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PREDICTORS OF WINTER ANURAN CALLING ACTIVITY IN THE NORTH CAROLINA PIEDMONT

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Abstract: Recent global amphibian declines have created an urgent need to monitor their populations. Anuran calling surveys are a widely used and accepted monitoring technique; however, habitat and weather variables influence anuran breeding distribution and timing and need to be considered when establishing monitoring efforts. The effects of both habitat and weather variables on detection probabilities and site occupancy estimates of winter-breeding anurans were studied in the western Piedmont of North Carolina. Calling surveys were conducted at 27 ponds in Mecklenburg County, NC and the program PRESENCE was used to evaluate how anuran detectability and site occupancy estimates were influenced by habitat type and weather variables. The best-fit model for each of the three species observed was determined. Upland chorus frog (*Pseudacris feriarum*) calling activity was best predicted by distance to nearest road and air temperature, spring peeper (*Pseudacris crucifer*) calling activity was best predicted by precipitation, and southern leopard frog (*Rana sphenocephala*) calling activity was best predicted by day of the year. Our results indicate that species' calling activities vary greatly in their associations with different habitat and weather variables. Models that incorporate these variables to describe anuran calling behavior can be used by monitoring programs to design species-specific survey protocols.

Key Words: Amphibian Monitoring; PRESENCE; Occupancy; Calling Survey; *Pseudacris feriarum*; *Pseudacris crucifer*; *Rana sphenocephala*.

INTRODUCTION

Anthropogenic disturbances have resulted in the widespread decline of amphibian populations (Alford and Richards, 1999; Delis et al., 1996). Consequently, scientists have increased amphibian monitoring efforts through the use of anuran calling surveys to help determine the extent of these declines. Anuran calling surveys have provided scientists with valuable data pertaining to amphibian population trends and have led to the implementation of management practices for amphibians (Mossman et al., 1998). Nevertheless, many factors influence anuran calling behavior and therefore it is important for scientists to consider these factors when developing and implementing monitoring programs.

Male anurans attract mates through vocal displays which are essential for reproduction, but can be energetically costly (Ryan et al., 1982). Male anurans should vocalize only when the potential benefits outweigh the costs. Anurans rely on environmental factors to determine the best times and places to breed (Brooke et al., 2000). Previous studies have found either temperature or rainfall to be the primary environmental influence on breeding activity in anurans (Bevier, 1997; Blankenhorn, 1971; Blaustein et al., 2001; Duellman and Lizana, 1994; Marsh, 2000; Navas and Bevier, 2001; Reading, 1998; Royle, 2004; Woolbright, 1985). Other studies have found single environmental variables such as wind (Henzi et al., 1995) or humidity (Bellis, 1962) to be triggers for anuran calling. Winter-breeding anurans may be strongly influenced by weather variables because of unpredictable weather fluctuations. Weather variables impact species detectablity (Blair, 1961; Oseen and Wassersug, 2002) and therefore species-weather correlations must be considered individually when developing monitoring programs.

Habitat surrounding a breeding site is an important determinant of the quality of the breeding site and hence the distribution of breeding anurans (Knutson et al., 2000). Habitat destruction around breeding sites is hypothesized to be a cause of some anuran declines (Delis et al., 1996). Yet, species differ greatly in their responses to habitat conditions. Rubbo and Kiesecker (2005), Knutson et al. (1999), Knutson et al. (2000), and Skelly et al. (1999) have found positive correlations between certain anuran species abundance and forested habitat, indicating that forests are important post-metamorphic habitats for some anurans. Other research has shown negative correlations between some anurans and "urban" land cover, because urban areas do not always provide suitable habitat for many anuran species during the terrestrial part of their life cycle (Knutson et al., 2000; Price et al., 2005; Rubbo and Kiesecker, 2005). The diversity of species-habitat relationships described in previous studies indicate that no single landscape variable can be strictly associated with all anuran species in a region, and that species tend to vary uniquely in their habitat associations (Johnson et al., 2003; Knutson et al., 2004; Price et al., 2005). Therefore, developing effective monitoring programs requires a species-specific understanding of the relative importance of these habitat variables as well as the appropriate weather conditions under which to monitor anurans.

