
DETECTING FROGS AND DETECTING DECLINES: AN EXAMINATION OF OCCUPANCY AND TURNOVER PATTERNS AT THE RANGE EDGE OF BLANCHARD'S CRICKET FROG (*ACRIS BLANCHARDI*)

RICHARD M. LEHTINEN^{1,3} AND JAMES R. WITTER²

¹Department of Biology, The College of Wooster, 931 College Mall, Wooster, Ohio 44691, USA

²Program Department, Wood County Park District, 18729 Mercer Road, Bowling Green, Ohio 43402, USA

³Corresponding author, e-mail: rlehtinen@wooster.edu

Abstract.—While geographically widespread, Blanchard's Cricket Frog (*Acris blanchardi*) has been declining recently in the northern portions of its range. No cause or causes have yet been definitively associated with this decline and few data are available regarding its current status. To provide data on recent trends in occupancy in the area of decline, we monitored 312 aquatic sites in three areas of western Ohio from 2004–2008 using calling surveys (1,807 surveys total). These sites were positioned surrounding the easternmost known populations identified in 2004 to allow us to detect ongoing decline, stasis, or recovery. Using occupancy modeling techniques, we estimated occupancy and turnover (extinction-colonization) rates and identified factors influencing occupancy, turnover, and detection probability. Site occupancy varied strongly by region but was stable or increasing in all monitoring areas during the study (north: 29% to 31%; central: 5% to 16%; south: 14% to 21%). Further, the easternmost known populations shifted eastward in two of the three monitoring areas, which together we interpret as potential evidence for limited recovery. We also detected population turnover with estimated annual colonization and extinction rates averaging 4% and 7%, respectively. Extinction rates were highest in ponds, lowest in streams, and intermediate in lakes, suggesting a possible source-sink population structure. The probability of detection was most heavily influenced by time of day and whether a broadcast of a breeding vocalization was played during the survey. Although these populations appear to be stable or expanding, they still occupy only a fraction of the species' historic range in Ohio. We advocate continued monitoring to detect future distributional shifts in this formerly common species.

Key Words.—amphibian declines; metapopulation dynamics; monitoring; occupancy modeling; source-sink dynamics

INTRODUCTION

In the last few decades, evidence has mounted for widespread declines and extinctions of amphibians (Stuart et al. 2004; Wake and Vredenburg 2008). In response, much effort has gone into constructing conservation strategies for affected species (Gascon et al. 2007). Amphibian conservation decisions, however, are frequently hampered by a lack of information. For example, distributional information about species of conservation concern is often inadequate. This is true even in reasonably well-studied areas and the information that does exist is often fragmentary, anecdotal, or at small spatial or temporal scales.

In the past, amphibian monitoring focused on getting long time series of detailed data from one or a few sites (e.g., Semlitsch et al. 1996; Werner et al. 2009). These long term data are frequently from protected areas and we therefore often have little idea of trends in landscapes with a large human presence. While the rich data available from such studies are extremely valuable, the results cannot often be extended meaningfully beyond the studied areas. As detecting declines and assessing the conservation status of species has become more

important, herpetologists have increasingly turned to occupancy as a state variable (Storfer 2003; Mazarolle et al. 2007). Occupancy is simply whether a given area (site) is occupied by a species of interest. Since comparatively little effort needs to be expended to determine occupancy, many more sites can be assessed in this way than if, for example, population size was to be estimated.

However, the probability of detecting the species of interest is almost always less than one. Therefore, detection probability becomes an important issue in occupancy studies as some sites classified as unoccupied may in fact be occupied (the species of interest was simply not detected during the survey, a false zero; MacKenzie et al. 2002). Underestimation of occupancy and overestimation of extinction and colonization rates can result from the failure to detect focal organisms when they are present (de Solla et al. 2005; Pellet and Schmidt 2005). Further, variation in detection probability over time makes it difficult to separate real changes in occupancy from changes in detectability (MacKenzie et al. 2006).

Fortunately, statistical modeling techniques have now become widely available that allow a more robust

estimate of occupancy that explicitly accounts for variation in the probability of detection (MacKenzie et al. 2006). These techniques allow investigators to evaluate variables that may influence both the probability of occupancy and the probability of detection as well as to model other processes (e.g., extinction and colonization). The use of these methods with appropriately designed field studies permits a more robust assessment of occupancy patterns in space and time for the species of interest. Despite the utility of these approaches in providing more reliable information about occupancy trends, they are just beginning to be widely incorporated into monitoring programs for amphibians and reptiles (Pellet and Schmidt 2005; Mazerolle et al. 2007).

For anurans, calling surveys (i.e., chorusing or listening surveys) are widely used both by professional herpetologists and by volunteer-based programs for monitoring purposes. These surveys have many desirable properties (e.g., they are generally effective, inexpensive and time efficient) and often work well with monitoring programs focused on occupancy trends. A number of studies have identified environmental variables that can influence detection of anurans in calling surveys. For example, Weir et al. (2005) presented evidence for the importance of season, time of day, air temperature, and moon illumination on detection probabilities when using calling surveys. Many studies have found evidence for the importance of these and other factors (e.g., humidity, water temperature, wind speed, barometric pressure, noise from traffic; Saenz et al. 2006; Dorcas et al. 2009; Steelman and Dorcas 2010). However, not all of these variables are influential for all species in all times and places and those variables which are important influences on calling activity are often species specific.

Blanchard's Cricket Frog (*Acris blanchardi*) is a species thought to be in decline throughout the northern portions of its range (Gray et al. 2005; Beauclerc et al. 2010). While these frogs apparently remain abundant in more southerly portions of its range, declines and/or extirpations have been reported from many other areas (e.g., Lannoo et al. 1994; Mierzwa 1998; Hammerson and Livo 1999; Lehtinen 2002; McLeod 2005). Many possible decline mechanisms have been proposed (see Gray and Brown 2005 and Lehtinen and Skinner 2006 for a summary) and there has been some initial exploration of a number of these hypotheses (e.g., McCallum and Trauth 2003 for abnormalities; Beasley et al. 2005 for trematodes and contaminants; Irwin 2005, Burdick and Swanson 2010 and Swanson and Burdick 2010 for overwintering mortality; Lehtinen and Skinner 2006 for habitat acidification; Steiner and Lehtinen 2008 for disease outbreaks; McCallum 2010 for climate change).

Despite these reports of declines and the availability of calling surveys as a monitoring tool, little effort has been put into monitoring populations of this formerly common species. To help fill this gap, we sampled east-west transects in Ohio in 2004 and found evidence for a 120 km westward range contraction at the northeastern range boundary (Lehtinen and Skinner 2006) compared to historical distributional patterns (Walker 1946; Davis and Menze 2000). Using these results as a starting point, we established 312 sites for monitoring in three areas of western Ohio that straddled this putative eastern range limit for Blanchard's Cricket Frog. Since these sites were positioned directly along the decline front, monitoring of these sites through time should provide evidence for continuing decline, stasis, or recovery.

