

# Copeia

*founded in 1913 by John Treadwell Nichols*

## Surveying a Threatened Amphibian Species through a Narrow Detection Window

Perry J. Williams<sup>1</sup>, Nathan J. Engbrecht<sup>2</sup>, Joseph R. Robb<sup>3</sup>, Vanessa C. K. Terrell<sup>4</sup>,  
and Michael J. Lannoo<sup>2</sup>



## Surveying a Threatened Amphibian Species through a Narrow Detection Window

Perry J. Williams<sup>1</sup>, Nathan J. Engbrecht<sup>2</sup>, Joseph R. Robb<sup>3</sup>, Vanessa C. K. Terrell<sup>4</sup>, and Michael J. Lannoo<sup>2</sup>

**Crawfish Frogs (*Lithobates areolatus*) are a relatively widespread but understudied North American species suspected to be in steep decline. Discussions to petition this species for federal listing have begun and therefore effective techniques to survey and monitor populations must be developed. Crawfish Frogs produce unusually loud breeding calls, making call surveys the most efficient way to assess populations; however, their peak breeding period lasts for only a few nights, sometimes for only one night. We used automated calling survey techniques at two wetlands where the numbers of Crawfish Frog males present were known ( $\pm 1\%$ ) for the entire length of the breeding season to examine detection probabilities in relation to season, time of day, weather variables, survey duration, and the numbers of males present. We then used these data to ask three simple but important questions: 1) When should researchers listen—that is, what times and under what environmental conditions should surveys for Crawfish Frogs take place? 2) How long should surveys last? and 3) What can call surveys tell us about the size of a population? The most supported model for detection included the quadratic relationship of time and date, a positive linear relationship with temperature, and a negative linear relationship with recent rain, while the most supported model for estimating abundance included the quadratic relationship of time and date, and call rate. Five-minute surveys should suffice during peak breeding for known large populations; 15-minute surveys with repeat visits should be used for small populations or when sampling new areas. These findings should improve manually collected (auditory) call survey efficiencies for Crawfish Frogs, surveys that are being organized to provide the first objective data on the status of this species across its range.**

OVER the past quarter of a century, concern over worldwide amphibian declines has led to considerable gains in our understanding of the biology of these animals (Wake, 1991; Houlihan et al., 2000; Alford et al., 2001; Wells, 2007; Collins and Crump, 2009; Wake, 2012). Despite these endeavors, status assessments and the relative importance of potential threats remain unevenly detailed across species (Stuart et al., 2004; IUCN Red List, 2012). In North America, where amphibians are generally well known (Lannoo, 2005), Crawfish Frogs (*Lithobates areolatus*) historically have been one of the most secretive and least understood amphibian species (Smith, 1950). Adults spend much of their lives in and around the entrances to crayfish burrows, quickly retreating into them when disturbed (Thompson, 1915; Hoffman et al., 2010; Engbrecht et al., 2012). Crawfish Frogs, along with their southern counterparts, Dusky Gopher Frogs (*L. sevosus*) and Gopher Frogs (*L. capito*), are species of conservation concern (Jensen and Richter, 2005; Richter and Jensen, 2005). Dusky Gopher Frogs are federally endangered and currently restricted to one moderately sized population, two smaller peripheral populations, and one repatriated population (USFWS, 2010). Gopher Frogs have been petitioned for federal listing. The status of Crawfish Frogs is similarly tenuous. Declines have occurred across their range; Crawfish Frogs are classified globally as Near Threatened (IUCN Red List, 2012), and listed as State Endangered in Indiana and Iowa (where they have not been seen since 1942) and as a Species in Need of Conservation in Kansas (Christiansen and Bailey, 1991; Minton, 2001; Collins et al., 2010). Discussions to petition Crawfish Frogs for federal listing have begun.

When not breeding, Crawfish Frog adults are extraordinarily difficult to detect (Bragg, 1953; Parris and Redmer, 2005; Heemeyer et al., 2012). Further, Crawfish Frog tadpoles are easily confused with those of Southern Leopard Frogs (*L. sphenoccephalus*; Smith et al., 1948; Trauth et al., 2004; Altig et al., 2012). Therefore, neither upland nor larval surveys offer promise for generally assessing or monitoring Crawfish Frog populations. In contrast, during their relatively short breeding season, male Crawfish Frogs can easily be detected by their loud (107.5 dB at 1 m; Gerhardt, 1975), distinct calls, which have considerable carrying power and can be heard at distances >1 km (Swanson, 1939; Minton, 2001). Perhaps no other Midwestern anuran species of conservation concern has such a deeply binary pattern of detectability; targeted call surveys designed to sample a large number of wetlands over a short period of time are the only practical way to assess the status of Crawfish Frog populations.

Call surveys have become widely used for monitoring frog and toad populations (Scott and Woodward, 1994; Zimmerman, 1994; Mossman et al., 1998; Weir and Mossman, 2005). Call surveys permit the standardized sampling of many sites over a relatively short period of time. For example, the North American Amphibian Monitoring Program (NAAMP) volunteers are asked to sample ten sites a night (Weir and Mossman, 2005). More broadly, NAAMP has coordinated standardized call survey techniques into a wide-ranging network adopted by many states in the United States (Weir and Mossman, 2005). Increasingly, automated recording systems (ARS) such as “frog-loggers” (Peterson and Dorcas, 1994; Corn et al., 2000; Saenz et al., 2006) are being used as a means of surveying and monitoring anuran

<sup>1</sup>Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, Colorado, 80523; E-mail: perry.williams@colostate.edu.

<sup>2</sup>Terre Haute Center for Medical Education, Indiana University School of Medicine, Rm 135 Holmstedt Hall—ISU, Terre Haute, Indiana 47809; E-mail: (NJE) nathanengbrecht@gmail.com; and (MJL) mlannoo@iupui.edu. Send reprint requests to MJL.

<sup>3</sup>Big Oaks National Wildlife Refuge, 1661 West JPG Niblo Road, Madison, Indiana 47250; E-mail: Joe\_Robb@fws.gov.

<sup>4</sup>Warnell School of Forestry and Natural Resources, University of Georgia, 180 Green Street, Athens, Georgia 30602; E-mail: vkinney@uga.edu.

Submitted: 26 November 2012. Accepted: 19 February 2013. Associate Editor: J. Kerby.

© 2013 by the American Society of Ichthyologists and Herpetologists DOI: 10.1643/CH-12-157

species (Bridges and Dorcas, 2000; Oseen and Wassersug, 2002; Waddle et al., 2009; Steelman and Dorcas, 2010). Automated recording systems allow researchers to compile large datasets that can be reviewed and analyzed as often as necessary. Automated recording systems also allow for the collection of a complete calling record (or chorusing profile) of selected species or study sites. Finally, ARS are the most effective method for surveying species that cease calling in response to disturbance, or with irregular or short breeding seasons (Dorcas et al., 2010).

In an effort to improve the efficiency of manual call surveys we examined the chorusing phenology of Crawfish Frogs at two breeding wetlands. This is the first study of any anuran species to couple the calling activity of frogs to known (rates of trespassing [i.e., crossing fences undetected] <1.0%; Kinney, 2011) numbers of males over the course of an entire breeding season. We use these data to address three simple but important questions: 1) When should researchers listen for Crawfish Frogs—that is, what times and under what environmental conditions should surveys take place to maximize detection probabilities? 2) How long, based on detection probabilities, should surveys last? and 3) What can call surveys tell us about the size of the population? To answer these questions, we use ARS techniques to examine Crawfish Frog calling behavior as it relates to season, time of day, weather variables, survey duration, and numbers of males present.

