter buffer	Proportion	NLCD
100.opn	Open land in 100-meter buffer	Proportion	NLCD
100.agr	Agriculture land in 100-meter buffer	Proportion	NLCD
100.wet	Wetlands in 100-meter buffer	Proportion	NLCD
250.dev	Low developed in 250-meter buffer	Proportion	NLCD
250.devhigh	High developed in 250-meter buffer	Proportion	NLCD
250.for	Forested land in 250-meter buffer	Proportion	NLCD
250.opn	Open land in 250-meter buffer	Proportion	NLCD
250.agr	Agriculture land in 250-meter buffer	Proportion	NLCD
250.wet	Wetlands in 250-meter buffer	Proportion	NLCD
500.dev	Low developed in 500-meter buffer	Proportion	NLCD
500.devhigh	High developed in 500-meter buffer	Proportion	NLCD
500.for	Forested land in 500-meter buffer	Proportion	NLCD
500.opn	Open land in 500-meter buffer	Proportion	NLCD
500.agr	Agriculture land in 500-meter buffer	Proportion	NLCD
500.wet	Wetlands in 500-meter buffer	Proportion	NLCD
beaver	Beaver activity presence or absence	0 (absence) 1 (presence)	WNF
dw	Distance to nearest adjacent wetland (m)	13.86–871.26 m	GE
dr	Distance to nearest road (m)	0–209.91 m	GE
Dd	Distance to nearest development including road (m)	0–209.91 m	GE
Num	Number of water sources to site	1–3 (numerical)	WNF

Inventory), nearest paved road, and other human development.

Statistical analysis.—To understand how occupancy has changed over time in southeast Ohio, we selected five species with enough detections to accommodate occupancy models: American Bullfrog (*Lithobates catesbeianus*), American Toad (*Anaxyrus americanus)*, Gray Tree Frog (*Hyla versicolor)*, Green Frog (*L. clamitans)*, and Pickerel Frog (*L. palustris)*. The most detected species, the Spring Peeper (*Pseudacris crucifer*), was excluded from the analysis due to its presence at most of the sites (typically > 90%) each year. As such, an occupancy analysis of this species was not adequate. Similarly, for species with only a few detections each year, occupancy models are also not suitable as they may fail to differentiate between non-detection and true absence due to the lack of variation in both detection and site-specific variables and zero-inflation. When dynamic occupancy models are used, biased detection estimates due to lack of observations can also lead to biased inferences on extinction and colonization probabilities.