Our specific goals were to: (1) provide robust estimates of occupancy over time for these areas and rigorously assess the conservation status of this species in Ohio; (2) determine the most important variables influencing the probability of detection of Blanchard's Cricket Frog using calling surveys; (3) assess whether the use of recorded playbacks during calling surveys increases detection probability; and (4) estimate turnover (extinction-colonization) rates from these data and examine potential influences on these processes. Lastly, since little is known about the relative timing and spatial extent of cricket frog declines in Ohio, we summarize historical information about their distribution in the state.

MATERIALS AND METHODS

Site selection and field surveys.—Using calling surveys along east-west transects in 2004, we identified the point in northwestern, west-central, and southwestern Ohio where cricket frogs became rare or undetectable (see Lehtinen and Skinner 2006 for details) and then established our study sites for long-term monitoring in three $30 \times 30 \text{ km}^2$ areas surrounding these putative range boundaries (Fig. 1). Within these areas, we identified all streams (2nd order or larger), ponds, and lakes using digitized US Geological Survey topographic maps and randomly selected which to include as study sites using a random number generator. To insure that study sites were independent of each other, we used 1.5 km as a minimum distance between sites. Lakes were arbitrarily defined as lentic water bodies > 4 ha in size (ponds < 4 ha). We treated large and small lentic water bodies separately as the former are often dominated by fish and are essentially permanent aquatic habitats while the latter are usually fishless and dry periodically (Wellborn et al. 1996). To insure accessibility, only sites that were located within 0.4 km of a public road were used. The northern monitoring area (portions of Wood and Hancock counties, centered at 41°05'N latitude) included 106 study sites. The central monitoring area (portions of

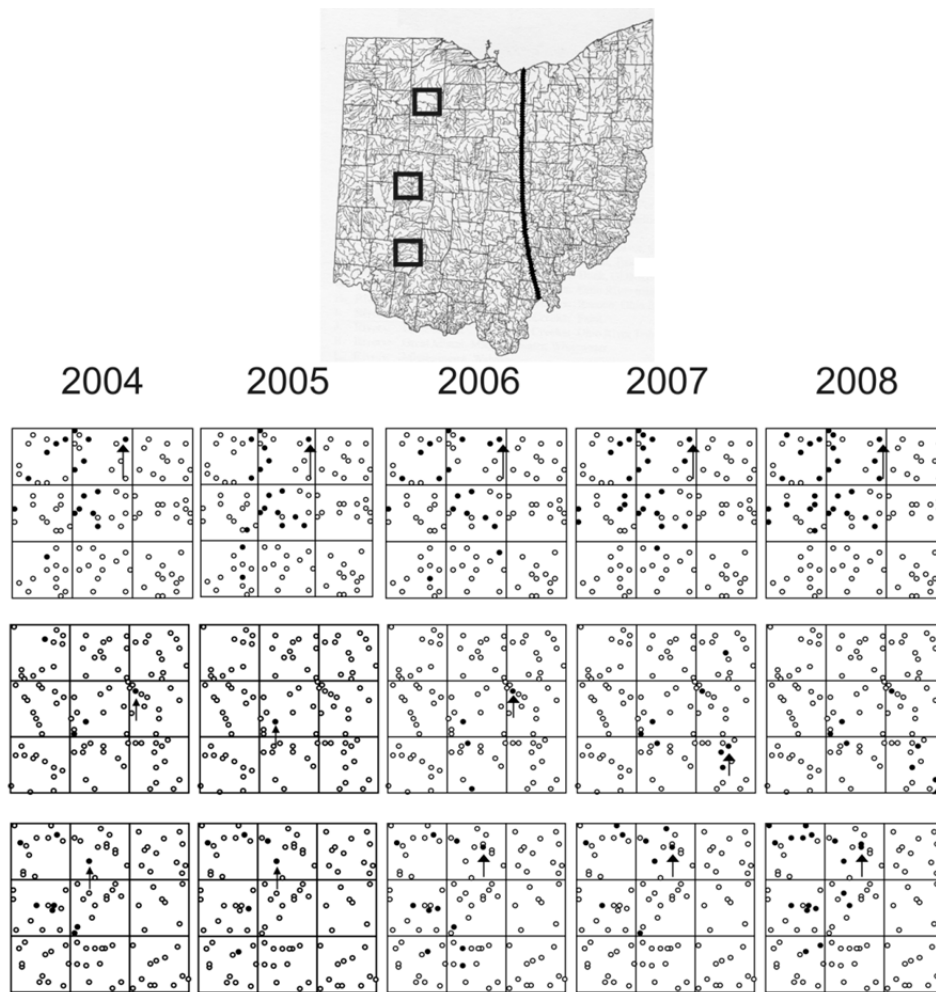


FIGURE 1. Top: Squares indicate the location of each 30×30 km monitoring area in the northern, central, and southern portions of western Ohio, USA, for Blanchard's Cricket Frog (*Acris blanchardi*). The solid line indicates approximate historical eastern range boundary (estimated from Walker 1946). Bottom: Locations of study sites within each monitoring area are shown as dots (northern monitoring area at top, central monitoring area in the middle, southern monitoring area at bottom). Filled dots were occupied in the given year, unfilled dots were unoccupied based on survey results. Arrows indicate the position of the easternmost known population in each year.

Champaign, Logan, Miami, and Shelby counties, centered at $40^{\circ}10'N$ latitude) included 105 study sites. The southern monitoring area (portions of Clinton, Greene, and Warren counties, centered at $39^{\circ}25'N$ latitude) included 101 study sites.

We used 8-min listening surveys to detect the presence of Blanchard's Cricket Frogs at each site with no acclimation period (Dorcas et al. 2009). We opted for relatively brief surveys to maximize our geographic coverage. Also, Pierce and Gutzwiller (2004) found that longer listening surveys did not increase detection efficiency, suggesting that short surveys should be adequate. Cricket frogs were recorded as present or absent at each site. The timing of our surveys was designed to coincide with the peak calling activity of Blanchard's Cricket Frogs in Ohio. While cricket frogs can be heard calling as early as April and as late as August, our experience indicates that in much of the state, June is the peak month for breeding activity (RML,

pers. obs.). The exact dates when surveys began varied somewhat from year to year based on climatic considerations but generally started in late May and concluded by late June or early July. We surveyed the most southerly sites first and then proceeded northward. We began site surveys at 1500 and continued until 2400, if weather conditions remained suitable (minimum air temperature $18^{\circ}C$, no heavy rain or high wind (< 15 km/h)). We surveyed during daylight hours as cricket frogs commonly call during the day (Bridges and Dorcas 2000; RML, pers. obs.) and previous analysis suggested that calling intensity did not differ over these hours (Lehtinen and Skinner 2006).