The effects of both habitat and weather variables on detection probabilities and site occupancy estimates of winter-breeding anurans were investigated in the western Piedmont of North Carolina. Our goal was to use knowledge of factors affecting calling activity to optimize the effectiveness of amphibian monitoring programs in this region using calling surveys.

METHODS

Study Sites

Anuran calling surveys were conducted at 27 ponds in Mecklenburg County, located in the western Piedmont of North Carolina. Region-wide urbanization has occurred rapidly and only small patches of farmland and secondary-growth forest remain between areas of development (Griffith et al., 2003). We selected study ponds from digital aerial photographs using a geographical information system (GIS; ArcView ver. 3.2, ESRI, Redlands, CA) and personal communication with the Mecklenburg County Natural Resources Division. Ponds were selected that were permanent and isolated from other study sites by at least 200 m.

Survey Protocol

Anuran calling surveys were conducted at each of the 27 study ponds from 25 January–13 March 2005. Several anurans begin calling as early as January in the Piedmont region of North Carolina. Calling surveys were based on the NAAMP protocol (Weir and Mossman, 2005), although some variations to the protocol were made to allow more sophisticated models to be developed. Surveys were conducted in all types of weather, regardless of adverse conditions for calling. Study ponds were divided into six routes based on driving proximity, with 3–5 ponds per route. Each pond was surveyed three times (once every two weeks) throughout the study period. Surveys were conducted at 1830, 2030, and 2230 hr. We randomly assigned days and times to routes, although we made sure that each route was surveyed once during each two-week interval. Listening for frog calls began immediately after arriving at each pond and lasted for 10 minutes. We recorded each species heard during the 10-minute survey. Environmental conditions were recorded and included a cloud cover estimate (0 = few clouds, 1 = partly cloudy sky, 2 = cloudy or overcast, 3 = fog or smoke), a wind speed estimate (0 = <1 mph, 1 = 1–3 mph, 2 = 4–7 mph, 3 = 8–12 mph, 4 = 13–18 mph), a precipitation estimate (0 = dry, 1= damp or fog, 2 = drizzle or light rain, 3 = rain, 4 = downpour or freezing rain, 5 = snow), relative humidity, air and water temperature, as well as the start time and end time of the survey.

Landscape Analysis

Two–hundred meter buffers were created around each pond from digital aerial photographs taken in 2002 of Mecklenburg County in the GIS. Buffer size was chosen because previous studies (Semlitsch and Bodie, 2003) have shown that small spatial scales such as 200 m are considered core habitat for amphibian populations. The area within the 200 m buffer zone for each pond was measured (to the nearest 0.1 ha) and expressed as percentage of that area which represented developed areas (considered "urban"), forest, water, and pasture/grassland. We also determined pond area and distance to nearest road using the GIS.

Data Analysis

The computer program PRESENCE (MacKenzie et al., 2002) was used to analyze our anuran calling data. PRESENCE utilizes a likelihood-based method to estimate the proportion of sites occupied when species detection probabilities are <1. All estimation models assume: 1) the species of interest remains in occupied sites for the duration of the survey; 2) species are not detected when absent, but species may or may not be detected when present; and 3) species detection at one site is independent of species detection at all other sites (MacKenzie et al., 2002). This method also requires at least two sample occasions per sampling period where detection/non-detection data are recorded for each species. PRESENCE gives the following estimable parameters: ψ_i, the probability that a species is present at site i, and p_{it}, the conditional probability that a species is detected at site i at time t, given it is present (MacKenzie et al., 2002). Both ψ_i and p_{it} can be expressed as a logit-function of site-specific covariates, such as habitat variables, and p_{it} may also be expressed as a function of sample-specific variables such as air temperature and weather conditions.