Because we were interested in determining the environmental conditions to best detect Crawfish Frogs, whether we could reliably predict their abundance based on calling rates, and the time it would reasonably take to detect them, we conducted multiple analyses. In the first, we assessed Crawfish Frog detectability in relation to environmental and temporal conditions; in the second, we compared the abundance of Crawfish Frogs at breeding wetlands in relation to calling metrics; in the third, we assessed Crawfish Frog detectability in relation to the amount of time spent surveying for frogs. This was an intensive survey effort meant to inform, and no doubt be modified by, future extensive surveys conducted across the range of this species. Data from such surveys conducted broadly will be critical in objectively evaluating the conservation status of this species. Further, this approach offers promise for surveying and monitoring other species, for example other ranids such as Wood Frogs (*Lithobates sylvaticus*; Redmer and Trauth, 2005) and members of the family Pelobatidae (Wells, 2007), with narrow detection windows.

## MATERIALS AND METHODS

**Data collection.**—We studied Crawfish Frog populations from two breeding wetlands located at Hillenbrand Fish and Wildlife Area (HFWA) in Greene County, Indiana, containing genetically distinct populations (Nunziata et al., 2013). The portion of HFWA used by Crawfish Frogs is situated on a reclaimed surface coalmine, and is managed by the Indiana Department of Natural Resources (Lannoo et al., 2009). The first site, Nate's Pond, is a shallow (<0.5 m) seasonal wetland approximately 0.14 ha in surface area that dries completely during late summer and early fall. The second site, Cattail Pond, is a relatively shallow (<1.0 m), semi-permanent wetland approximately 0.33 ha in surface area. The two wetlands are approximately 0.9 km apart. These wetlands are important, supporting the largest Crawfish Frog breeding aggregations in Indiana (Engbrecht

and Lannoo, 2010), and are being studied as part of a larger effort examining the population biology of Crawfish Frogs (Kinney and Lannoo, 2010; Heemeyer and Lannoo, 2012; Heemeyer et al., 2012). Drift fences were constructed around the perimeters of both wetlands and checked daily, giving us a running tally of the number of animals in each wetland (Kinney, 2011). Rates of trespassing at these drift fences have been estimated to be <1.0% (Terrell, unpubl. data).

Crawfish Frog calling activity was recorded using Song Meter (models SM1 and SM2, Wildlife Acoustics Inc., Concord, MA) ARS units. Chorusing data were collected for two months in 2010, from 1 March to 30 April. Units were set out prior to first calling and left out for 2 weeks following last calling. One unit was placed adjacent (<5 m) to each wetland shoreline on the ground hidden by vegetation, near areas where Crawfish Frog choruses were heard in 2009 (Kinney, 2011). Song Meter units were programmed to record continuously for 8 h segments beginning at 1900 hrs EST and ending at 0300 hrs the following morning, a time frame corresponding to the daily calling period (up to several hours after sunset) noted previously by others (Busby and Brecheisen, 1997; Minton, 2001) as well as by us in 2009 (Engbrecht, 2010; Kinney, 2011).

We recorded air temperature, relative humidity, rainfall amount, and wind speed at 10 min intervals throughout the study using a HOBO Micro Station (Onset Computer Corporation, Pocasset, MA) located at a secure site approximately 3.5 km from Nate's Pond and 3.2 km from Cattail Pond. Water temperatures of each wetland were recorded at 30 min intervals using submerged HOBO Pendant Data Loggers. Data from each of these environmental measurements, with the exception of rainfall, were linearly interpolated to 1 min intervals in order to match the resolution of the Crawfish Frog calling data. Rainfall amounts were averaged to 1 min resolution. We examined correlations between our metrics and found that water temperatures were correlated with air temperatures ( $P < 0.001$ ,  $n = 21,017$ ,  $R = 0.72$ , Spearman Rank Order Correlation), and because we were interested in the application of easily estimated environmental variables to call surveys, we focused on air temperatures, which can be generally measured.

**Data analyses.**—Recordings were analyzed manually (both audibly and visually) by inspecting audio spectrograms produced by Song Scope software. The typical breeding call of Crawfish Frogs consists of a single, distinct snore (Minton, 2001; Elliot et al., 2009), allowing for the identification of individual calls (exceptions occurred during especially dense [ $>100$  calls/min] chorusing). Call count rates (calls/min; Duellman and Trueb, 1986; Nelson and Graves, 2004; Wells, 2007) were compiled by downloading each digital recording to Song Scope software and examining the record. Only the typical snore call was counted (i.e., we excluded the prolonged aggressive calls produced during male to male encounters; Elliot et al., 2009). Although time consuming, manual enumeration gave much more accurate counts than we could obtain through two automated call recognition programs (Song Scope and Raven [www.birds.cornell.edu/raven]; Waddle et al., 2009), even after consulting with the respective software designers and/or their troubleshooters. Due to this effort being a part of a larger project studying the biology of

**Table 1.** Model Selection Results for Models Estimating Detection Probability in a 20 min Interval by Crawfish Frogs in Breeding Wetlands, Southwestern Indiana, USA. Time and date were temporal variables for the time of night and day of year, rain was whether it was raining during the survey, rain prev 24 hrs was the amount of rain in the 24 hours preceding the survey, site was an indicator variable for which pond it was, and temp was temperature.

Covariates	K	$-2\log(L)$	$\Delta AIC$	$\omega_i$
Time, time <sup>2</sup> , date, date <sup>2</sup> , rain prev 24 hrs, temp, site	8	1681.42	0.00	0.71
Time, time <sup>2</sup> , date, date <sup>2</sup> , rain, rain prev 24 hrs, temp, site	9	1681.23	1.81	0.29
Date, date <sup>2</sup> , time, time <sup>2</sup> , site	6	1787.45	102.04	0.00
Date, date <sup>2</sup> , site	4	1835.53	146.11	0.00
Rain, rain prev 24 hrs, temp, site	5	3380.20	1692.78	0.00
Time, time <sup>2</sup> , rain, rain prev 24 hrs, temp, site	7	3376.34	1692.92	0.00
Time, time <sup>2</sup> , rain, temp, site	6	3417.45	1732.03	0.00
Temp, site	3	3428.77	1737.36	0.00
Rain prev 24 hrs, site	3	3502.63	1811.21	0.00
Date, site	3	3528.04	1836.62	0.00
Time, site	3	3540.27	1848.85	0.00
Time, time <sup>2</sup> , site	4	3540.24	1850.82	0.00
Rain, site	3	3557.82	1866.40	0.00
Null	1	3831.44	2136.02	0.00

Crawfish Frogs (Hoffman et al., 2010; Kinney, 2011; Heemeyer and Lannoo, 2012; Heemeyer et al., 2012), researchers were sometimes present monitoring drift fence arrays at wetlands during recording sessions; Crawfish Frogs cease calling in response to disturbance (Wright and Meyers, 1927; Swanson, 1939; Redmer, 2000). These disturbance times (including a 5 min lag time after calling had resumed) were removed before analyses were conducted.