To allow for the estimation of detection probability and for a robust estimate of occupancy, we visited a randomly selected subset (about 20%) of our study sites three times each year in the years 2006–2008 (a double sampling design, see MacKenzie et al. 2006). Given

limited time and resources, we opted to survey more sites at the expense of fewer surveys per site since our primary goal was to assess occupancy patterns over a large spatial extent. For sites that received multiple site visits in a given year, we separated site visits by at least 24 h except in a small number of cases (< 20). We visited study sites a single time in 2004 and 2005 but these are included in our analysis because occupancy modeling procedures (see below) are robust to this type of missing data. During the 5-y period, we visited each of the 312 study sites a minimum of five times and a maximum of 11 times resulting in a total of 1,807 site visits.

In addition to cricket frog presence or absence, we also recorded a number of variables that may influence detection probability. In all years, we recorded time of day (24 h clock), day of the year (Julian scale), air temperature ($^{\circ}$ C), and the moon phase (% of full illumination, using data from the U.S. Naval Observatory: <http://tycho.usno.navy.mil/vphase.html>) for each survey. Starting in 2006, we added two additional variables that were recorded for each survey: relative humidity (%) and barometric pressure in mm Hg (1 mm Hg = 1.333 kPa). We measured these variables using Kestrel 3000 or 3500 portable weather meters (Nielsen Kellerman Company, Boothwyn, Pennsylvania, USA). These variables have been found by other studies to influence calling activity of North American anurans (e.g., Weir et al. 2005; Saenz et al. 2006; Steelman and Dorcas 2010). To mitigate the impact of false positives, we only surveyed for the focal species and we trained and tested the hearing acuity of all observers as recommended by McClintock et al. (2010). In addition, most of our surveys (about 65%) had the same observer (RML) present in all years. Either one or two surveyors was present on each site visit and all either had previous experience with identifying Blanchard's Cricket Frog vocalizations or had received detailed training prior to beginning survey work. If two surveyors were present during a survey, and they differed in their determination of presence or absence, a consensus was reached on the occupancy status of the site before moving on or, lacking consensus, the site was re-surveyed.

Additionally, we randomly selected a subset of site visits (44 in 2006, 89 in 2007, and 48 in 2008; 181 total) to include a 30-s broadcast of a cricket frog breeding vocalization. We played this broadcast from a portable stereo at about 90 dB (measured at 1 meter distance with a sound level meter; RadioShack Corporation, Fort Worth, Texas, USA) pointed in the direction of the aquatic habitat being surveyed. The recording was played 5 min into the calling survey. For site visits that included a broadcast in a given year, we randomly determined on which site visit the broadcast occurred.

Data analysis and model selection.—We developed a statistical model to estimate Blanchard's Cricket Frog occupancy for our study sites in each year and to provide estimates of extinction and colonization rates between years using a multi-season analysis in the program Presence, version 6.2 (Hines 2006). The initial occupancy parameterization for a multi-season model was used for all models. Using data from all five years, we first modeled variables influencing detection probability (P) using four covariates: time of day, day of the year (Julian day), air temperature, and moon phase. We initially considered both linear and quadratic formulations of Julian day, time of day, and air temperature. However, a linear formulation of Julian day and time of day and a quadratic formulation of air temperature had the most explanatory power and subsequently we only considered those variable formulations. We fit all additive models with different combinations of these four covariates and ranked them according to Akaike's Information Criterion (AIC). Next, we used the best model for P (i.e., the model with the lowest AIC score) to construct models for occupancy (ψ). To model ψ , we identified two *a priori* variables that we suspected might influence the probability of occupancy: the geographic region (northern, central, or southern Ohio) and the aquatic habitat type (pond, lake, or stream). We created additive models for ψ for all possible combinations of these variables. Then, using the best model for ψ , we created models first for colonization (γ) and subsequently for extinction (ϵ) using all possible combinations of these same two covariates (region and aquatic habitat type). Parameter estimates (proportion of sites occupied, extinction and colonization rates) are reported from the overall best model. All five years of survey data are analyzed here (despite the fact that multiple site visits only occurred in 2006–2008) on the assumption that the detection process was not markedly different in 2004 and 2005. We make this assumption based on two pieces of information. First, estimated detection probability did not vary much in 2006–2008 and in a preliminary analysis when year was included as a covariate in models for P, it had very little explanatory power. Note that model selection criteria like AIC only allow models to be compared to one another but provide no information on the fit of the model to the data. There currently are no goodness-of-fit tests available to examine the fit of multi-season occupancy models.

To model detection probability (P) for the additional covariates recorded in 2006–2008, we fit all additive models with different combinations of six different covariates (time of day, day of the year (Julian day), air temperature, moon phase, barometric pressure, and breeding vocalization playback) using the approach described above. In this analysis, a linear formulation of time of day and air temperature and a quadratic

formulation of Julian day was used as these had the most explanatory power. Relative humidity was not included as a covariate as this variable was highly correlated with air temperature ($r = 0.73$). To keep the number of candidate models for P manageable, we did not model the number of observers in our models for P, as preliminary analysis suggested this was unimportant. We also did not model any interactions among covariates. Continuous covariates were normalized before analysis and categorical covariates were coded as dummy variables. Coding categorical covariates as dummy variables created $n - 1$ covariates, where n is the number of categories. This approach influences the number of parameters in the resulting model as each dummy variable has an associated parameter. When parameter estimates are given these were obtained from the best supported model of the relevant analysis. Model-selection uncertainty was low in all analyses, and consequently, we did not use model-averaging to derive estimates of parameters.

To estimate the relative importance of modeled variables, we summed the AIC weight (w_i) for every model in which a given covariate occurred (following Burnham and Anderson 2002). If a covariate occurred in most or all of the best models, it would have a high relative variable importance and be supported as an influential variable. Similarly, if a covariate only occurred in the models with relatively weak explanatory power, it would have a low relative variable importance and be assumed unimportant. We also calculated estimates of lambda (λ) using the best overall model. Lambda was suggested by MacKenzie et al. (2003) as a measure of the rate of change in occupancy such that a stable set of populations should have an estimated λ of approximately 1.0 (declining occupancy < 1 , increasing occupancy > 1). Following MacKenzie et al. (2003), λ was calculated for each pair of successive years as ψ_{t+1} / ψ_t . For a full treatment and justification of these modeling approaches and model selection procedures, see Burnham and Anderson (2002) and MacKenzie et al. (2006).