Detection Probabilities (p) and Site Occupancy Estimates (ψ)

PRESENCE was used to estimate p and ψ for the winter-breeding anuran species detected at our 27 ponds. The importance of sample and site covariates on p and ψ was explored by first modeling p as a logit function of survey effects and each sample covariate separately. Sample (weather) covariates included air temperature, water temperature, humidity, and precipitation, wind, and sky conditions. To develop the model of survey effects on p, we held the proportion of sites occupied constant, $\psi(\cdot)$, and allowed p to vary with time (survey effects) and each covariate separately, p(t) and p(Cov). Each model was ranked according to Akaike Information Criteron (AIC) values (Akaike, 1973; Burnham and Anderson, 1998) calculated by PRESENCE. The lowest ranked sample covariate model for each species was then combined with each site (habitat) covariate. The lowest ranked sample and site covariate model was considered to be the model of "best" fit for that species. The "best" model does not necessarily represent all environmental or biological processes that influence site occupancy or detection probabilities (Bailey et al., 2004).

Possible survey-specific effects on detection probability were defined (i.e., different detection probabilities for each sample occasion) using a predefined model with survey-specific p, $\psi(\cdot)p(\mathrm{t})$. Our model assumed that ψ is the same for all sites, but p differed between the three sampling occasions. Our model allowed us to calculate detection probabilities for each species during each of the three surveys within our sampling period. The equations we used to calculate survey-specific p (for our three surveys) were:

$$p_{t=1} = e^{int+\beta1}/1 + e^{int+\beta1}$$
$$p_{t=2} = e^{int+\beta2}/1 + \mathrm{e}^{int+\beta2}$$
$$p_{t=3} = e^{int}/1 + \mathrm{e}^{int}$$

where *site-int* was the intercept for site covariates, *int* was the intercept for sampling covariates, and βi was the sampling covariate coefficient for survey i (MacKenzie et al., 2002).

RESULTS

During our six-week sampling period three vocalizing anuran species were detected and included spring peepers (*Pseudacris crucifer*, detected at 16 sites), upland chorus frogs (*Pseudacris ferarium*, detected at 14 sites), and southern leopard frogs (*Rana sphenocephala*, detected at 8 sites). No vocalizing anurans were heard during survey one at any pond, and there were four ponds where no frogs were heard during any survey.

During survey one, the air temperatures ranged from –2.4 to 4.1°C, the water temperatures from 0.4 to 7.1°C, the humidity from 27% to 53%, and the precipitation code from 1 (dry) to 4 (rain or sleet). During survey two air temperatures ranged from 6.4 to 15.1°C, water temperatures from 8.5 to 12.1°C, humidity from 26% to 74%, and the precipitation code from 1 to 4. During survey three, the air temperature ranged from –2.0 to 15.0°C, the water temperature from 9.0 to 17.4°C, the humidity from 29% to 71%, and the precipitation code from 1 to 3.

Spring peeper calling activity was best predicted by precipitation code ($w_i = 0.2$, Table 1), with spring peepers calling more frequently on rainy evenings. Chorus frogs were most often heard on warmer nights and were also predicted by distance to nearest road ($w_i = 0.1$). Southern leopard frogs were best predicted by day of year ($w_i = 0.54$).

All species were most detectable during survey three and had 0% detection probability during survey one, when no species were heard calling (Fig. 1). Leopard frogs had the highest detection probability during survey three (1.00), followed by spring peepers (0.73) and chorus frogs (0.55). Detectability of both spring peepers and leopard frogs increased substantially from survey 2 to survey 3, although detectability of chorus frogs increased only slightly (Fig. 1). Spring peepers had the highest overall proportion of sites occupied (0.77 ± 0.15) followed by chorus frogs (0.70 ± 0.15) and leopard frogs (0.32 ± 0.51, Fig. 2).