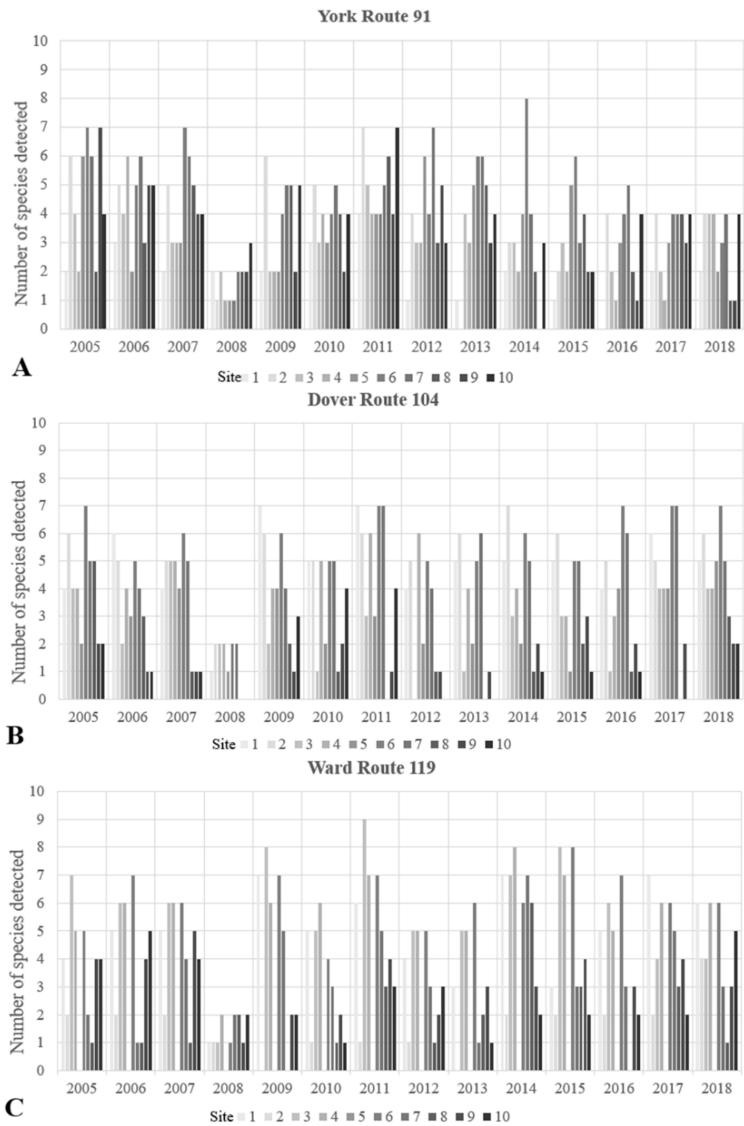

Figure 2. Naïve species richness of anurans by year for 30 ponds (10 sites for each of three areas, A = York Route 91, B = Dover Route 104, C = Ward Route 119) in Wayne National Forest in southeastern Ohio, USA.

To evaluate the trends in site occupancy through time, as well as colonization (γ) and extinction (ε) rates, we used a Multi-season (Dynamic) Occupancy Model (MacKenzie et al. 2003; MacKenzie and Royle 2005; Schmidt and Pellet 2005; Popescu et al. 2012) implemented using package unmarked (Fiske and Chandler 2011) for program R (R Core Team 2021). This allowed us to estimate initial occupancy (Ψ) at a given site for a given species while accounting for imperfect detection (p), which we modeled as a function of survey specific variables recorded during each call survey (Table 2), standardized by centering on the mean and dividing by the standard deviation. We first identified the best covariates for detection for each species from the four detection variables (month, time after sunset, air temperature, and sky conditions) using a full model for occupancy and null models for extinction and colonization. We ranked models by their AICc values to determine which covariates were the most important for detection probability (p; Burnham and Anderson 2002). We then ran Spearman Correlation tests using package Hmisc (Harrell 2021) to test for correlations between site-specific variables. Using uncorrelated variables (Spearman *rho* < |0.7|), we fit 22 models for each species using combinations of land cover proportions extracted at different scales and other variables and ranked them using AICc (Hurvich and Tsai 1989;

Murray et al. 2015) using the package MuMIn (Barton 2020). For each species, we ran half of the models (n = 11) with an intercept-only for extinction (ε = 1) and the other half (n = 11) allowed for extinction to vary by year (ε = YEARS), to account for annual changes in extinction probability. For each species we also then calculated mean ±1 standard error (SE) colonization (γ), extinction (ε), and derived yearly occupancy probability (Ψ) from the top model. We drew inference on whether occupancy showed a significant trend by examining the overlap between 95% confidence intervals around mean predicted occupancy.

Results

Species richness.—We detected 13 species of pond-breeding anurans, of 14 species historically present on WNF (Table 1); Eastern Spadefoot Toads (*Scaphiopus holbrookii*) were not detected. The mean ± standard error of species richness across the survey period for the York Route 91 sites was 3.5 ± 0.14, 3.5 ±0.17 for the Dover Route 104 sites, and 3.5 ± 0.20 for Ward Route 119 sites. The maximum species detected at a site across transects occurred at Ward Route 119, site 3 in 2011, where nine species were detected over the 4-mo period. Mean species richness at this site was 5.8 ± 0.55.

There was great variation in the number of species detected within sites in a route (Fig. 2). York Route 91 had a maximum mean species richness at site 7 of 4.9 ± 0.36, and a minimum species richness at site 1 of 1.9 ± 0.27. Dover Route 104 had a maximum mean species richness at site 6 of 5.7 ± 0.27 and a minimum at site 8 of 1.4 ± 0.39 and at site10 of 1.4 ± 0.37. Ward Route 119 had a maximum mean species richness at site 3 of 5.7 ± 0.55 and at site 6 of 5.8 ± 0.46, and a minimum at a site 5 with zero detections across the surveys (Fig. 2). There were 30 instances where no species were detected at a site for an entire year. This occurred three times on Route 91, nine times on Route 104, and 18 times on Route 119.