Historical distribution and timing of declines.—To better quantify the timing of Blanchard’s Cricket Frog declines in Ohio, we assembled data on the dates of last known occurrence for the 61 counties in Ohio for which cricket frogs have been known to occur historically. We also tallied the total number of unique localities from which cricket frogs were collected in Ohio prior to 1960. We accepted records as valid if they met one or more of the following criteria: (1) they were based on data reported in peer-reviewed journals or in government or technical publications; (2) they included museum voucher specimens or call recordings that had been verified by ourselves or another herpetologist; or (3) they were based on our own fieldwork. For the purposes of statistical analysis, we split all counties into two categories, western Ohio or central Ohio, as declines are thought to have occurred in the latter but not the former (Lehtinen and Skinner 2006). A county was considered in western Ohio if at least a portion of its boundaries was located west of 83°40'W longitude. All other counties were classified as being in central Ohio. A non-parametric Mann-Whitney test was used to examine differences in the year of last known cricket frog occurrence for counties in central and western Ohio. Chi-square goodness-of-fit tests were used to examine differences in the number of reported localities in central and western Ohio in two time periods (pre-1960 and post-1960).

RESULTS

Occupancy patterns varied by region but all were stable or increasing over time (Table 1). The greatest proportion of occupied sites was consistently found in the northern monitoring area, with the central and southern monitoring areas having somewhat fewer extant populations in all years. The proportion of extant populations was stable in the northern monitoring area (0.29 in 2004 to 0.31 in 2008) and increased in the central and southern monitoring areas (0.05 in 2004 to 0.16 in 2008 and 0.14 in 2004 to 0.21 in 2008,

TABLE 1. Occupancy estimates (ψ) of Blanchard’s Cricket Frogs (*Acris blanchardi*) at 312 sites in three monitoring areas in Ohio, USA (2004–2008). Standard error and 95% confidence interval estimates can be found next to and below each ψ estimate, respectively.

	2004	2005	2006	2007	2008
North	0.29 (0.06) (0.19–0.41)	0.30 (0.05) (0.20–0.39)	0.30 (0.04) (0.21–0.39)	0.30 (0.04) (0.22–0.39)	0.31 (0.04) (0.23–0.39)
Central	0.05 (0.03) (0.02–0.13)	0.08 (0.02) (0.04–0.13)	0.11 (0.02) (0.07–0.16)	0.14 (0.03) (0.09–0.19)	0.16 (0.03) (0.10–0.22)
South	0.14 (0.04) (0.07–0.24)	0.16 (0.04) (0.09–0.23)	0.18 (0.03) (0.11–0.25)	0.20 (0.03) (0.13–0.26)	0.21 (0.03) (0.15–0.28)

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TABLE 2. Model sets and rankings for evaluating covariate effects on Blanchard's Cricket Frog (*Acris blanchardi*) probability of detection (P), with the models for all other parameters held constant. The dataset is based on 1,807 surveys of 312 sites from 2004–2008. For each model we present the number of parameters (K), Akaike's Information Criterion (AIC), the difference between the model AIC and the best fit model AIC (Δ AIC), and the Akaike weight of the model (w_i). We also present the summed Akaike weights (Σw_i) for each covariate to estimate relative variable importance.

Model	AIC	Δ AIC	w_i	K	Variable	Σw_i
$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), P(\text{time of day} + \text{temperature} + \text{temperature}^2)$	1085.77	0.00	0.2645	7	Time of Day	1.00
$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), P(\text{time of day} + \text{temperature} + \text{temperature}^2 + \text{moon phase})$	1085.91	0.14	0.2466	8	Air Temperature	0.72
$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), P(\text{time of day} + \text{moon phase})$	1087.30	1.53	0.1231	6	Moon Phase	0.51
$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), P(\text{time of day} + \text{temperature} + \text{temperature}^2 + \text{Julian day})$	1087.40	1.63	0.1171	8	Julian Day	0.29
$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), P(\text{time of day} + \text{temperature} + \text{temperature}^2 + \text{Julian day} + \text{moon phase})$	1087.87	2.10	0.0926	9		
$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), P(\text{time of day})$	1088.26	2.49	0.0762	5		
$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), P(\text{time of day} + \text{Julian day} + \text{moon phase})$	1089.28	3.51	0.0457	7		
$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), P(\text{time of day} + \text{Julian day})$	1089.86	4.09	0.0342	6		
$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), P(\text{temperature} + \text{temperature}^2)$	1160.25	74.48	0	6		
$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), P(\text{temperature} + \text{temperature}^2 + \text{moon phase})$	1160.28	74.51	0	7		
$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), P(\text{temperature} + \text{temperature}^2 + \text{Julian day})$	1161.28	75.51	0	7		
$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), P(\text{temperature} + \text{temperature}^2 + \text{Julian day} + \text{moon phase})$	1161.87	76.10	0	8		
$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), P(\text{moon phase})$	1167.58	81.81	0	5		
$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), P(\cdot)$	1168.05	82.28	0	4		
$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), P(\text{Julian day})$	1168.76	82.99	0	5		
$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), P(\text{Julian day} + \text{moon phase})$	1169.24	83.47	0	6		

respectively; Table 1).

In the detection probability (P) models constructed from data from all five years (these included the linear form of Julian day, moon phase, time of day, and the quadratic form of air temperature), time of day was identified as an important variable ($\Sigma w_i = 1.0$). Air temperature during the survey also seemed to have an influence on detection ($\Sigma w_i = 0.72$) but moon phase and Julian day were not influential ($\Sigma w_i = 0.51$ and 0.29 , respectively; Table 2). The overall estimated probability of detection in our surveys was 0.51 ($SE = 0.032$, 95% C.I. = 0.45 – 0.58).

Reflecting the regional variation in occupancy, occupancy models (ψ) with the region covariate performed markedly better ($\Sigma w_i = 1.0$) than those models without it (Table 3). Occupancy was consistently highest in the northern monitoring area, lowest in the central monitoring area, and intermediate in the southern monitoring area (Fig. 2). Occupancy models with the habitat type covariate also performed well ($\Sigma w_i = 0.85$; Table 3). Over all regions and years, occupancy was always highest in lakes (Fig. 2). Cricket frog occupancy of ponds and streams was lower but comparable to one

another, though occupancy among these habitat types varied over time and in different regions.

Our analysis also provided evidence of population turnover during this 5-y period. Overall colonization rates were estimated at 0.04 ($SE = 0.01$, 95% CI = 0.02 – 0.06). Colonization (ψ) models including the region or habitat type covariates performed worse than a model without covariates (Table 4). In contrast, the best model of extinction (ε) included both the habitat type and region covariates ($\Sigma w_i = 0.97$ and 0.90 , respectively; Table 5). The overall estimated extinction rate was 0.07 ($SE = 0.03$, 95% CI = 0.03 – 0.14). Estimated extinction rates in the different habitat types were 0.14 ($SE = 0.05$, 95% CI = 0.07 – 0.26) in ponds, 0.08 ($SE = 0.06$, 95% CI = 0.02 – 0.31) in lakes, and zero (0.00) in streams ($SE = 0.00$).