**Modeling detection probability ( $p$ ).—**We assessed Crawfish Frog detectability in relation to environmental and temporal conditions. To do this we developed a *a priori* suite of alternative hypotheses and then compared these hypotheses using an information-theoretic approach. We developed our hypotheses from other research on calling amphibians, and our experience. We hypothesized that detection probability would be positively correlated with ambient temperature and the amount of rain in the previous 24 hrs. Additionally, we thought that detection probability would be positively correlated with the time of night, or have a quadratic relationship with time of night (i.e., calling would increase immediately after sunset to a peak, and then decrease thereafter). We hypothesized detection probability might have a quadratic relationship with day of year (reaching a maximum in the middle of the calling season; Dodd and Scott, 1994; Minton, 2001; Oseen and Wassersug, 2002; Todd et al., 2003; Engbrecht, 2010; Williams et al., 2012). In addition to these variables, we included hypotheses based on three other observations, as follows. The first, that Crawfish Frog calling was positively correlated with recent rainfall, current rainfall, temperature, and time of night (Busby and Brecheisen, 1997). The second, that calling was positively related to temperature, had a quadratic relationship to time, and was negatively related to current rainfall, and disturbance (Engbrecht, 2010). And the third, that detection probability was positively correlated with temperature, the amount of rain in the previous 24 hrs, and time, and had a quadratic relationship with the day of year (Williams et al., 2012). In addition to these variables, we included a global model/hypothesis that was an additive combination of all the metrics listed above.

Next, we built statistical models that represented our hypotheses, and ranked the estimated parsimony between our models and our data. We used generalized linear regression models with a binomial distribution for the detection of calls. That is,

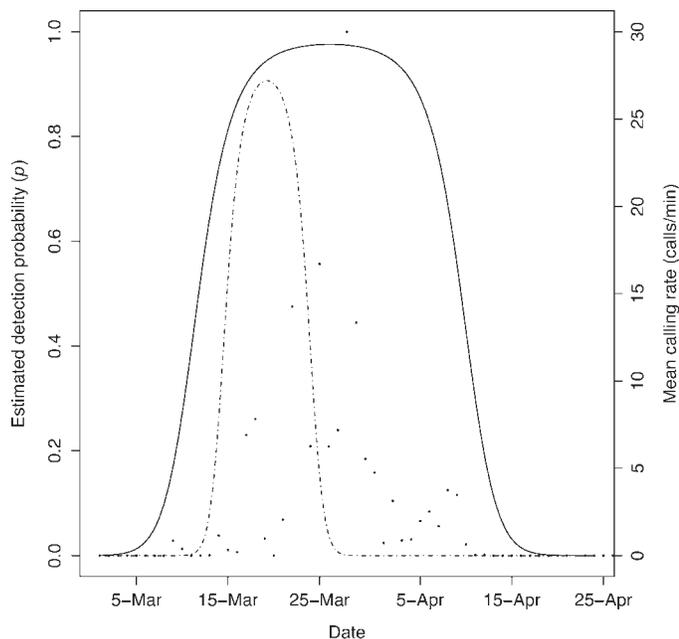
$$y \sim \text{Binomial}(1, p)$$

$$E(y) = p \text{ and } \text{var}(y) = p(1-p)$$

$$\log \text{it}(p) = X\beta$$

where  $y$  was a vector of whether frogs were detected (detected = 1, undetected = 0) in a 20 min period,  $p$  was the estimated detection probability,  $X$  was the design matrix, and  $\beta$  were our parameters to be estimated. From our hypotheses, we had 14 different models with various combinations of  $X\beta$  (Table 1). We fit our models to our data using Program R (R Version 2.14.1; R Development Core Team, 2012). We estimated the parsimony of each model using Akaike's Information Criterion (AIC), and assessed its relative support using Akaike weights ( $\omega$ ). We used parameter estimates from our top model. Finally, we compared our model selection results for detection probability to previous model selection results from a similar analysis in a different part of the state (Fig. 1; Williams et al., 2012).

**Modeling abundance.—**We modeled Crawfish Frog abundance using a similar approach to our detection-probability modeling. That is, we developed conceptual hypotheses relating Crawfish Frog abundance to environmental and temporal variables, quantified our hypotheses using statistical models and an information theoretic approach, and then made inference based on our top model. Our hypotheses consisted of all our hypotheses from the detection-probability modeling listed above, plus one additional hypothesis: that higher call rates by Crawfish Frogs would be indicative of more frogs in the pond. We examined our hypotheses using linear regression models with the number of frogs as the response variable. We evaluated the assumptions of our models by examining



**Fig. 1.** Estimated detection probability of calling Crawfish Frogs as a function of date (solid line and left vertical axis). Time, temperature, and rain in the previous 24 hours were also included in the model and were set to their mean values resulting in the function:  $\text{logit}(p) = -11.69 + 0.94(\text{date}) - 0.02(\text{date})^2 + 3.07(\text{pond})$ . Shown is the function for Nate's Pond ( $\text{pond} = 1$ ). Also shown are 1) the estimated detection probability for Crawfish Frogs in southeastern Indiana (dotted line; Williams et al., 2012) whose model selection procedure resulted in a similar model being selected as our study, and 2) mean calling rates across the season (points and right vertical axis). The mean calling rates were estimated for each night.

residual plots and auto-correlation plots. Our auto-correlation plots suggested that abundance had a high degree of temporal auto-correlation. Therefore, we included a residual correlation structure in each of our statistical models for abundance data. To select the correlation structure we fit our global model to the compound symmetry and the autoregressive model of order 1 (AR-1) auto-correlation structures. We used AIC to compare the parsimony of each correlation structure and used the correlation structure with the lowest AIC for the remaining models in our model suite. The AR-1 correlation structure was most parsimonious. Thus our models for abundance were:

$$\text{Frogs} = \mathbf{X}\boldsymbol{\beta} + \boldsymbol{\varepsilon}$$

$$\boldsymbol{\varepsilon} = \rho\boldsymbol{\varepsilon}_{t-1} + \boldsymbol{\eta}_t$$

where  $\rho$  as a parameter that estimated the correlation between the residuals for one unit measure in time and  $\boldsymbol{\eta}_t$  was noise (Zuur et al., 2009). Based on our hypotheses we had models representing 13 combinations of  $\mathbf{X}\boldsymbol{\beta}$  or abundance models (Table 2). We approximated the parsimony of each of these 13 models using AIC, and estimated the relative support using Akaike weights ( $\omega$ ). We examined the fit of our top model by comparing predicted values and actual values of abundance. We made inferences based on estimates from our top model (i.e., the model with the lowest AIC value; Burnham and Anderson, 2002).

**Estimating survey length.**—We assessed Crawfish Frog detectability in relation to the amount of time spent surveying for

frogs. To examine the length of time required to detect frogs, we compared detection rates to varying survey lengths. To assess survey duration, we isolated calling activity at each wetland into early season (initial calling) and peak periods and chose three consecutive days from each period (for a total of 12 samples). For each day and in each wetland we knew the number of Crawfish Frogs present. From each day, we randomly chose 15 times (hr/min/sec) between 2000 and 2300 hrs (peak calling during each night; see below) and determined the time from each of these points to when the first call was heard (i.e., we mimicked a quiet surveyor arriving at a breeding wetland). We scored these intervals for each night at each wetland as the number of times Crawfish Frogs were heard calling within 5 min, 10 min, and 20 min. These scores allowed us to calculate detection probabilities (number of intervals heard at each time period/15) based on survey durations.

## RESULTS

**Descriptive summary of calling.**—Chorusing dates during the 2010 breeding season ranged from 11 March–14 April at Nate's Pond and from 16 March–4 April at Cattail Pond (Fig. 1). Chorusing levels varied within the breeding season with peak chorusing (calls/min) occurring in both wetlands during the same 4 d period between 30 March and 2 April. The beginning of the breeding season at each site was marked by a gradual increase in chorusing levels interrupted by nights of little to no calling. After peak breeding, calling activity dropped off sharply at both wetlands (Fig. 1).