Table 3. Naïve (observed) occupancy by five anuran species at 30 sites in Wayne National Forest, Ohio, USA, between 2005 and 2018. The values in parentheses are the total number of detections across all sites during the four surveys conducted each year. The Total row shows the sum of detections across the study period (in parentheses) and the total number of sites at which the species was detected at least once between 2005 and 2018. The Naïve (observed) occupancy of the nine species not selected for study was calculated and reported using identical methods in Appendix Table. Species are American Bullfrog (*Lithobates catesbeianus*) American Toad (*Anaxyrus americanus*), Gray Tree Frog (*Hyla versicolor*), Green Frog (*L. clamitans*), and Pickerel Frog (*L. palustris*).

Year	American Toad	American Bullfrog	Gray Treefrog	Green Frog	Pickerel Frog
2005	11(20)	12(23)	11(16)	17(38)	9(19)
2006	4(8)	10(19)	9(20)	17(43)	9(13)
2007	22(40)	13(22)	9(13)	17(41)	12(21)
2008	9(18)	12(27)	12(26)	20(51)	10(15)
2009	19(19)	13(23)	11(19)	16(37)	9(14)
2010	3(4)	12(19)	10(15)	14(33)	7(16)
2011	15(24)	13(24)	10(23)	19(42)	8(16)
2012	2(3)	12(19)	12(13)	15(34)	11(19)
2013	3(6)	11(13)	8(10)	14(28)	10(14)
2014	10(11)	12(23)	8(15)	17(35)	10(11)
2015	6(9)	5(8)	10(11)	13(25)	12(17)
2016	11(14)	7(12)	6(7)	14(38)	12(25)
2017	12(15)	10(16)	7(13)	16(39)	11(23)
2018	1(1)	10(19)	13(26)	15(28)	4(7)
Total	28(192)	22(267)	28(227)	28(512)	24(230)

Anuran occupancy.—Of the 13 species detected during the course of the surveys, the Spring Peeper was the most detected species (detections at 19–27 sites per year). The American Bullfrog, American Toad, Gray Tree Frog, Green Frog, and Pickerel Frog were among the most detected species (Table 3, Appendix Table). The mean occupancy probabilities for the five species modeled here were high: American Bullfrog Ψ in year 1 (2005) = 0.557 0.109 American Toad Ψ = 0.896 0.078, Gray Tree Frog Ψ = 0.715 0.125, Green Frog Ψ = 0.658 0.100 and Pickerel Frog Ψ = 0.625 0.086 (Fig. 3). The best predictor for site occupancy across all species was distance to nearest wetland, which was negatively associated with occupancy for the American Toad, Gray Tree Frog and the Pickerel Frog and positively associated for the American Bullfrog and Green Frog (Table 4). Site occupancy was also positively associated with distance to nearest road for all species (Table 4; Fig. 4); however, none of the occupancy parameter estimates were statistically significant.

Anuran detection probabilities.—Of the four survey specific variables, air temperature and month of the year together were the most important factors in detection probability (*p*) for the American Bullfrog, American Toad, and Gray Tree Frog, while time and month of the year were the most important factors in detection probability of the Green Frog