DISCUSSION

Winter-breeding anuran species varied uniquely in their responses to habitat and weather variables. No single variable was found to substantially affect all three anuran

Table 1. Relative differences in AIC (ΔAIC), AIC model weights (w_i), detection probabilities for surveys 1, 2, and 3 (p_1, p_2, p_3), overall estimates of proportion of sites occupied by each species (ψ), and associated standard error [SE(ψ)]. Any model with a ΔAIC of <3 is considered a good model. The best-fit models are shown for each species in order of importance, plus the constant model if it was not included in the top two models of best-fit.

Model, by Species	ΔAIC	w_i	p_1	p_2	p_3	ψ	SE(ψ)
Spring peeper							
$\psi(\cdot)$ p(precipitation)	0.00	0.20	0.00	0.31	0.73	0.77	0.15
$\psi(\cdot)$ p(t)	0.14	0.19	0.00	0.29	0.67	0.84	0.22
ψ(water) p(precipitation)	1.46	0.07	0.00	0.32	0.75	0.75	0.14
Upland chorus frog							
ψ(near-road) p(airtemp)	0.00	0.10	0.00	0.52	0.55	0.70	0.15
$\psi(\cdot)$ p(airtemp)	0.03	0.19	0.00	0.47	0.50	0.78	0.20
$\psi(\cdot)$ p(t)	0.26	0.17	0.00	0.47	0.50	0.78	0.20
Southern leopard frog							
$\psi(\cdot)$ p(Julian day)	0.00	0.54	0.00	0.20	1.00	0.32	0.51
ψ(pasture/grass) p(Julian day)	0.69	0.12	0.00	0.20	1.00	0.32	0.48
$\psi(\cdot)$ p(t)	4.03	0.07	0.00	0.12	1.00	0.32	0.09

species. Species also differed greatly in their site occupancy estimates: spring peepers and upland chorus frogs were detected throughout our study area, but southern leopard frogs were only detected at a few sites. Our results emphasize the importance of evaluating habitat and weather variables independently for each species.

Spring peeper calling activity was best predicted by precipitation. Jones and Brattstrom (1961) found temperature to be a primary factor in determining calling behavior for spring peepers. Oseen and Wassersug (2002) found that spring peepers were more sensitive to meteorological variables later in the breeding season, indicating that this species may be slightly more selective about when to call later in the breeding period. The association

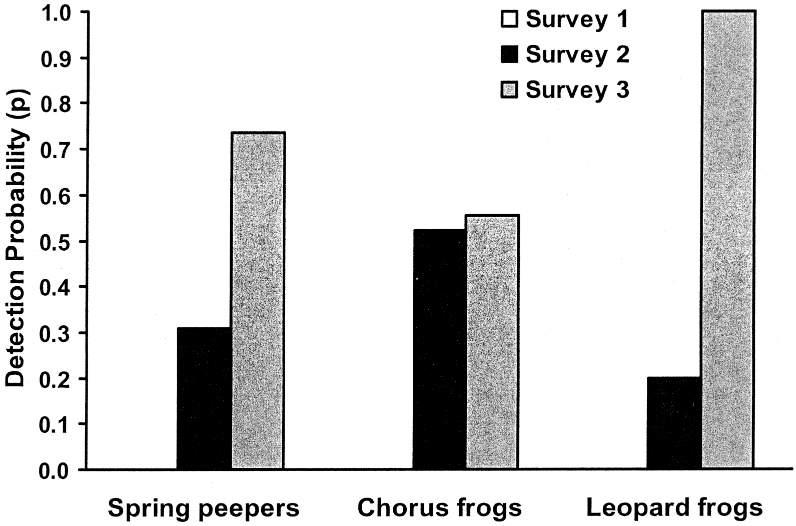

FIG. 1. Detection probabilities (p) for spring peepers, chorus frogs, and leopard frogs for each of three sampling occasions at our 27 study ponds using PRESENCE models of best fit, p(Cov)ψ(Cov). Note that no calling anurans were detected during survey 1.