The eastern-most known population in the northern monitoring area did not change over five years of monitoring. However, the eastern-most known population in the southern monitoring area shifted eastwards by about 4 km during the study. In the central monitoring area, the eastern-most known population shifted eastwards by about 7 km. In agreement with

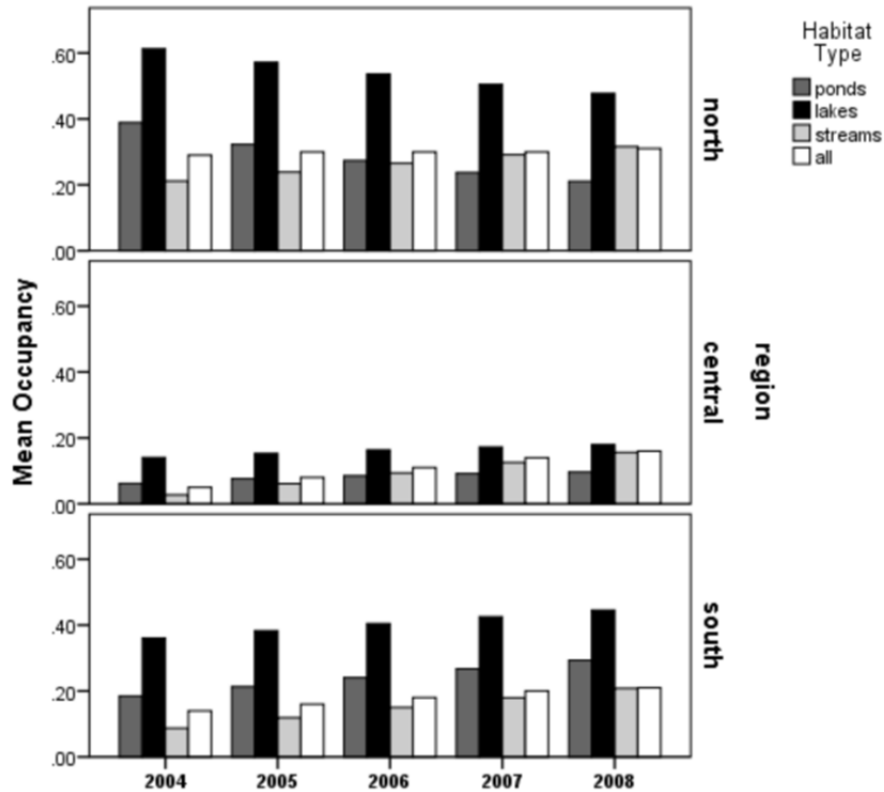


FIGURE 2. Estimated proportion of sites occupied by Blanchard’s Cricket Frogs (*Acris blanchardi*) in each region (panels) and habitat type (bars), 2004–2008. Estimates were taken for the best model in Table 5.

these observations, the estimates of λ suggested that despite turnover, at a regional level, the situation was stable (northern monitoring area average $\lambda = 1.02$) or expanding (central and southern monitoring areas, average $\lambda = 1.34$ and 1.12 , respectively; Table 6). In all regions, λ was highest for stream habitats and lower for ponds and lakes (Table 6).

In the expanded detection probability models for the years 2006–2008 (which added barometric pressure and whether a breeding call playback occurred), the most

supported model contained the covariates time of day, air temperature, Julian day, and playback (Table 7). There is strong evidence that breeding vocalization playbacks positively influenced detection probability ($\Sigma w_i = 0.96$). Estimated detection probability without vocalization playbacks was 0.47 (SE = 0.04). With playbacks, detection probability increased to 0.60 (SE = 0.05). In contrast, there was little evidence to suggest that barometric pressure or moon phase influenced detection ($\Sigma w_i = 0.27$ and 0.28 , respectively; Table 7).

TABLE 3. Model sets and rankings for evaluating covariate effects on Blanchard’s Cricket Frog (*Acris blanchardi*) probability of occupancy (ψ). Models compared here include time of day and the quadratic form of air temperature as these were identified as influential on the probability of detection, with the models for all other parameters held constant. The dataset is based on 1,807 surveys of 312 sites from 2004–2008. For each model, we present the number of parameters (K), Akaike’s Information Criterion (AIC), the difference between the model AIC and the best fit model AIC (ΔAIC), and the Akaike weight of the model (w_i). We also present the summed Akaike weights (Σw_i) for each covariate to estimate relative variable importance.

Model	AIC	ΔAIC	w_i	K	Variable	Σw_i
$\psi(\text{habitat type} + \text{region}), \gamma(\cdot), \epsilon(\cdot), P(\text{time of day} + \text{temperature} + \text{temperature}^2)$	1069.77	0.00	0.8487	11	habitat type	0.85
$\psi(\text{region}), \gamma(\cdot), \epsilon(\cdot), P(\text{time of day} + \text{temperature} + \text{temperature}^2)$	1073.23	3.46	0.1505	9	region	1.00
$\psi(\text{habitat type}), \gamma(\cdot), \epsilon(\cdot), P(\text{time of day} + \text{temperature} + \text{temperature}^2)$	1084.24	14.47	0.0006	9		
$\psi(\cdot), \gamma(\cdot), \epsilon(\cdot), P(\text{time of day} + \text{temperature} + \text{temperature}^2)$	1085.77	16.00	0.0003	7		

The year of last known cricket frog occurrence was significantly more recent in the western part of Ohio than in central Ohio (Mann-Whitney U = 157, $P < 0.001$). The mean year of last known occurrence in western Ohio was 1999 (95% C.I. = 1994–2003, median year = 2004, $n = 31$). The mean year of last known occurrence in central Ohio was 1973 (95% C.I. = 1965–1982, median year = 1970, $n = 31$). The number of unique locality records before 1970 ($n = 158$) was not significantly different in the western (82 records) and central (76 records) portions of Ohio ($\chi^2 = 0.228$, $df = 1$, $P = 0.633$). Considering only unique records before 1960 yields a similar result: 86 total records, 39 from western Ohio, and 47 from central Ohio ($\chi^2 = 0.744$, $df = 1$, $P = 0.393$). See Appendix 1 for a listing of the year of last known occurrence by county.