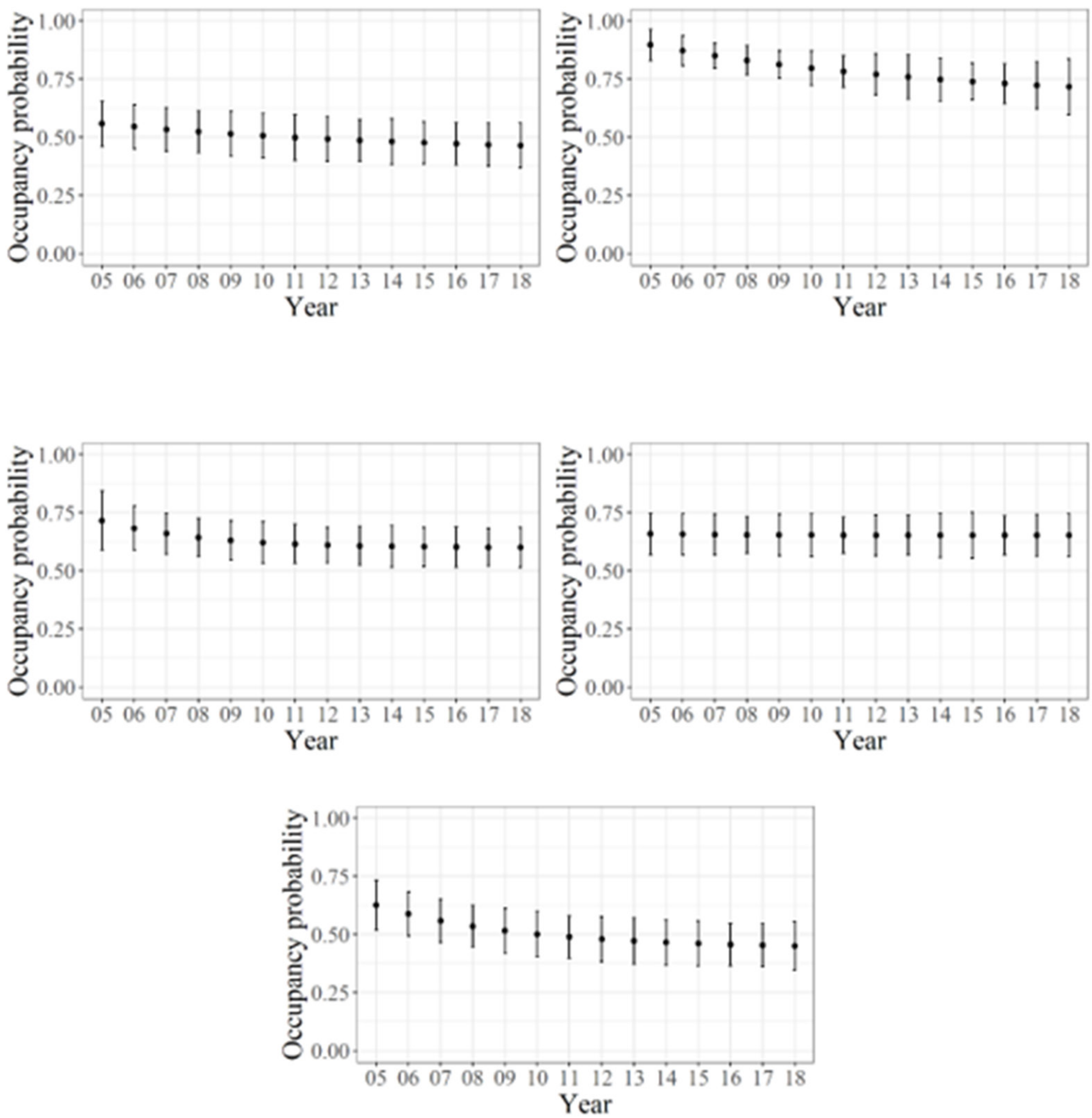

Figure 3. Mean occupancy probability (± 2 standard errors) for five anuran species at 30 ponds in southeastern Ohio, USA, from 2005 through 2018. (A) American Bullfrog (*Lithobates catesbeianus*), (B) American Toad (*Anaxyrus americanus*), (C) Gray Tree Frog (*Hyla versicolor*), (D) Green Frog (*L. clamitans*), (E) Pickerel Frog (*L. palustris*).

and Pickerel Frog (Table 4). Air temperature was positively associated with detection probability for the American Toad, American Bullfrog, and Gray Tree Frog, and time of the survey was negatively associated with detection probability for the Green Frog and Pickerel Frog. Detection probabilities varied by month and species from March through June: American Toad and Pickerel Frog detections were highest in March and April, and lowest in May and June, while American Bullfrogs, Green Frogs and Gray Tree Frogs had the highest detections in May and June (Table 5). Overall, the most detectable species across the survey period was the Green Frog (p = 0.463), while American Toads and Gray Tree Frogs had lower detection probability overall (p = 0.144 and 0.221, respectively; Table 5).