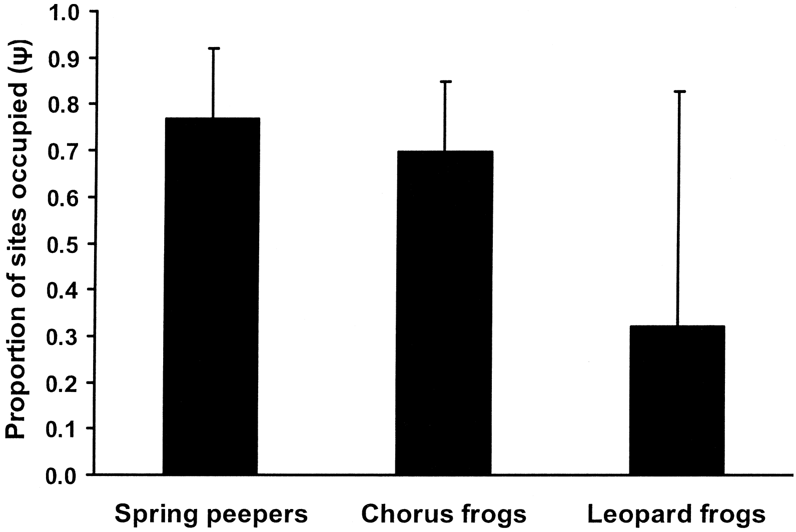

FIG. 2. Proportion of sites occupied (ψ) by spring peepers, chorus frogs, and leopard frogs using PRESENCE models of best fit, $p(\text{Cov})\psi(\text{Cov})$, for each species. Proportion of sites occupied incorporates data from all three sampling occasions as well as detection probability. Error bars equal to ± standard error.

between calling activity of spring peepers and precipitation may be because many species are known to call more intensely after periods of heavy rain (Bevier, 1997; Blair, 1961; Duellman and Lizana, 1994; Marsh, 2000). Spring peeper occupancy was predicted by percent water within a 200 m buffer. Although many studies have found spring peepers to be associated with forest (Johnson et al., 2003; Knutson, 2000; Price et al., 2005), others have found them to be fairly insensitive to loss of forest habitat (Gibbs, 1998). Mann et al. (1991) found that the probability of some anuran species occurrence increases as the number of pools increases, a result consistent with our findings. Knutson et al. (2004) found that spring peepers were associated with distance to nearest wetland (includes all types of wetlands).

Upland chorus frog occurrence and calling activity was best predicted by distance to nearest road and air temperature. Air temperature has been found to be associated with anuran calling behavior for many species (Fukuyama and Kusano, 1992; Navas, 1996; Navas and Bevier, 2001; Woolbright, 1985) and anurans can increase their call duration and rate at higher temperatures (Navas and Bevier, 2001). We detected upland chorus frogs calling from roadside ditches and small runoff streams during our entire study period, indicating that this species may actually be more prevalent in areas with high road densities. Chorus frogs are known to be forest-floor dwellers and to breed in semi-permanent pools (Martof et al., 1980). They may utilize the roadside ditches that occur along forested roads as breeding sites rather than breeding strictly at ponds. Therefore, the closer the nearest road, the more likely it is that chorus frogs would be detected by observers.