Within each night, mean calling intensity increased during the first hour of sampling (1900–2000 hrs) and after a period of peak chorusing lasting about 1–2 hrs grew weaker as night progressed (Fig. 2). On average, calling rates at Nate's Pond abruptly rose from scattered calling (<5 calls/min) around 1900 hrs to peak calling (>25 calls/min) around 1945–2045, then gradually tapered off to <10 calls/min at 0300 hrs. Average calling rates at Cattail Pond steadily rose during the first 30 min of sampling and peaked (>10 calls/min) for about 2 hrs. Low-level calling (<5 calls/min) continued after 2200 hrs. Crawfish Frogs called significantly less during human-induced disturbances (15.0 calls/min) than when undisturbed (42.7 calls/min;  $P < 0.001$ ; Independent t-test). As noted above, all times when human disturbance affected call rates (including a 5 min lag time after calling had resumed) were removed before analyses were performed.

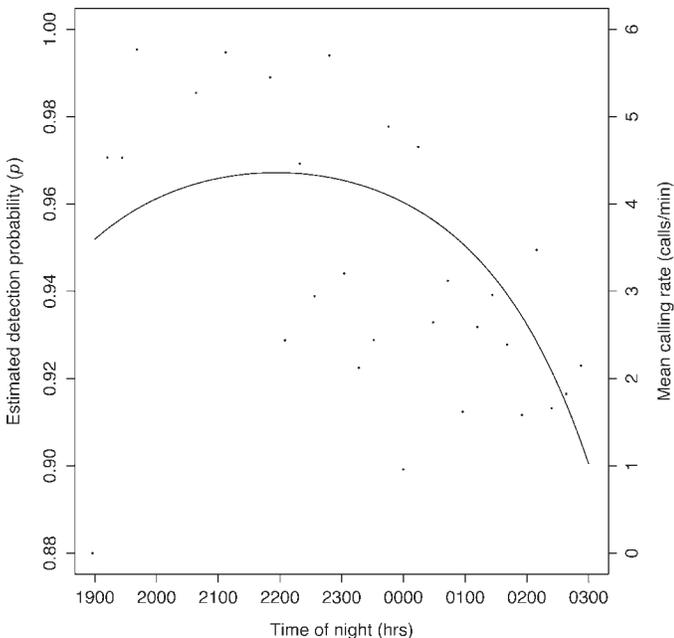
**Model-selection results and inference.**—The most supported model for Crawfish Frog detection probability included terms for the quadratic relationship of time and date, a positive linear relationship with temperature, and a negative linear relationship with rain in the previous 24 hrs (Table 1; Figs. 1, 2). The model containing these variables was 1.81 AIC units better than the next best model and accounted for 71% of the AIC weight (Table 1). The second best model from our model selection procedure included all of the variables from our top model but also included a variable for rain during the survey. While the model contained 29% of the AIC weight, the 95% confidence interval for rain overlapped zero ( $\beta_{\text{rain}} = -0.17$ , 95% CI =  $-0.93$ – $0.59$ ). Therefore we concluded that rain during surveys did not substantially affect calling probabilities, and retained only our top model for inference. Average values for the continuous variables used to estimate detection probability

**Table 2.** Model Selection Results for Models Comparing Crawfish Frog Abundance in Breeding Wetlands, Southwestern Indiana, USA. Time and date were temporal variables for the time of night and day of year, call rate was the mean calling rate for the night, rain was whether it was raining during the survey, rain prev 24 hrs was the amount of rain in the 24 hours preceding the survey, site was an indicator variable for which pond it was, and temp was temperature.

Covariates	K	$-2\log(L)$	$\Delta AIC$	$\omega_i$
Date, date <sup>2</sup> , time, time <sup>2</sup> , call rate, site	9	7513.38	0	0.82
Date, date <sup>2</sup> , call rate, site	7	7520.53	3.15	0.17
Time, time <sup>2</sup> , date, date <sup>2</sup> , rain prev 24 hrs, temp, call rate, site	11	7518.35	8.97	0.01
Time, time <sup>2</sup> , date, date <sup>2</sup> , rain, rain prev 24 hrs, temp, call rate, site	12	7520.17	12.79	0.00
Time, time <sup>2</sup> , call rate, site	7	7621.57	104.19	0.00
Call rate, site	5	7629.05	107.67	0.00
Rain prev 24 hrs, call rate, site	6	7628.43	109.05	0.00
Rain, call rate, site	6	7630.94	111.56	0.00
Time, time <sup>2</sup> , rain, temp, call rate, site	9	7629.43	116.05	0.00
Temp, call rate, site	6	7636.06	116.68	0.00
Time, time <sup>2</sup> , rain, rain prev 24 hrs, temp, call rate, site	10	7628.8	117.42	0.00
Rain prev 24 hrs, rain, temp, call rate, site	8	7637.32	121.94	0.00
Null	3	10540.62	3015.24	0.00

were: temperature = 9°C, and rain in previous 24 hrs = 0.0 cm. Thus, we based our inference for average detection probability from these point estimates. Temperatures higher than 9°C had a higher estimated detection probability; rain in the previous 24 hrs produced detection probability estimates lower than average estimates.

Based on our top model, detection probability was relatively high between mid-March and early April, peaking on 26 March (Fig. 1). Within nights, detection probability was highest between 1900 and 2300 hrs. Within these time frames the mean detection probability was 0.89 (compared to an overall mean of 0.47) when temperatures were >9°C



**Fig. 2.** Estimated detection probability of calling Crawfish Frogs as a function of time (solid line and left vertical axis). Date, temperature, and rain in the previous 24 hours were also included in the model but were set to their mean values resulting in the function:  $\text{logit}(p) = -21.85 + 2.02(\text{time}) - 0.046(\text{time})^2 + 3.07(\text{pond})$ . Also shown is the mean calling rate across the night. The mean calling rate was estimated for each 10 min interval during the night using all nights surveyed.

and there had been no rain in the previous 24 hrs; detection probability was >0.89 when temperatures were >9°C, and <0.89 when it had rained in the previous 24 hrs.

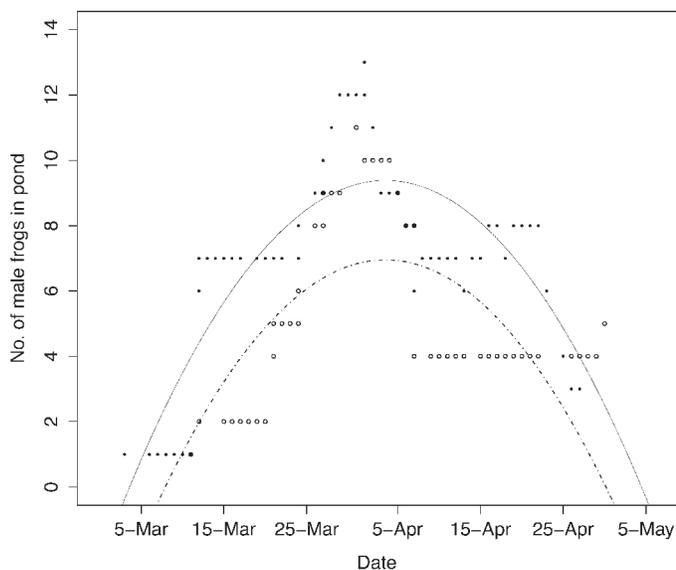
The most supported model for estimating Crawfish Frog abundance included the variables date, date<sup>2</sup>, time, time<sup>2</sup>, and the call rate (i.e., calls heard in a one-minute interval). This model was 3.15 AIC units better than the second ranked model, and had 82% of AIC weight (Table 2). The correlation between two residuals one time-step apart ( $\rho$ ) was estimated to be 0.87. The model-predicted abundance based on a quadratic relationship to date appeared to fit the data well (Fig. 3). However, neither time of night nor calling rate by themselves were good predictors of Crawfish Frog abundance. The 95% CI for each of these coefficients overlapped zero (Table 3), and the predicted estimates did not fit the actual data well. Among the single variables, Crawfish Frog abundance was best predicted by the date, not calling rates.