Colonization and extinction probabilities.—Extinction and colonization rates for all species did not vary across years; intercept-only extinction models had the lowest AICc (Table 4). In general, colonization and extinction rates were low (i.e., low turnover; Table 5). Extinction rates were slightly higher than colonization rates for American Bullfrogs

Table 4. The top three models that may explain occupancy for anuran species of interest in Wayne National Forest, Ohio, USA. Variable abbreviations are dw = distance to nearest wetland, dr = distance to nearest road, dd = distance to nearest human development (structure), 500.dev = low developed in 500-meter buffer, 500.opn = open land in 500-meter buffer, 500.devhigh = high developed in 500-meter buffer. Heading abbreviations are df = degrees of freedom, LogLik = log likelihood, AICc = second-order Akaike Information Criterion. Species are American Bullfrog (*Lithobates catesbeianus*) American Toad (*Anaxyrus americanus*), Gray Tree Frog (*Hyla versicolor*), Green Frog (*L. clamitans*), and Pickerel Frog (*L. palustris*).

Initial occupancy(Ψ)	Extinction (ε)	df	LogLik	AICc	ΔAICc	AICc Weight
American Bullfrog - detection (p): TEMP + MONTH						
Dw	1	10	-378.2	788.0	0.00	0.531
dw + dr +dd	1	12	-373.8	790.0	1.94	0.202
dw + dr	1	11	-376.7	790.1	2.05	0.191
American Toad - detection (p): TEMP + MONTH						
dw	1	10	-456.7	945.0	0.00	0.626
dw + dr	1	11	-455.5	957.6	2.62	0.169
dw + dd	1	11	-455.7	948.1	3.10	0.133
Gray Tree Frog - detection (p): TEMP + MONTH						
dw	1	10	-503.7	1039	0.00	0.557
500.dev + 500.opn+.500.devhigh	1	12	-499.0	1040	1.51	0.262
dw + dr	1	11	-503.1	1043	4.01	0.075
Green Frog - detection (p): TIME + MONTH						
dw	1	10	-623.9	1279	0	0.634
dw + dr	1	11	-622.5	1282	2.23	0.208
dw + dd	1	11	-623.1	1283	3.46	0.11
Pickerel Frog - detection (p): TIME + MONTH						
dw	1	10	-429.6	890.7	0	0.693
dw + dr	1	11	-428.4	893.4	2.66	0.183
dw + dd	1	11	-429.3	895.3	4.60	0.096

($\gamma = 0.043 \pm 0.017$; $\varepsilon = 0.056 \pm 0.019$) and Pickerel Frogs ($\gamma = 0.0884 \pm 0.026$ and $\varepsilon = 0.112 \pm 0.035$). For all the other species considered here, colonization rates were higher than extinction rates (Table 5). Despite the variation in extinction and colonization rates, there were no strong trends in occupancy through time (Fig. 3). The occupancy of most species stayed stable or showed a slight decline, but none of the occupancy parameter estimates were significantly different.

Discussion

This study was the first to explore anuran community occupancy dynamics in southeast Ohio, USA, using long-term data collected on the WNF. Thirteen of the 14 species present in Ohio were detected over the 14-y study duration, with the exception of the Eastern Spadefoot Toad, an endangered species in the state of Ohio (Smith et al. 1973). For five species with sufficient data to parameterize Dynamic Occupancy Models, we found that the occupancy probability of all five species was stable throughout the study period. Colonization and local extinction rates were low, suggesting low turnover in these species in WNF; however, the surveys started at the end of March each year and likely missed some early breeding species in some instances (e.g., Wood Frogs, *L. sylvaticus*, which are early breeders).