Southern leopard frogs began calling later in the year (February 23) than spring peepers and upland chorus frogs (February 8), indicating that our study period coincided with the beginning of leopard frogs' breeding season. Todd et al. (2003) also found southern leopard frogs to begin breeding about this time in the same study area. Because of the later start of the southern leopard frogs' breeding season, we may not have detected them at every site at which they were present. This is likely why the proportion of sites occupied for southern leopard frogs has such a high standard error (Fig. 2). During the study period, southern leopard frog calling activity was best predicted by day of the year, indicating that they may use some factor that changes in correlation to the day of the year as a cue to begin calling. Later in their breeding season other factors such as weather and/or temperature may become more important. Southern leopard frog occurrence was also associated with pasture/grassland and forest, pasture/grassland being the more important variable. Knutson et al. (2000) and Knutson et al. (2004) found the northern leopard frog (*Rana pipiens*) to be associated with grassland and forest. Southern leopard frogs venture far from water to forage for insects (Martof et al., 1980), indicating that upland habitats such as grassland and forest are essential for this species' life history and behavioral characteristics.

Many previous studies have found that time of day is an important determinant of anuran calling behavior (Bridges and Dorcas, 2000; Mohr and Dorcas, 1999; Oseen and Wassersug, 2002; Todd et al., 2003). Since our study was conducted only between 1830 and 2400 hr, within the peak calling hours of all three species as determined by Todd et al. (2003), time of day had little importance in predicting calling behavior. Often when the temperature drops below freezing at night, winter breeding anurans will only call during the day when the temperatures are warmer. Anurans called consistently during the day throughout our study. Therefore, if we had conducted surveys during the day, we may have found differences in anuran calling activity because of time of day, especially during survey one when no anurans were observed during the evening study hours. Also, Bridges and Dorcas (2000) found that during the summer, southern leopard frogs called consistently from midnight until dawn. Although their study was conducted in July, it is possible that southern leopard frogs call past midnight during late winter also, and therefore may have been calling at many of our study sites after the survey hours. Further studies could use automated recording systems to monitor anurans continuously to see if the diel variation found by Todd et al. (2003) and Bridges and Dorcas (2000) could be incorporated into our models.

Oseen and Wassersug (2002) found that prolonged-breeding species (the three species investigated are prolonged breeders) responded differently to environmental variables over the course of the breeding season. During the latter half of the breeding season these species were affected by different variables than in the beginning of the season. Our study did not cover the entire breeding season of any of the three species; if we had conducted surveys later into the year, we may have found different weather variables to be important calling predictors.

Detection probabilities varied among species throughout the study period, indicating that it is impossible to assign an overall detection probability to each species included in a monitoring program. No species were detected during survey one. This is likely because we began our surveys during a period in January when temperatures never rose above 4.1°C (and were frequently below 0°C) in the evenings surveyed. Many of our study ponds contained substantial ice coverage during this time. Night-time surveys during periods early in the season may not be good for calling activity and thus may not provide much data useful for monitoring.

Todd et al. (2003) found that even during the same night, anurans of the same species called from some ponds but not other ponds that were in close proximity and that were known to be occupied by the species. These results implied that considerable variation existed in anuran calling behavior between ponds despite similar weather conditions, which might explain some of the low detection rates we documented.

Our results indicate that species' calling activities vary greatly in their associations with different habitat and weather variables and thus, broad generalizations about anuran calling activity should only be made with caution. Certain habitat and weather variables affect the times and places at which winter-breeding anurans breed. Monitoring programs must be designed to account for variation among species. Models that incorporate habitat and weather variables in order to describe anuran calling behavior can be used by monitoring programs to design species-specific survey protocol.

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LITERATURE CITED

AKAIKE, H. 1973. Information theory as an extension of the maximum likelihood principle. Pp. 267–281 in B. N. Petrov and F. Csaki (eds.), 2nd International Symposium on Information Theory. Akademiai Kiado, Budapest.

ALFORD, R. A., AND S. J. RICHARDS. 1999. Global amphibian declines: a problem in applied ecology. Ann. Rev. Ecol. Syst. 30:133–165.

BAILEY, L. L., T. R. SIMONS, AND K. H. POLLOCK. 2004. Estimating detection probability parameters for *Plethodon* salamanders using the robust capture-recapture design. J. Wildl. Mgt. 68:1–13.