DISCUSSION

Blanchard’s Cricket Frogs have declined dramatically in Ohio in the last 40 y and much of this decline has been concentrated along their eastern range boundary in the central part of the state. Based on the last known date of occurrence data, this decline probably occurred

in the 1970s. Prior to 1970, there was no significant difference in the number of reported localities in the western and central parts of the state. Despite this large reduction in their geographic range in Ohio, our study suggests that this decline may have slowed, halted, or even partially reversed. One of our monitoring areas (north) showed a stable occupancy pattern over the duration of the study and the two others (central and south) showed increases. The λ estimates also indicate that, at least for the years examined, these sets of populations appear stable or increasing over time ($\lambda > 1.0$). In two of the three monitoring areas, the easternmost known population shifted eastward during the study (there was no net movement in the third). This could suggest the beginnings of an eastward recolonization of some of its unoccupied former range.

While we cannot speculate on the status of Blanchard’s Cricket Frogs beyond the end of our surveys, there seems to be little evidence for further declines in Ohio as of 2008. Since our data were collected from sites randomly selected from those available before surveys began, we believe that these conclusions should be broadly applicable to other similar areas. Further, as our study sites were generally not

TABLE 4. Model sets and rankings for evaluating covariate effects on Blanchard’s Cricket Frog (*Acris blanchardi*) colonization (γ), 2004–2008. Models compared here include time of day and the quadratic form of air temperature (as covariates for detection probability) and habitat type and region (as covariates for occupancy) as these were identified as influential in previous models, with the models for all other parameters held constant. The dataset is based on 1,807 surveys of 312 sites from 2004–2008. For each model, we present the number of parameters (K), Akaike’s Information Criterion (AIC), the difference between the model AIC and the best fit model AIC (Δ AIC), and the Akaike weight of the model (w_i). We also present the summed Akaike weights (Σw_i) for each covariate to estimate relative variable importance.

Model	AIC	Δ AIC	w_i	K	Variable	Σw_i
$\psi(\text{habitat type} + \text{region}), \gamma(\cdot), \varepsilon(\cdot), P(\text{time of day} + \text{temperature}^2)$	1069.77	0	0.6416	11	habitat	0.23
$\psi(\text{habitat type} + \text{region}), \gamma(\text{habitat type}), \varepsilon(\cdot), P(\text{time of day} + \text{temperature} + \text{temperature}^2)$	1072.25	2.48	0.1857	13	region	0.17
$\psi(\text{habitat type} + \text{region}), \gamma(\text{region}), \varepsilon(\cdot), P(\text{time of day} + \text{temperature} + \text{temperature}^2)$	1072.99	3.22	0.1283	13		
$\psi(\text{habitat type} + \text{region}), \gamma(\text{habitat type} + \text{region}), \varepsilon(\cdot), P(\text{time of day} + \text{temperature} + \text{temperature}^2)$	1075.11	5.34	0.0444	15		

TABLE 5. Model sets and rankings for evaluating covariate effects on Blanchard’s Cricket Frog (*Acris blanchardi*) extinction (ε), 2004–2008. Models compared here include time of day and the quadratic form of air temperature (as covariates for detection probability) and habitat type and region (as covariates for probability of occupancy) as these were identified as influential in previous models, with the models for all other parameters based held constant. The dataset is 1,807 surveys of 312 sites from 2004–2008. For each model, we present the number of parameters (K), Akaike’s Information Criterion (AIC), the difference between the model AIC and the best fit model AIC (Δ AIC), and the Akaike weight of the model (w_i). We also present the summed Akaike weights (Σw_i) for each covariate to estimate relative variable importance.

Model	AIC _{ε}	Δ AIC	w_i	K	Variable	Σw_i
$\psi(\text{habitat type} + \text{region}), \gamma(\cdot), \varepsilon(\text{habitat type} + \text{region}), P(\text{time of day} + \text{temperature} + \text{temperature}^2)$	1060.20	0	0.8709	15	habitat	0.97
$\psi(\text{habitat type} + \text{region}), \gamma(\cdot), \varepsilon(\text{habitat type}), P(\text{time of day} + \text{temperature} + \text{temperature}^2)$	1064.64	4.44	0.0946	13	region	0.90
$\psi(\text{habitat type} + \text{region}), \gamma(\cdot), \varepsilon(\text{region}), P(\text{time of day} + \text{temperature} + \text{temperature}^2)$	1067.13	6.93	0.0272	13		
$\psi(\text{habitat type} + \text{region}), \gamma(\cdot), \varepsilon(\cdot), P(\text{time of day} + \text{temperature} + \text{temperature}^2)$	1069.77	9.57	0.0073	11		

TABLE 6. Estimates of the rate of change in occupancy (λ) for each successive pair of years for each region and habitat type. Values of 1.0 suggest stable occupancy patterns; values greater and less than one suggest increasing and decreasing occupancy patterns, respectively. The standard error and 95% confidence interval are given in parentheses next to and below each estimate, respectively.

		2004–2005	2005–2006	2006–2007	2007–2008
North	ponds	0.83 (0.09) (0.65–1.01)	0.85 (0.08) (0.69–1.01)	0.87 (0.07) (0.73–1.00)	0.89 (0.06) (0.77–1.00)
	lakes	0.93 (0.09) (0.75–1.12)	0.94 (0.09) (0.76–1.11)	0.94 (0.08) (0.78–1.10)	0.95 (0.08) (0.79–1.10)
	streams	1.13 (0.06) (1.02–1.25)	1.11 (0.04) (1.03–1.20)	1.10 (0.03) (1.03–1.16)	1.09 (0.03) (1.03–1.14)
	all sites	1.02 (0.04) (0.94–1.10)	1.02 (0.04) (0.95–1.09)	1.02 (0.03) (0.96–1.08)	1.02 (0.03) (0.96–1.07)
Central	ponds	1.23 (0.39) (0.47–1.99)	1.12 (0.19) (0.76–1.49)	1.07 (0.11) (0.86–1.29)	1.05 (0.07) (0.91–1.19)
	lakes	1.09 (0.19) (0.71–1.47)	1.07 (0.14) (0.79–1.35)	1.05 (0.11) (0.84–1.26)	1.04 (0.08) (0.88–1.21)
	streams	2.26 (0.85) (0.59–3.93)	1.54 (0.16) (1.23–1.85)	1.34 (0.06) (1.21–1.46)	1.24 (0.03) (1.18–1.31)
	all sites	1.62 (0.40) (0.83–2.40)	1.34 (0.13) (1.08–1.60)	1.23 (0.07) (1.10–1.36)	1.16 (0.04) (1.09–1.24)
South	ponds	1.15 (0.08) (1.00–1.31)	1.13 (0.06) (1.02–1.24)	1.11 (0.04) (1.03–1.19)	1.10 (0.03) (1.03–1.16)
	lakes	1.06 (0.05) (0.97–1.15)	1.06 (0.04) (0.98–1.14)	1.05 (0.03) (0.98–1.12)	1.05 (0.03) (0.99–1.11)
	streams	1.37 (0.19) (0.99–1.75)	1.26 (0.10) (1.06–1.45)	1.20 (0.06) (1.08–1.31)	1.16 (0.04) (1.08–1.24)
	all sites	1.17 (0.11) (0.95–1.38)	1.13 (0.07) (0.99–1.27)	1.10 (0.05) (1.00–1.20)	1.08 (0.04) (1.00–1.15)

from protected areas but rather were primarily on privately owned land in a typical Midwestern landscape with a heavy human presence, we believe that these patterns are likely reflective of what is actually occurring at the landscape level. Given that we found occupancy and turnover patterns to be region-specific, we suspect that these patterns may differ markedly in other regions. Unfortunately, similar large-scale monitoring data from other areas of its range are currently not available for comparison.