The distance to nearest wetland was the top variable for explaining occupancy for all five species of interest, although it was not statistically significant for any species. This finding, however, corroborates previously studies in other locations and species of anurans in the eastern U.S. (Hamer and Mahony 2010; Scherer et al. 2012). The positive association to the nearest wetland for the American Bullfrog and Green Frog needs to be further examined as there could be other factors not assessed in this survey. The freshwater systems in southeast Ohio are heavily

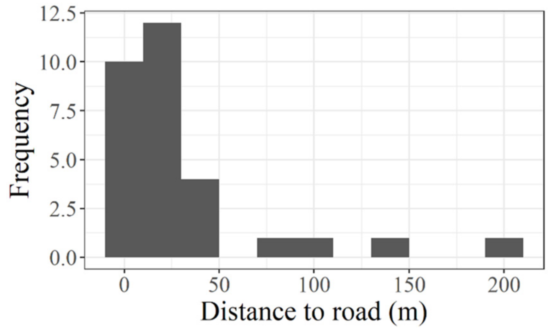

Figure 4. Distance (m) from the nearest road for 30 anuran monitoring sites in Wayne National Forest, Ohio, USA.

impacted by acid mine drainage runoff (Calhoun and Kinney 2016). At the same time, there is a legacy of decades-long oil and gas exploration and exploitation, and hydraulic fracturing and wastewater injection wells have also been expanding in the broader region (although not allowed on WNF-managed lands). While efforts to recover streams affected by acid drainage from mines are underway, the legacies of past freshwater impacts and current development could potentially deter migration between sites. This indicates that connectivity and distance to other wetlands are important factors affecting the persistence of these species in the WNF. The loss of wetlands could affect the overall occupancy of these species due to fewer dispersal opportunities for those species whose occupancy is negatively correlated to distance to the nearest wetland (i.e., American Toad, Gray Tree Frog, Pickerel Frog). Wetlands are some of the most imperiled habitats on the planet, with a net loss in the U.S. of 3.64 million ha (9 million ac), or 10% of their wetlands occurring in the mid to late 20th Century (Tiner 1984). Because access to wetlands can be difficult due to geographic characteristics or denial by landowners, the full extent of wetlands status is unknown in the U.S. currently. Therefore, the monitoring and conservation of the accessible (public) lands and species within it is important (Olsen et al. 2019).

Occupancy was also positively, but not significantly, associated with the distance to the nearest roads within our top models for all species. This result could be an artifact of selecting survey sites in close proximity to roads due to logistics. In our study region, which is unglaciated and has high topographic fragmentation, both roads and wetlands occur in similar geographic and geologic locations, specifically along valleys. As such, the variation in distance to roads was not high in our study (also due to feasibility considerations in sampling design). Nonetheless, roads can have high impacts on amphibian dispersal, mortality, and occupancy (Hopkins et al. 2019; Harman et al. 2023). Landscapes in southeast Ohio are also fragmented by a dense network of roads with varying traffic intensity. Roads are known to pose challenges to amphibian conservation, as they are often one of the main sources of mortality, particularly during breeding migrations (Fahrig et al. 1995; Gibbs 1998; Carr and Fahrig 2001; Gibbs and Shriver 2005; Eigenbrod et al. 2008). Roads also have a strong influence on ecosystems, an effect that is often negatively correlated with species richness and individual fitness (Forman and Alexander 1998; Trombulak and Frissell 2000). The lack of declining trends in the five species analyzed here, however, suggests that roads in our area are not likely to affect pond-breeding anuran populations. The roads in our study are classified as township roads by the Ohio Department of Transportation, and they have low vehicle traffic (median = 38 vehicles; Bencin et al. 2018) during nighttime, when amphibian migration movements typically occur.

Detection of the five species considered here varied with air temperature during the survey and month of the year. For three of the five species of interest, time after sunset and month of the year together were most important in determining detection probability for two of the species. Temperature and month were the most important factors for the American Toad, the American Bullfrog, and the Gray Tree Frog, while

Table 5. Occupancy and detection probabilities, colonization, and extinction rates (mean ± standard error) for five anuran species in Wayne National Forest, Ohio, USA, from 2005 through 2018. Species are American Bullfrog (*Lithobates catesbeianus*) American Toad (*Anaxyrus americanus*), Gray Tree Frog (*Hyla versicolor*), Green Frog (*L. clamitans*), and Pickerel Frog (*L. palustris*).