BELLIS, E. D. 1962. The influence of humidity on wood frog activity. Am. Mid. Nat. 68:139–148.

BEVIER, C. R. 1997. Breeding, activity and chorus tenure of two neotropical hylid frogs. Herpetologica 53: 297–311.

BLACKENHORN, H. J. 1972. Meteorological variables affecting onset and duration of calling in *Hyla arborea* L. and *Bufo calamita* Laur. Oecologia 9:223–234.

BLAIR, W. F. 1961. Calling and spawning seasons in a mixed population of anurans. Ecology 42:99–110.

BLAUSTEIN, A. R., L. K. BELDEN, D. H. OLSON, D. M. GREEN, T. L. ROOT, AND J. M. KIESECKER. 2001. Amphibian breeding and climate change. Conserv. Biol. 15:1804–1809.

BRIDGES, A. S., AND M. E. DORCAS. 2000. Temporal variation in anuran calling behavior: implications for surveys and monitoring programs. Copeia 2000:587–592.

BROOKE, P. N., R. A. ALFORD, AND L. SCHWARZKOPF. 2000. Environmental and social factors influence chorusing behavior in a tropical frog: examining various temporal and spatial scales. Behavioral Ecol. Sociobiol. 49:79–87.

BURNHAM, K. P., AND D. R. ANDERSON. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, 353p.

DELIS, P. R., H. R. MUSHINSKY, AND E. D. MCCOY. 1996. Decline of some west-central Florida anuran populations in response to habitat degradation. Biodiversity Conserv. 5:1579–1595.

DUELLMAN, W. E., AND M. LIZANA. 1994. Biology of a sit-and-wait predator, the leptodactylid frog *Ceratophrys cornuta*. Herpetologica 50:51–64.

FUKUYAMA, K., AND T. KUSANO. 1992. Factors affecting breeding activity in a stream-breeding frog, *Buergeria buergeri*. J. Herpetology. 26:88–91.

GIBBS, J. P. 1998. Distribution of woodland amphibians along a forest fragmentation gradient. Landscape Ecol. 13:263–268.

GRIFFITH, J. A., S. V. STEHMAN, AND T. R. LOVELAND. 2003. Landscape trends in Mid-Atlantic and Southeastern United States ecoregions. Envir. Mgt. 32:572–588.

HENZI, S. P., M. L. DYSON, S. E. PIPER, N. E. PASSMORE, AND P. BISHOP. 1995. Chorus attendance by male and female painted reed frogs (*Hyperolius marmoratus*): environmental factors and selection pressures. Functional Ecol. 9:485–491.

JOHNSON, C. M., L. B. JOHNSON, C. RICHARDS, AND V. BEASLEY. 2002. Predicting the occurrence of amphibians: an assessment of multiple-scale models. Pp.157–170 in Predicting Species Occurrences: Issues of Accuracy and Scale. Island Press, Washington, D.C.

JONES, J., AND B. H. BRATTSTROM. 1961. The call of the spring peeper, *Hyla crucifer*, in response to a recording of its own voice. Herpetologica 17:246–250.

KNUTSON, M. G., J. R. SAUER, D. A. OLSEN, M. J. MOSSMAN, L. M. HEMESATH, AND M. J. LANNOO. 1999. Effects of landscape composition and wetland fragmentation on frog and toad abundance and species richness in Iowa and Wisconsin, USA. Conserv. Biol. 13:1437–1446.

———, ———, ———, ———, ———, AND ———. 2000. Landscape associations of frog and toad species in Iowa and Wisconsin, USA. J. Iowa Acad. Sci. 107:134–145.

———, W. B. RICHARDSON, D. M. REINEKE, B. R. GRAY, J. R. PARMELEE, AND S. E. WEICK. 2004. Agricultural ponds support amphibian populations. Ecol. Applications 14:669–684.