**Survey duration.**—Detection probabilities varied with time within the calling season (Table 4). Using 20 min durations, detection probabilities during early season surveys (the second or third week in March) ranged from 0.00 (with seven males present) to 1.00 (with one male present) at Nate's Pond, and from 0.27 to 0.47 (with two males present in both cases) at Cattail Pond. Detection probabilities during peak breeding surveys were 1.00 within 5 min at Nate's Pond and 1.00 within 10 min at Cattail Pond.

Doubling the survey period from 5 to 10 min did not increase the detection probability in 7 of 12 samples from both wetlands (primarily during peak breeding times); in the five samples where detection probabilities increased the average increase was 9% (Table 4). Quadrupling the survey period from 5 to 20 min again did not increase the detection probability in the majority of samples (7 of 12); in the five samples where detection probabilities increased, the average increase was 17% (Table 4).

## DISCUSSION

Petitioning a species for federal protection under the US Endangered Species Act is both a time- and labor-intensive process, driven by the best available data. For species with



**Fig. 3.** Estimated abundance (solid and dashed lines) and actual abundance (circles) of male Crawfish Frogs from data collected during March and April 2010 at two wetlands at Hillenbrand Fish and Wildlife Area in southwestern Indiana, USA. The solid line and closed circles are from Nate's Pond. The dashed line and open circles are from Cattail Pond. We estimated the abundance with the function:  $Y = -4.75 + 0.68(\text{date}) - 0.0098(\text{date})^2 + 2.43(\text{pond})$ , where  $\text{pond} = 1$  for Nate's Pond and  $0$  for Cattail Pond.

wide geographic distributions suspected to be declining over large areas, the ideal data for assessment are the results of standardized survey and monitoring efforts across a species' range coupled with a consideration of threats from known dangers. The problem with determining the conservation status of Crawfish Frogs has been overcoming the challenge of surveying and monitoring geographically scattered populations when peak calling occupies a narrow detection window. Here we offer a specific solution to this problem, although our approach can be generalized to other cryptic species, including Wood Frogs and spadefoot toads, with limited detection windows (Redmer and Trauth, 2005; Wells, 2007).

Three studies previously examined Crawfish Frog calling (Busby and Brecheisen, 1997; Engbrecht, 2010; Williams et al., 2012). Our analyses supplement these studies in three ways. First, our data provide a test of whether the predictive models for Crawfish Frog calling probability (Busby and Brecheisen, 1997; Williams et al., 2012) apply to other Crawfish Frog populations (i.e., do the results of our intensive surveys have range-wide relevance?). Second, our models supplement a previous analysis (Engbrecht, 2010), which was based on data continuously collected across time but not in a predictive model, and thus our analyses provide models with parameter estimates. Third, because we knew the number of frogs at the ponds at any given time ( $\pm 1\%$ ), we could compare model predicted results to actual values to assess the goodness of fit of our predictive model.

**When should researchers listen for Crawfish Frogs?**—Our dataset indicates that at northern latitudes (Illinois, Indiana, northern Missouri) surveyors should listen for Crawfish Frogs seasonally from early March to mid-April (e.g., 1 March–10 April in 2010). Surveyors farther south should begin earlier. For example, in 2012 Crawfish Frogs in Texas—the southern-most populations of this species—

**Table 3.** Parameter Estimates and 95% Confidence Intervals for the Most Parsimonious Models for Estimating Calling Probability and Abundance from Tables 1 and 2, Respectively for Crawfish Frogs in Breeding Wetlands, Southwestern Indiana, USA. Time and date were temporal variables for the time of night and day of year, call rate was the mean calling rate for the night, rain was whether it was raining during the survey, rain prev 24 hrs was the amount of rain in the 24 hours preceding the survey, site was an indicator variable for which pond it was, and temp was temperature.

Detection probability		
Coefficient	Value	95% CI
Intercept	−25.38	(−36.44, −14.45)
Time	29.49	(6.89, 52.25)
Time <sup>2</sup>	−16.62	(−28.47, −4.87)
Date	0.94	(0.86, 1.03)
Date <sup>2</sup>	−0.02	(−0.02, −0.02)
Rain prev 24 hrs	−0.24	(−0.33, −0.16)
Temp	0.10	(0.07, 0.12)
Site	3.06	(2.75, 3.40)
Abundance		
Coefficient	Value	95% CI
Intercept	3.86	(−11.28, 19.00)
Date	0.68	(0.61, 0.74)
Date <sup>2</sup>	−0.01	(−0.01, −0.01)
Time	−18.16	(−50.04, 13.72)
Time <sup>2</sup>	9.47	(−7.15, 26.10)
Call rate	0	(0.00, 0.00)
Site	2.43	(2.36, 2.50)

began calling on 18 January; P. Crump, pers. obs.). Within the day of survey, investigators should listen between 1900 and 2300 hrs. During these optimal periods, and when temperatures were  $>9^{\circ}\text{C}$  with no rain in the previous 24 hrs, detection probabilities were  $>0.89$ . Human disturbance reduces Crawfish Frog call rates (Wright and Myers, 1927; Swanson, 1939; Redmer, 2000; Minton, 2001; Engbrecht, 2010).

Our results were generally consistent with data from southeastern Indiana (Williams et al., 2012). Our most supported model for Crawfish Frog detection probability was a similar model selected (Williams et al., 2012) at a location where Crawfish Frog individual breeding pond populations were smaller but more numerous than at our study site (Engbrecht and Lannoo, 2010). In this model, Crawfish Frogs had a mean detection probability of 0.45, and were similarly affected by season, time of night, and temperature (Williams et al., 2012). The main difference between the detection probabilities found in our study and the previous model (Williams et al., 2012) was that in the previous study rain during the previous 24 hrs increased detection probabilities. One reason for this difference might be that rain will trigger Crawfish Frog migrations (Heemeyer et al., 2010, 2012; Heemeyer and Lannoo, 2012), and that in the smaller populations studied previously (Williams et al., 2012) recent recruits immigrating during rains began calling immediately and disproportionately increased detection probabilities for breeding ponds that were recently occupied by newly arriving males.

**How long should each Crawfish Frog call survey be conducted?**—Previous workers (Busby and Brecheisen, 1997) used

**Table 4.** Crawfish Frog Detection Probabilities as a Function of Call Survey Duration (5, 10, and 20 min) for Two Ponds (Nate's and Cattail) at the Early Portion of the Breeding Season and at Peak Breeding. Durations were calculated by selecting 15 random times between 2000 and 2300 hr and noting the time to hear first call (see text for additional details). Note that while detectability is high during peak breeding, it can be low and unpredictable during the early season. Doubling survey duration from 5 to 10 min altered detectability in 5 of 12 samples with a mean increase of 0.09. Quadrupling survey duration from 5 to 20 min again altered detectability in 5 of 12 samples with a mean increase of 0.17.