Species Name	Initial Occupancy Probability (psi)	Mean Detection Probability (*p*)	Colonization (γ)	Extinction (ε)
American Bullfrog	0.557 ± 0.109	0.317 0.008	0.043 0.017	0.056 0.019
American Toad	0.896 0.078	0.144 0.004	0.068 0.058	0.035 0.022
Gray Tree Frog	0.715 0.125	0.221 0.005	0.166 0.047	0.111 0.037
Green Frog	0.658 0.100	0.463 0.008	0.176 0.042	0.094 0.024
Pickerel Frog	0.625 0.086	0.276 0.005	0.088 0.026	0.112 0.035

time and month were the most important factors for the Green Frog and Pickerel Frog. Air temperature was positively associated with detection probability for the American Toad, American Bullfrog, and Gray Tree Frog. Time was negatively associated with detection probability for the Green Frog and Pickerel Frog. Air temperature is an important factor in amphibian calling activity (Gayou 1984), and it is important to monitor changes in breeding phenology of amphibians (Cohen et al. 2018). In addition, the timing of surveys (i.e., month of survey) played an important role in species detection. Therefore, it is important frog call surveys are implemented at appropriate times to increase detection probability and to limit imperfect detection (MacKenzie et al. 2002, 2003). Some early breeding species, such as Wood Frogs, were likely missed by the current survey design as Wood Frog breeding season is subject to high variability based on ambient temperature (Benard 2015; Larsen et al. 2021) and is very brief (typically about 1 week) in our study area (pers. obs.). Thus, we recommend that anuran surveys in southeast Ohio should start one month earlier (in February) to both include early breeding species and detect potential changes in breeding phenology that may occur due to climate change. These surveys likely missed the earliest breeding species, the wood frog, in many years. In addition, breeding phenology shifts have been shown for many anurans, with many species breeding earlier in the season due to climate change (Gibbs and Breisch 2001; Beebee 2002; Paton and Crouch 2002; Todd et al. 2011; Rudolf 2018).

We found that colonization rates were greater than the extinction rates for the American Toad and Gray Tree Frog, yet we observed a stable or slightly declining trend in occupancy through time. While colonization enables the larger population to persist, the values were quite low for both parameters, and there is likely an un-modeled heterogeneity in these parameters that could not be captured by our variables. In contrast, colonization rates were lower than extinction rates for the American Bullfrog, showcasing a slight decline in occupancy through time. Green Frogs had a relatively stable occupancy over time, suggesting latent factors may be affecting occupancy, and not allowing for the species to expand to other sites.

Our study had a limited spatial extent (30 sites selected based on accessibility in a relatively homogenous landscape), thus the inferences drawn here have limitations. To improve our inference, there is a need to increase the number and spatial extent of survey sites. Our study is, however, based on long-term data collection (14 y) and there are ongoing surveys after a 2-y hiatus due to COVID restrictions and other logistical issues (2019–2020).

***Management and conservation implications*.**—Long-term surveys have the potential to fill gaps in knowledge on breeding amphibians and provide information on how climate change and land management strategies may affect anuran occupancy. As the first long-term amphibian monitoring program in WNF, this work provides a baseline on anuran occupancy, and on breeding seasonality. We recommend that land managers continue to monitor trends and changes in colonization and extinction rates and determine how land management strategies can be effective. We also recommend that future anuran call surveys in WNF account for potential phenology shifts in breeding due to climate change, start 1 mo earlier (in February), and increase surveys to twice a month to aid in detecting species with short breeding periods. Monitoring phenology changes and increasing detection of early breeding species has the potential to improve inference on changes in anuran communities and in occupancy of species most affected by climate warming. The lack of a declining trend in the species analyzed via Dynamic Occupancy Models reflect stable anuran populations in WNF and corroborates findings from other NAAMP studies across broader spatial scales (Weir et al. 2009, 2014). As the first long-term anuran monitoring program in WNF specifically, this study also provides a baseline for future analysis on the baseline occupancy of Ohio anurans in the region.