Our models of occupancy suggest that occupancy patterns differed strongly by region. This result is not surprising as the northern monitoring area had consistently higher occupancy throughout the study than either of the other two areas and landscape context is known to be important to the dynamics of amphibian populations (Werner et al. 2009). Interestingly, the northern monitoring area had consistently higher occupancy despite being a more agriculturally intensive region than the other monitoring areas. Thus, while the mechanisms causing the initial declines cannot be definitively identified in this study, decline mechanisms

directly related to agriculture (e.g., habitat loss, impacts from pesticides) are not implicated by our results.

Our probability of detection (0.51) was somewhat lower than those reported in some other studies on *Acris* (Pierce and Gutzwiller 2004; Gooch et al. 2006; Brander et al. 2007; range: 0.66–0.92) but substantially higher than those reported by Walls et al. (2011; range: 0.11–0.25). The prime importance of time of day in our models of detection probability suggests that, despite the results of Lehtinen and Skinner (2006), daytime surveys were typically less effective at detecting Blanchard’s Cricket Frogs than ones later in the day. Therefore, it would seem that future monitoring efforts should concentrate survey effort later in the day (after 1800) for maximum probability of detection.

Our analysis also indicated that broadcasting breeding vocalizations during the survey strongly increased detection probability. These results are probably conservative, as in some surveys Blanchard’s Cricket Frogs were detected calling before the call was broadcast. This playback technique has long been used in surveys for secretive birds and other organisms (e.g.,

TABLE 7. Model sets and rankings for evaluating covariate effects on Blanchard’s Cricket Frog (*Acris blanchardi*) probability of detection (P) with all other parameters held constant. For each model we present the number of parameters (K), Akaike’s Information Criterion (AIC), the difference between the model AIC and the best fit model AIC (Δ AIC), and the Akaike weight of the model (w_i). We also present the summed Akaike weights (Σw_i) for each covariate to estimate relative variable importance. The dataset is 1,188 surveys of 312 sites from 2006–2008 only and are not directly comparable to the model sets presented in previous tables. Only the top 15 models are shown. Jd = Julian day.

Model	K	AIC	Δ AIC	w_i	Variable	Σw_i
P(time of day + Jd + Jd ² + temperature + playback)	9	838.13	0	0.45	Time of Day	1.00
P(time of day + Jd + Jd ² + temperature + playback + barometric pressure)	10	839.99	1.86	0.18	Air Temperature	0.98
P(time of day + Jd + Jd ² + temperature + playback + moon phase)	10	840.05	1.92	0.17	Moon Phase	0.28
P(time of day + Jd + Jd ² + temperature + playback + moon phase + barometric)	11	841.88	3.75	0.07	Julian Day Barometric Pressure	0.92
P(time of day + temperature + playback)	7	843.02	4.89	0.04	Pressure	0.27
P(time of day + Jd + Jd ² + temperature)	8	844.63	6.50	0.02	Playback	0.96
P(time of day + temperature + moon phase + playback)	8	845.01	6.88	0.01		
P(time of day + Jd + Jd ² + playback)	8	846.00	7.87	0.01		
P(time of day + temperature + moon phase + playback + barometric pressure)	9	846.22	8.09	0.01		
P(time of day + Jd + Jd ² + temperature + moon phase)	9	846.55	8.42	0.01		
P(time of day + Jd + Jd ² + temperature + barometric pressure)	9	846.59	8.46	0.01		
P(time of day + playback)	6	846.83	8.70	0.01		
P(time of day + playback + barometric pressure)	7	848.43	10.30	0.00		
P(time of day + Jd + Jd ² + temp + barometric pressure + moon phase)	10	848.49	10.36	0.00		
P(time of day + temperature)	6	848.64	10.51	0.00		
P(.)	4	928.45	90.32			

Conway 2011) but to our knowledge is not used widely in anuran monitoring. Our results (see also Sung et al. 2005; Mannan et al. 2014) suggest that such playbacks may be useful in increasing detection and anuran monitoring programs should consider their use. Many studies have reported on the importance of season (e.g., Weir et al. 2005) on frog calling activity. We found that day of year was not important in the 5-y analysis but was somewhat important in the 3-y analysis. These results confirm that we were surveying at the peak breeding season for Blanchard’s Cricket Frogs in Ohio. Had surveys started earlier in the spring or extended later into the summer, there undoubtedly would have been a stronger seasonal effect. A number of other variables found to be important influences on detection in other studies (e.g., barometric pressure, moon phase; Weir et al. 2005; Saenz et al. 2006; Grant et al. 2009; Steelman and Dorcas 2010) were not important in our study. We attribute these results to species differences in calling behavior.

Analysis of the turnover dynamics of these populations indicated a moderate rate of annual local

extinction and colonization (0.07 and 0.04, respectively). Local extinction rates exceeded the recolonization rate, yet the 95% confidence interval for these estimates overlapped. The magnitude of turnover seems to be within the range of what has been reported for other taxa using similar methods. For example, for a suite of different frog species in Ontario, de Solla et al. (2006) found extinction and colonization rates 1.5 to 19.5% per year. However, Brander et al. (2007) showed much higher colonization rates on average for six species in a Maryland protected area (range 0.77–1.00) compared to extinction rates (range 0.02–0.13). Perhaps substantial annual turnover is not surprising as many amphibians may have metapopulation structure (Marsh and Trenham 2001). Additionally, Blanchard’s Cricket Frogs have very short life cycles (Burkett 1984; McCallum et al. 2011). In a 6-y mark-recapture study, Lehtinen and MacDonald (2011) found no evidence for survival beyond 1 y; this brief life span could further predispose these populations to rapid turnover.