MACKENZIE, D. I., J. D. NICHOLS, G. B. LACHMAN, S. DROEGE, J. A. ROYLE, AND C. A. LANGTIMM. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83: 2248–2255.

———, ———, J. E. HINES, M. G. KNUTSON, AND A. B. FRANKLIN. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84:2200–2207.

MANN, W., P. DORN, AND R. BRANDL. 1991. Local distribution of amphibians: the importance of habitat fragmentation. Global Ecol. Biogeogr. Lett. 1:36–41.

MARSH, D. M. 2000. Variable responses to rainfall by breeding tungara frogs. Copeia 4:1104–1108.

MARTOF, B. S., W. M. PLAMER, J. R. BAILEY, AND J. R. HARRISON, III. 1980. Amphibians and Reptiles of the Carolinas and Virginia. Chapel Hill, North Carolina: The University of North Carolina Press, 264 p.

MOHR, J. R., AND M. E. DORCAS. 1999. A comparison of anuran calling patterns at two Carolina bays in South Carolina. J. Elisha Mitchell Sci. Soc. 115:63–70.

MOSSMAN, M. J., L. M. HARTMAN, R. HAY, J. R. SAUER, AND B. J. DHUEY. 1998. Monitoring long-term trends in Wisconsin frog and toad populations. Pp. 169–198 in M. J. Lannoo (ed.), Status and Conservation of Midwest Amphibians. University Iowa Press, Ames, IA.

NAVAS, C. A. 1996. The effect of temperature on the vocal activity of tropical anurans: a comparison of high and low-elevation species. J. Herpetology 30:488–497.

———, AND C. R. BEVIER. 2001. Thermal dependency of calling performance in the eurythermic frog *Colostethus subpunctatus*. Herpetologica 2001:384–395.

OSEEN, K. L., AND R. J. WASSERSUG. 2002. Environmental factors influencing calling in sympatric anurans. Oecologia 133:616–625.

PRICE, S. J., D. R. MARKS, R. W. HOWE, J. M. HANOWSKI, AND G. J. NIEMI. 2005. The importance of spatial scale for conservation and assessment of anuran populations in coastal wetlands of the Western Great Lakes, USA. Landscape Ecol. 20:441–454.

READING, C. J. The effect of winter temperatures on the timing of breeding activity in the common toad *Bufo bufo*. Oecologica 117:469–475.

ROYLE, J. A. 2004. Modeling abundance index data from anuran calling surveys. Conserv. Biol. 18:1378–1385.

RUBBO, M. J., AND J. M. KIESECKER. 2005. Amphibian breeding distribution in an urbanized landscape. Conserv. Biol. 19:504–511.

RYAN, M. J., M. D. TUTTLE, AND A. S. RAND. 1982. Bat predation and sexual advertisement in a neotropical frog. Am. Nat. 119:136–139.

SEMLITSCH, R. D., AND J. R. BODIE. 2003. Biological criteria for buffer zones around wetland and riparian habitats for amphibians and reptiles. Conserv. Biol. 17:1219–1228.

SKELLY, D. K., E. E. WERNER, AND S. A. CORTWRIGHT. 1999. Long-term distributional dynamics of a Michigan amphibian assemblage. Ecology 80:2326–2337.

TODD, M. J., R. R. COCKLIN, AND M. E. DORCAS. 2003. Temporal and spatial variation in anuran calling activity in the Western Piedmont of North Carolina. J. N. Car. Acad. Sci. 199:103–110.

WEIR, L. A., AND M. J. MOSSMAN. 2005. North American Amphibian Monitoring Program (NAAMP). Pp. 307–313 in M. J. Lanoo (ed.), Amphibian Declines: Conservation Status of United States Species. Univ. of California Press.

WOOLBRIGHT, L. L. 1985. Patterns of nocturnal movement and calling by the tropical frog *Eleutherodactylus coqui*. Hepetologica 41:1–9.

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