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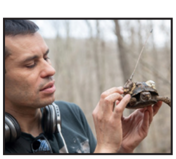
Appendix Table. Naïve (observed) occupancy by nine anuran species at 30 sites in Wayne National Forest, Ohio, USA, between 2005 and 2018. The values in parentheses are the total number of detections across all sites during the four surveys conducted each year. The Total row shows the sum of detections across the study period (in parentheses) and the total number of sites at which the species was detected at least once between 2005 and 2018. Species are Cope's Gray Treefrog (*H. chryoscelis*), Blanchard's Cricket Frog (*Acris blanchardi*), Fowler's Toad (*A. fowleri*), Leopard Frog (*Rana pipiens*), Mountain Chorus Frog (*P. brachyphona*), Eastern Spadefoot Toad (*Scaphiopus holbrookii*), Spring Peeper (*P. crucifer*), Western Chorus Frog (*P. triseriata*), and Wood Frog (*L. sylvaticus*).

Year	Cope's Gray Treefrog	Blanchard's Cricket Frog	Fowler's Toad	Leopard Frog	Mountain Chorus Frog	Eastern Spadefoot Toad	Spring Peeper	Western Chorus Frog	Wood Frog
2005	6(7)	1(1)	0(0)	1(1)	1(2)	0(0)	27(66)	0(0)	3(3)
2006	4(6)	0(0)	0(0)	2(2)	3(6)	0(0)	24(69)	0(0)	4(4)
2007	2(2)	0(0)	0(0)	2(3)	2(3)	0(0)	26(63)	0(0)	1(1)
2008	3(3)	0(0)	0(0)	3(3)	1(1)	0(0)	26(68)	4(4)	4(7)
2009	5(6)	0(0)	1(1)	0(0)	2(3)	0(0)	22(53)	0(0)	5(5)
2010	7(13)	0(0)	1(1)	0(0)	1(1)	0(0)	24(67)	0(0)	2(3)
2011	6(12)	0(0)	2(3)	3(6)	3(5)	0(0)	27(74)	1(1)	4(4)
2012	2(2)	0(0)	1(1)	1(1)	8(9)	0(0)	24(60)	0(0)	0(0)
2013	12(15)	0(0)	0(0)	0(0)	2(2)	0(0)	19(55)	0(0)	3(3)
2014	11(15)	0(0)	0(0)	0(0)	2(4)	0(0)	24(71)	0(0)	8(8)
2015	8(9)	0(0)	1(1)	0(0)	1(2)	0(0)	26(80)	0(0)	13(16)
2016	3(3)	0(0)	1(1)	0(0)	0(0)	0(0)	23(66)	0(0)	2(3)
2017	5(9)	0(0)	0(0)	1(1)	1(2)	0(0)	24(68)	0(0)	2(2)
2018	13(22)	1(1)	0(0)	3(3)	3(4)	0(0)	23(70)	2(2)	6(6)
Total	27(124)	2(2)	7(8)	11(20)	16(44)	0(0)	29(930)	72(7)	24(65)

Andrew Connolly received his B.S.in Wildlife and Conservation Biology from Ohio University, Athens, Ohio, USA, where he completed research in the laboratory of Dr. Viorel Popescu. He is a Zoo Educator at the Beardsley Zoo, Bridgeport, Connecticut, USA, where he coordinates the Peabody-Beardsley-Maritime chapter of FrogWatch USA. Andrew has largely worked in the fields of herpetology and wildlife education, and his research interests include amphibian behavior and phenology, citizen science data utilization, and occupancy modeling. (Photographed by Jack Bradley).



Viorel Popescu is a Research Scientist in the Department of Ecology, Evolution and Environmental Biology at Columbia University (formerly at Ohio University, Athens, Ohio, USA), New York City, New York, USA. He received his Ph.D. from the University of Maine, Orono, Maine, USA (2011), where he studied the effects of forestry on vernal pool breeding amphibians. He was a David H. Smith Conservation Research Fellow (2012–2014) and is a lifetime member of the Society for Conservation Biology. His research has a focus on the ecology and conservation of amphibians, including experimental studies on multiple stressors affecting pond-breeding anurans and in situ conservation of Eastern Hellbender populations. (Photographed by Ben Siegel).