Pond	Time	# Males present	Detection probabilities			$\Delta$ Detection probabilities	
			5 min	10 min	20 min	5–10 min	5–20 min
Nate's	Early season						
	11 March	1	0.80	0.87	1.00	0.07	0.20
	12 March	6	0.07	0.13	0.26	0.06	0.19
	13 March	7	0.00	0.00	0.00	0.00	0.00
	Peak						
	30 March	12	1.00	1.00	1.00	0.00	0.00
	31 March	12	1.00	1.00	1.00	0.00	0.00
1 April	12	1.00	1.00	1.00	0.00	0.00	
Cattail	Early season						
	16 March	2	0.20	0.40	0.47	0.20	0.27
	17 March	2	0.20	0.20	0.20	0.00	0.00
	18 March	2	0.27	0.27	0.27	0.00	0.00
	Peak						
	31 March	11	1.00	1.00	1.00	0.00	0.00
	1 April	10	0.87	1.00	1.00	0.13	0.13
2 April	10	0.93	1.00	1.00	<u>0.07</u> 0.09	<u>0.07</u> 0.17	

survey periods typically  $\leq 3$  min when surveying for Crawfish Frogs in eastern Kansas. In contrast, more recent workers (Williams et al., 2012), following Pierce and Gutzwiller (2004), suggested 15 min surveys for detecting small populations of Crawfish Frogs in southeastern Indiana. Our data (Table 4) indicate that small survey times (Busby and Brecheisen, 1997) might typically be sufficient for detecting Crawfish Frogs during peak breeding, but would miss populations exhibiting sporadic early or late season calling. A 15 min survey period (Williams et al., 2012) would be excessive during peak breeding but would increase chances of detecting populations, especially small populations, during early and late season calling. However, because early season calling periods are characterized by nights of no calling, if suspected populations go undetected, sites should be revisited.

The results of our study support the sampling period protocols currently used by NAAMP (30 min after sunset to 0100 hrs; Fig. 2), but not the survey duration (5 min; Weir and Mossman, 2005). Nor do we recommend the 3 min survey duration of Shirose et al. (1997) and Hemesath (1998). We suggest adopting the 15 min survey length (Williams et al., 2012), while recognizing that many potential breeding wetlands must be sampled in a relatively narrow peak calling period. Therefore, once Crawfish Frogs are detected during a 15 min survey at one site, surveyors should move to the next site, allowing efficient use of survey time. Conducting multiple surveys at each site over the course of the breeding season will increase detections. We suggest candidate wetlands be surveyed at least three times during the breeding season, with as many surveys as possible done during peak breeding.

**Determining abundance.**—Because of the tenuous status of many amphibian populations it is desirable to have quick, accurate methods for assessing population size. The NAAMP

index-based protocol (Weir and Mossman, 2005) is quick but imprecise (Nelson and Graves, 2004). Other methods for assessing amphibian population sizes, including drift fences/pitfall traps (Dodd and Scott, 1994; Wilson and Gibbons, 2010), mark–recapture (Donnelly and Guyer, 1994; Corn et al., 2000; Nelson and Graves, 2004; Bailey and Nichols, 2010), and egg-mass counts (Crouch and Patton, 2000; Richter et al., 2003; Patton and Harris, 2010), are more precise but time consuming. For breeding amphibians with narrow detection windows such as Crawfish Frogs, assessments of abundance at any given site must be done quickly if multiple sites are to be surveyed.

Abundance estimates based on call rates will typically describe the number of males in a population, since female anurans usually do not call and would not be directly represented (Wells, 2007). However, drift fence data collected at Nate's and Cattail ponds have shown that while Crawfish Frogs have male-biased operational sex ratios during most of the breeding season (males tend to remain in breeding ponds longer than females), absolute sex ratios for populations are approximately 1:1 (Kinney, 2011). Overall population estimates accounting for both males and females can then be calculated by doubling the estimated number of males.

In our study, the length of the calling period appeared to have a positive linear relationship with the number of calling Crawfish Frog males (and thus breeding adults). At Nate's Pond, with a population of 22 males, calling lasted 35 days (a ratio of 1.6 days calling/male present), while at Cattail Pond, with a population of 14 males, calling lasted 20 days (1.4 days calling/male present; Fig. 1). At smaller populations sampled previously (Williams et al., 2012), calling periods were shorter, lasting between 1 and >14 d depending on the pond. This finding suggests that within years, relative sizes of Crawfish Frog populations can be estimated if their length of calling period can be accurately

determined. Because breeding period shows an inverse relationship with temperature (M.J.L., pers. obs.), and temperatures vary across years, the slope of the relationship we observed (no. days calling/1.5 = no. of calling males for southern Indiana in 2010) will undoubtedly vary across years and across regions within years.

**Scope and limitations.**—To our knowledge, this study is the first to couple the relationship between anuran calling activity and the number of known males for the duration of a breeding season. As mentioned above, we feel that this approach could be useful for surveying other anuran species with short breeding seasons. We understand that our data, which were collected at two wetlands over the course of a single breeding season, represent a small temporal and geographic sampling size, and that data from additional sites and years would likely enhance our results. Drift fence techniques, however, are time consuming and operating drift fence arrays at additional sites was beyond the scope of our study. Other studies using ARS to analyze anuran chorusing patterns have also used data from one or two wetlands during a single field season (Mohr and Dorcas, 1999; Bridges and Dorcas, 2000; Oseen and Wassersug, 2002; Steelman and Dorcas, 2010). Because our chorusing data were based on call counts (calls/min) calculated from lengthy (8 h) recordings, they represent a continuous record (not a sample) of calling activity from 1900 to 0300 h during the breeding season. We feel that the high resolution of our dataset at least partially offsets its spatial and temporal limitations.

Currently, detectability in Crawfish Frogs has been examined in Indiana (Engbrecht, 2010; Williams et al., 2012) and Kansas (Busby and Brecheisen, 1997), all in areas where the northern subspecies *L. a. circulosus* occurs (Parris and Redmer, 2005). Research conducted in other regions, particularly within the range of the southern subspecies (*L. a. areolatus*), will likely enhance our understanding of detectability in this species.

**Conclusions and recommendations.**—Crawfish Frog choruses can be heard at least 0.5 km away in the absence of interference (i.e., traffic sounds), several times that distance under ideal acoustic conditions. To optimize survey and monitoring efforts, we recommend that surveys for Crawfish Frogs begin immediately after males are known or suspected to be in breeding wetlands. Detectability increases when temperatures are  $>9^{\circ}\text{C}$  (although temperature appeared less important than the timing of sampling, which should be done during peak breeding). Surveyors should be quiet, and take care not to disturb frogs by having their car stereos on, slamming car doors, engaging in conversations, or approaching wetlands on foot. Surveys of 5 min duration should suffice when sampling large populations during peak breeding, but surveys should last 15 min when sampling unknown or small populations. Conducting surveys when Crawfish Frogs are most easily detected will help researchers optimize their time, enabling them to visit additional sites, and allowing re-sampling. We trust these recommendations will assist in the estimation of the status of Crawfish Frog populations across their range, and provide the data necessary to objectively assess their conservation status.