To explain the mysterious decline of Blanchard’s Cricket Frog in the upper Midwest, Lannoo (1998)

argued that permanent water bodies are demographic sinks and that reproduction in these habitats is unsuccessful because of the presence of fish. Less permanent (fishless) aquatic habitats were argued to be sources. The data presented here are the first test of this hypothesis and are indeed suggestive of a source-sink population structure but with an alternative configuration than that envisioned by Lannoo (1998). Our data indicate that permanent aquatic habitats such as lakes were consistently more likely to be occupied than ponds or streams (see also Lehtinen and Skinner 2006). Further, we found that less permanent aquatic habitats (ponds) had relatively high annual extinction rates (overall mean 14%), streams had very low annual extinction rates (overall mean about 0%), and lakes were intermediate (overall mean 8%). The lambda (λ) estimates also support this view with stream habitats always having the most strongly positive occupancy patterns over time. Thus, habitat type appears to strongly influence both occupancy patterns and local extinction rates and permanent aquatic habitats such as streams and lakes are the sources and semi-permanent aquatic habitats like ponds are the sinks. While many other frog species are unable to coexist with fish in permanent aquatic habitats (Kats et al. 1988; Gunzberger and Travis 2005), recent research has identified several mechanisms by which Blanchard's Cricket Frog tadpoles do so (Carfagno et al. 2011).

Source-sink population structure in amphibians has not been extensively studied empirically, but several suggestive examples are available (Hels 2002; Greenberg and Tanner 2005; Martinez-Solano and Gonzalez 2008). If Blanchard's Cricket Frogs have a source-sink population structure and permanent aquatic habitats are sources and semi-permanent ones are sinks, this scenario makes several predictions (assuming habitat quality is static): (1) recruitment should be more consistent and greater on average in permanent aquatic habitats (lakes and streams) than in semi-permanent ones (ponds); (2) dispersal should primarily flow from streams and/or lakes to ponds (not vice versa); and (3) extinction rates should be lower in lakes and streams than ponds. In this study, we have provided evidence for the third prediction but further research is necessary to test the other two. This is a promising area for future work that could greatly aid our ability to understand and predict the dynamics of this species.

The data presented here represent the results of the first large-scale monitoring effort specifically targeted at Blanchard's Cricket Frog. These data suggest that populations of this species are dynamic and vary in meaningful ways both regionally and among different habitat types. At a time when most amphibian conservation news is sobering, it is encouraging that populations of Blanchard's Cricket Frogs in western Ohio are not continuing to decline and there is even

some evidence of recovery, at least as of 2008. However, this conclusion was only reached after substantial field effort and utilizing modern analytical techniques to correct for variation in detection probability. While these data provide an important historical baseline, detecting future changes in space and time will require additional monitoring work and we encourage these activities throughout the range of this species.

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Herpetological Conservation and Biology



Richard M. Lehtinen (“Rick”) received a B.S. degree in Biology from Winona State University, an M.S in Conservation Biology from the University of Minnesota, and a Ph.D. in Biology from the University of Michigan. In addition to his work in the USA, he has conducted studies on the ecology, evolution, and conservation of amphibians and reptiles in Madagascar, Taiwan, and Trinidad and Tobago. He is currently an Associate Professor of biology at the College of Wooster (Ohio, USA). (Photographed by Marcy Campbell).



James R. Witter (pictured here with a Barred Owl, *Strix varia*) is a Naturalist with the Wood County Park District in Perysburg, Ohio, USA. He received a B.A. from The College of Wooster in Biology (2007) where his research focused on the Blanchard’s Cricket Frog in Western Ohio. His interests include outdoor education and bird watching. (Photographed by Lara Simmons).

APPENDIX 1. Dates of last known occurrence in 61 Ohio counties known to historically have Blanchard's Cricket Frogs (*Acris blanchardi*). Numbers indicate museum voucher specimens (CMC = Cincinnati Museum Center, CMNH = Cleveland Museum of Natural History, CM = Carnegie Museum, CW = College of Wooster, DATM = Dayton Museum of Natural History, OSU = Ohio State University Museum, OUZ = Ohio University Zoology collection, UMMZ = University of Michigan Museum of Zoology). Note: these data were assembled in 2006 and may not reflect current distribution patterns.

County	Last Sighting	Part of Range	Source	County	Last Sighting	Part of Range	Source
Adams	2003	Western	CMC 9283	Licking	1969	Central	CM 89134
Allen	1960	Western	OSU 2324	Logan	1997	Western	CMC 6463
Athens	unknown	Central	OUZ 928	Lorain	1961	Central	OSU 2794
Auglaize	2005	Western	CMC, pending	Lucas	2005	Western	CMC 10279
Brown	1971	Western	DATM Z3378	Madison	unknown	Central	OSU 741.3
Butler	2005	Western	CMC 10001	Mahoning	1999	Central	CMC 7679
Champaign	2005	Western	RML, calling record	Marion	1964	Central	OSU 3647
Clark	1999	Western	CMC 7501	Mercer	2000	Western	CMC 7874
Clermont	1998	Western	CMC 7264	Miami	2005	Western	CMC 9929
Clinton	2005	Western	RML, calling record	Montgomery	2005	Western	CMC 10028
Crawford	1964	Central	OSU 4096	Morrow	1940	Central	OSU 2362
Darke	2004	Western	RML, calling record	Ottawa	1970	Central	CW AN241
Defiance	1997	Western	CMC 6602	Paulding	2004	Western	RML, calling record
Delaware	1967	Central	OSU 4085	Perry	unknown	Central	OSU 119.1
Erie	1959	Central	CMNH 1474	Pickaway	1999	Central	CMC 7561
Fairfield	1928	Central	OSU 622	Pike	1967	Central	DATM Z2492
Fayette	1946	Central	UMMZ 111846	Preble	2005	Western	CMC 9942
Franklin	2005	Central	M. Albin, calling record	Putnam	2004	Western	G. Lipps, calling record
Fulton	2005	Western	CMC 10287	Ross	1998	Central	CMC 7112
Gallia	2004	Central	A. Skinner, calling record	Sandusky	1999	Central	CMC 7801
Greene	2005	Western	RML, calling record	Scioto	1973	Central	OSU 4968
Hamilton	2005	Western	CMC 10172	Seneca	1998	Central	G. Lipps, calling record
Hancock	2005	Western	RML, calling record	Shelby	1999	Western	CMC 7438
Hardin	1998	Western	CMC 7280	Union	2001	Central	CMC 7983
Henry	1997	Western	G. Lipps, calling record	Van Wert	1961	Western	OSU 2381
Highland	2004	Western	CMC 9847	Vinton	1998	Central	CMC 7108
Hocking	1972	Central	OSU 4046	Warren	2005	Western	CMC 10041
Huron	1946	Central	OSU 76.3	Williams	1999	Western	CMC 7802
Jackson	2004	Central	A. Skinner, calling record	Wood	2005	Western	RML, calling record
Knox	1940	Central	OSU 2367	Wyandot	1979	Central	OSU 4777
Lawrence	2004	Central	K. Flegel, calling record				