#### ACKNOWLEDGMENTS

We thank K. Smith, B. Feaster, and R. Ronk of the Indiana Department of Natural Resources for their support, and for

allowing us to work at the Hillenbrand Fish and Wildlife Area. We also thank J. Heemeyer, T. Wheat, and S. Lannoo for their field assistance, and A. Royle for the statistical consultation. B. Gerber and F. Graybill at the statistical Laboratory at Colorado State University provided suggestions for data analysis. This project was supported by State Wildlife Grant (SWG) Number E2-08-WDS13 awarded by the Indiana Department of Natural Resources. All research described here was conducted under IACUC number 3-24-2008 issued by Indiana State University, and Scientific Purposes License Permit number 09-0084 issued by Indiana Department of Natural Resources.

#### LITERATURE CITED

- Alford, R. A., P. M. Dixon, and J. H. K. Pechmann. 2001. Ecology: global amphibian population declines. *Nature* 412:499–500.
- Altig, R., R. W. McDiarmid, K. A. Nichols, and P. C. Ustach. 2012. Tadpoles of the United States and Canada: a tutorial and key. <http://www.pwrc.usgs.gov/tadpole/>, Accessed 17 March 2012.
- Bailey, L. L., and J. D. Nichols. 2010. Capture–mark–recapture, removal sampling, and occupancy models, p. 447–463. *In: Amphibian Ecology and Conservation: A Handbook of Techniques*. C. K. Dodd (ed.). Oxford University Press, New York.
- Bragg, A. N. 1953. A study of *Rana areolata* in Oklahoma. *Wasmann Journal of Biology* 11:273–319.
- Bridges, A. S., and M. E. Dorcas. 2000. Temporal variation in anuran calling behavior: implications for surveys and monitoring programs. *Copeia* 2000:587–592.
- Burnham, K. P., and D. R. Anderson. 2002. *Model Selection and Multimodal Inference: A Practical Information-Theoretic Approach*. Springer, New York.
- Busby, W. H., and W. R. Brecheisen. 1997. Chorusing phenology and habitat associations of the Crawfish Frog, *Rana areolata* (Anura: Ranidae), in Kansas. *Southwest Naturalist* 42:210–217.
- Christiansen, J. L., and R. M. Bailey. 1991. *The Salamanders and Frogs of Iowa*. Iowa Department of Natural Resources, Nongame Technical Series Number 3, Des Moines, Iowa.
- Collins, J. P., and M. L. Crump. 2009. *Extinction in Our Times: Global Amphibian Declines*. Oxford University Press, New York.
- Collins, J. T., S. L. Collins, and T. W. Taggart. 2010. *Amphibians, Reptiles, and Turtles in Kansas*. Eagle Mountain Publishing, Eagle Mountain, Utah.
- Corn, P. S., E. Muths, and W. M. Iko. 2000. A comparison in Colorado of three methods to monitor breeding amphibians. *Northwest Naturalist* 81:22–30.
- Crouch, W. B., III, and P. W. C. Patton. 2000. Using egg mass counts to monitor Wood Frog populations. *Wildlife Society Bulletin* 28:895–901.
- Dodd, C. K., and D. E. Scott. 1994. Drift fences encircling breeding sites, p. 125–130. *In: Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*. W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L.-A. C. Hayek, and M. S. Foster (eds.). Smithsonian Institution Press, Washington, D.C.
- Donnelly, M. A., and C. Guyer. 1994. Mark–recapture, p. 183–200. *In: Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*. W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L.-A. C. Hayek, and

- M. S. Foster (eds.). Smithsonian Institution Press, Washington, D.C.
- Dorcas, M. E., S. J. Price, S. C. Walls, and W. J. Barichivich.** 2010. Auditory monitoring of anuran populations, p. 281–298. *In: Amphibian Ecology and Conservation: A Handbook of Techniques.* C. K. Dodd (ed.). Oxford University Press, New York.
- Duellman, W. E., and L. Trueb.** 1986. *Biology of Amphibians.* McGraw-Hill, New York.
- Elliot, L., C. Gerhardt, and C. Davidson.** 2009. *The Frogs and Toads of North America: A Comprehensive Guide to Their Identification, Behavior, and Calls.* Houghton Mifflin Harcourt, Boston.
- Engbrecht, N. J.** 2010. The status of Crawfish Frogs (*Lithobates areolatus*) in Indiana, and a tool to assess populations. Unpubl. M.S. thesis, Indiana State University, Terre Haute, Indiana.
- Engbrecht, N. J., J. L. Heemeyer, V. C. Kinney, and M. J. Lannoo.** 2012. *Lithobates areolatus* (Crawfish Frogs). Thwarted predation. *Herpetological Review* 43:323–324.
- Engbrecht, N. J., and M. J. Lannoo.** 2010. A review of the status and distribution of Crawfish Frogs (*Lithobates areolatus*) in Indiana. *Proceedings of the Indiana Academy of Science* 119:64–73.
- Gerhardt, H. C.** 1975. Sound pressure levels and radiation patterns of the vocalizations of some North American frogs and toads. *Journal of Comparative Physiology* 102:1–12.
- Heemeyer, J. L., V. C. Kinney, N. J. Engbrecht, and M. J. Lannoo.** 2010. The biology of Crawfish Frogs (*Lithobates areolatus*) prevents the full use of telemetry and drift fence techniques. *Herpetological Review* 41:42–45.
- Heemeyer, J. L., and M. J. Lannoo.** 2012. Breeding migrations in Crawfish Frogs (*Lithobates areolatus*): long-distance movements, burrow philopatry, and mortality in a near-threatened species. *Copeia* 2012:440–450.
- Heemeyer, J. L., P. J. Williams, and M. J. Lannoo.** 2012. Obligate crayfish burrow use and core habitat requirements of Crawfish Frogs. *Journal of Wildlife Management* 76:1081–1091.
- Hemesath, L. M.** 1998. Iowa's frog and toad survey, 1991–1994, p. 206–216. *In: Status and Conservation of Midwestern Amphibians.* M. J. Lannoo (ed.). University of Iowa Press, Iowa City, Iowa.
- Hoffman, A. S., J. L. Heemeyer, P. J. Williams, J. R. Robb, D. R. Karns, V. C. Kinney, N. J. Engbrecht, and M. J. Lannoo.** 2010. Strong site fidelity and a variety of imaging techniques reveal around-the-clock and extended activity patterns in Crawfish Frogs (*Lithobates areolatus*). *Bioscience* 60:829–834.
- Houlahan, J. E., C. S. Findlay, B. R. Schmidt, A. H. Meyer, and S. L. Kuzmin.** 2000. Quantitative evidence for global amphibian population declines. *Nature* 404:753–755.
- IUCN (International Union for the Conservation of Nature) Red List.** 2012. IUCN Red List of threatened species. <http://www.iucnredlist.org>, Accessed 17 March 2012.
- Jensen, J. B., and S. C. Richter.** 2005. *Rana capito*, Gopher Frog, p. 536–538. *In: Amphibian Declines: The Conservation Status of United States Species.* M. J. Lannoo (ed.). University of California Press, Berkeley, California.
- Kinney, V. C.** 2011. Adult survivorship and juvenile recruitment in populations of Crawfish Frogs (*Lithobates areolatus*), with additional consideration of the population sizes of associated pond breeding species. Unpubl. M.S. thesis, Indiana State University, Terre Haute, Indiana.
- Kinney, V. C., and M. J. Lannoo.** 2010. *Lithobates areolatus* (Northern Crawfish Frog). Breeding. *Herpetological Review* 41:197–198.
- Lannoo, M. J. (ed.).** 2005. *Amphibian Declines: The Conservation Status of United States Species.* University of California Press, Berkeley, California.
- Lannoo, M. J., V. C. Kinney, J. L. Heemeyer, N. J. Engbrecht, A. L. Gallant, and R. W. Klaver.** 2009. Mine spoil prairies expand critical habitat for endangered and threatened amphibian and reptile species. *Diversity* 1:118–132.
- Minton, S. A., Jr.** 2001. *Amphibians and Reptiles of Indiana.* Second edition. Indiana Academy of Science, Indianapolis, Indiana.
- Mohr, J. R., and M. E. Dorcas.** 1999. A comparison of anuran calling patterns at two Carolina bays in South Carolina. *The Journal of the Elisha Mitchell Scientific Society* 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, p. 169–198. *In: Status and Conservation of Midwestern Amphibians.* M. J. Lannoo (ed.). University of Iowa Press, Iowa City, Iowa.
- Nelson, G. L., and B. M. Graves.** 2004. Anuran population monitoring: comparison of the North American amphibian monitoring program's calling index with mark-recapture estimates for *Rana clamitans*. *Journal of Herpetology* 38:355–359.
- Nunziata, S. O., M. J. Lannoo, J. R. Robb, D. R. Karns, S. L. Lance, and S. C. Richter.** 2013. Population and conservation genetics of Crawfish Frogs, *Lithobates areolatus*, at their northeastern range limit. *Journal of Herpetology* 47:361–368.
- Oseen, K. L., and R. J. Wassersug.** 2002. Environmental factors influencing calling in sympatric anurans. *Oecologia* 133:616–625.
- Parris, M. J., and M. Redmer.** 2005. *Rana areolata*, Crawfish Frog, p. 256–258. *In: Amphibian Declines: The Conservation Status of United States Species.* M. J. Lannoo (ed.). University of California Press, Berkeley, California.
- Patton, P. W. C., and R. N. Harris.** 2010. Egg mass and nest counts, p. 143–163. *In: Amphibian Ecology and Conservation: A Handbook of Techniques.* C. K. Dodd (ed.). Oxford University Press, New York.
- Peterson, C. R., and M. E. Dorcas.** 1994. Automated data acquisition, p. 47–57. *In: Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians.* W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L.-A. C. Hayek, and M. S. Foster (eds.). Smithsonian Institution Press, Washington, D.C.
- Pierce, B. A., and K. J. Gutzwiller.** 2004. Auditory sampling of frogs: detection efficiency in relation to survey duration. *Journal of Herpetology* 38:495–500.
- R Development Core Team.** 2012. R: A language and environment for statistical computing. R Project for Statistical Computing. <http://www.r-project.org>, Accessed 27 February 2012.
- Redmer, M.** 2000. Demographic and reproductive characteristics of a southern Illinois population of the Crayfish Frog, *Rana areolata*. *Journal of the Iowa Academy of Science* 107:128–133.
- Redmer, M., and S. E. Trauth.** 2005. *Rana sylvatica*, Wood Frog, p. 590–593. *In: Amphibian Declines: The Conserva-*

- tion Status of United States Species. M. J. Lannoo (ed.). University of California Press, Berkeley, California.
- Richter, S. C., and J. B. Jensen.** 2005. *Rana sevos*, Dusky Gopher Frog, p. 584–586. *In: Amphibian Declines: The Conservation Status of United States Species.* M. J. Lannoo (ed.). University of California Press, Berkeley, California.
- Richter, S. C., J. E. Young, G. N. Johnson, and R. A. Seigel.** 2003. Stochastic variation in reproductive success of a rare frog, *Rana sevos*: implications for conservation and for monitoring amphibian populations. *Biological Conservation* 111:171–177.
- Saenz, D., L. A. Fitzgerald, K. A. Baum, and R. N. Conner.** 2006. Abiotic correlates of anuran calling phenology: the importance of rain, temperature, and season. *Herpetological Monographs* 20:64–82.
- Scott, N. J., and D. B. Woodward.** 1994. Surveys at breeding sites, p. 118–125. *In: Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians.* W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L.-A. C. Hayek, and M. S. Foster (eds.). Smithsonian Institution Press, Washington, D.C.
- Shirose, L. J., C. A. Bishop, D. M. Green, C. J. MacDonald, R. J. Brooks, and N. J. Helferty.** 1997. Validation tests of an amphibian call count survey technique in Ontario, Canada. *Herpetologica* 53:312–320.
- Smith, H. M.** 1950. *Handbook of Amphibians and Reptiles of Kansas.* University of Kansas Museum of Natural History, Miscellaneous Publication Number 2, Lawrence, Kansas.
- Smith, H. M., C. W. Nixon, and P. E. Smith.** 1948. A partial description of the tadpole of *Rana areolata circulosa* and notes on the natural history of the race. *American Midland Naturalist* 39:608–614.
- Steelman, C. K., and M. E. Dorcas.** 2010. Anuran calling survey optimization: developing and testing predictive models of anuran calling activity. *Journal of Herpetology* 44:61–68.
- Stuart, S. N., J. S. Chanson, J. A. Cox, B. E. Young, A. S. L. Rodrigues, D. L. Fischman, and R. W. Waller.** 2004. Status and trends of amphibian declines and extinctions worldwide. *Science* 306:1783–1786.
- Swanson, P. L.** 1939. Herpetological notes from Indiana. *American Midland Naturalist* 22:684–695.
- Thompson, C.** 1915. Notes on the habits of *Rana areolata* Baird and Girard. *Scientific Papers of the University of Michigan* 10:1–7.
- 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. *Journal of the North Carolina Academy of Science* 119:103–110.
- Trauth, S. E., H. W. Robison, and M. V. Plummer.** 2004. *The Amphibians and Reptiles of Arkansas.* University of Arkansas Press, Fayetteville, Arkansas.
- USFWS (United States Fish and Wildlife Service).** 2010. Endangered and threatened wildlife and plants: designation of critical habitat for Mississippi Gopher Frog. *Federal Register* 106:31387–31411.
- Waddle, J. H., T. F. Thigpen, and B. M. Glorioso.** 2009. Efficacy of automatic vocalization recognition software for anuran monitoring. *Herpetological Conservation and Biology* 4:384–388.
- Wake, D. B.** 1991. Declining amphibian populations. *Science* 253:860.
- Wake, D. B.** 2012. Facing extinction in real time. *Science* 335:1052–1053.
- Weir, L. A., and M. J. Mossman.** 2005. North American amphibian monitoring program, p. 307–313. *In: Amphibian Declines: The Conservation Status of United States Species.* M. J. Lannoo (ed.). University of California Press, Berkeley, California.
- Wells, K. D.** 2007. *The Ecology and Behavior of Amphibians.* University of Chicago Press, Chicago.
- Williams, P. J., J. R. Robb, and D. R. Karns.** 2012. Occupancy dynamics of breeding Crawfish Frogs in southeastern Indiana. *Wildlife Society Bulletin* 36:350–357.
- Wilson, J. D., and J. W. Gibbons.** 2010. Drift fences, coverboards, and other traps, p. 229–245. *In: Amphibian Ecology and Conservation: A Handbook of Techniques.* C. K. Dodd (ed.). Oxford University Press, New York.
- Wright, H. P., and G. S. Myers.** 1927. *Rana areolata* at Bloomington, Indiana. *Copeia* 1927:173–175.
- Zimmerman, B. L.** 1994. Audio strip transects, p. 92–97. *In: Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians.* W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L.-A. C. Hayek, and M. S. Foster (eds.). Smithsonian Institution Press, Washington, D.C.
- Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith.** 2009. *Mixed Effects Models and Extensions in Ecology with R.* Springer, New York.