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Original Article

Occupancy Dynamics of Breeding Crawfish Frogs in Southeastern Indiana

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ABSTRACT We studied the occupancy dynamics of breeding crawfish frogs (*Lithobates areolatus*) at 45 randomly selected grasslands across 208 km^2 at Big Oaks National Wildlife Refuge, in southeastern Indiana, USA, during March 2010 and 2011. We developed a suite of hypotheses explaining the relationship between occupancy, detection, and environmental covariates. We fit our hypotheses using multiseason occupancy models, and compared them in an information-theoretic, model-selection framework. Our top model suggested that the detection probability had a positive, linear relationship with time, temperature, and the amount of rain 24 hours before the survey, and had a quadratic relationship with date, which peaked on 19 March. Our top model supported our hypothesis that occupancy probability was positively correlated with grassland size; larger grasslands were more likely to be occupied by crawfish frogs. Based on our results, we recommend that managers conserve large tracts of grasslands near breeding sites. We recommend that in southeastern Indiana crawfish frog-breeding surveys be conducted in mid- to late-March, and that each call point be surveyed for 15 minutes. We provide a model to increase the precision of detection probability estimates for call surveys that target calling crawfish frogs. Published 2012. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS amphibians, call surveys, detection, grassland size, Indiana, *Lithobates areolatus*, multi-season occupancy.

Crawfish frog (*Lithobates areolatus*) populations have declined substantially across their range (Hammerson and Parris 2004, Parris and Redmer 2005). As a result, they have been listed as state-endangered in Indiana and Iowa, USA, and are listed as near-threatened on the International Union for Conservation of Nature red list of threatened species (Christiansen and Bailey 1991, Minton 2001, Hammerson and Parris 2004). They are solitary secretive animals that rely on crayfish burrows for their entire life cycle, with the exception of an abbreviated breeding period in the spring (Smith 1950, Busby and Brecheisen 1997, Hoffman et al. 2010, Heemeyer 2011, Kinney 2011). Because of their secretive nature, detecting crawfish frogs at their burrows is difficult and impractical (Thompson 1915, Smith 1950, Minton 2001, Parris and Redmer 2005). Therefore, assessing population status and trends must be conducted during their short breeding period.

Crawfish frogs breed in ephemeral, temporary, and seasonal wetlands usually in open, damp grasslands, but occasionally in wooded habitat (Minton 2001; Williams et al., in press). Although periodic calling from wetlands can occur for up to 55 days, their peak chorusing period generally lasts <2 weeks during March and/or April (Busby and Brecheisen 1997, Engbrecht 2010). While breeding, adult male frogs make a loud, resonant, snore-like call that can carry up to 1 km and is easily identifiable (Swanson 1939, Minton 2001).

Calling rates by crawfish frogs depend on several temporal and weather covariates, and detection probability is usually <1 (Busby and Brecheisen 1997, Minton 2001, Engbrecht 2010). Occupancy models are popular in amphibian monitoring programs because they allow for imperfect detection, more precise parameter estimates, and improved understanding of population trends (MacKenzie et al. 2006, Mazerolle et al. 2007, Walls et al. 2011). By using occupancy models, we can better understand the influences of the environment on occupancy and detection, as well as other population parameters. Understanding these influences can be used to improve survey efficacy and help identify management priorities. Therefore, we designed crawfish frog call surveys at Big Oaks National Wildlife Refuge (BONWR), Indiana, with 3 specific objectives. They were to 1) to estimate the occupancy, detection, persistence, and colonization probabilities of breeding male crawfish frogs; 2) estimate and rank the support of a priori hypotheses relating environmental covariates to detection probability; and 3) identify physical characteristics or management regimes of grasslands that were associated with crawfish frog occupancy.

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STUDY AREA

We conducted our study at BONWR (208 km^2; 85°25′, 38°57′) in southeastern Indiana. Big Oaks National

Wildlife Refuge was the eastern limit of the crawfish frog range; the next closest confirmed population was 90 km to the west (Monroe County, IN; Engbrecht and Lannoo 2010). Big Oaks National Wildlife Refuge has what is likely the largest assemblage of crawfish frog-breeding sites of any contiguous area in Indiana (see Engbrecht and Lannoo [2010] for species accounts outside BONWR). Big Oaks National Wildlife Refuge was the former site of Jefferson Proving Ground, a U.S. Army military-ordnance testing facility where approximately 25 million rounds of artillery were discharged from 1941 to 1994. To meet their objectives with testing artillery, the U.S. Army maintained a network of >90 grasslands using prescribed fire, disking, mowing, and persistent herbicides. Total grassland area was 2,480 ha ($\bar{x}$ = 35.0 ha; range = 0.5–312 ha). Grasslands were interspersed among forest and shrub cover types. The continuous impact of artillery on grasslands resulted in a dynamic system of artificially created ephemeral, temporary, and seasonal wetlands used by crawfish frogs and other breeding amphibians. When Jefferson Proving Ground closed in 1995, ordnance testing ended, as did the capacity to use the mechanized management tools (i.e., disking and mowing) due to risks with remnant unexploded ordnance.

When BONWR was established in 2000, U.S. Fish and Wildlife Service staff maintained grasslands (i.e., prevented woody encroachment), primarily with prescribed fire or aerially applied herbicides; the only 2 logistically feasible management tools available. Big Oaks National Wildlife Refuge staff burned an average of 3,440 ha/year from 2001 to 2010. Climate at BONWR was characterized as having warm ($\bar{x}$ temp = 22° C), humid summers and cold winters ($\bar{x}$ temp = 1° C). Annual precipitation ranged from 98.8 cm to 180.6 cm between 2004 and 2010. Grasslands were characterized as having poorly drained acidic, clay soils. Vegetation was dominated by broomsedge (*Andropogon virginicus*) and steeplebush (*Spiraea tomentosa*), and to a lesser extent, spike-rush (*Eleocharis tenuis*), early goldenrod (*Solidago juncea*), beard-tongue (*Penstemon digitalis*), narrow-leaved mountain mint (*Pycnanthemum tenuifolium*), boneset (*Eupatorium perfoliatum*), and round-leaved boneset (*E. rotundifolium*). Woody encroachment by black locust (*Robinia pseudoacacia*), sweet gum (*Liquidambar styraciflua*), winged sumac (*Rhus copallina*), persimmon (*Diospyros virginania*), red maple (*Acer rubrum*), and oak (*Quercus* spp.) was common in grasslands.

METHODS

Pre- and Post-Survey Monitoring

Each day, 30 minutes after sunset, for 1 week prior to the start of our sampling, 1–4 observers visited grasslands that had a history of abundant, calling crawfish frogs and opportunistically listened to see if frogs had begun calling. Also, to examine when frogs moved to breeding ponds, we placed minnow traps in >10 breeding ponds to capture frogs upon their arrival. Additionally, this study occurred concurrently with a habitat selection study with telemetered crawfish frogs (Williams et al., in press). Using data from that study, we were able to identify when radiomarked frogs left breeding ponds. When all frogs left the monitored breeding ponds, we concluded that the primary breeding season had ended.

Sampling Design and Data Collection

We used grasslands as our sampling unit to estimate occupancy and detection. We used grasslands instead of breeding ponds because grasslands often contained several breeding ponds that we could not uniquely identify from our call points during surveys (unexploded ordnance precluded us from walking in many grasslands to confirm exact breeding ponds). We randomly selected 45 of the >90 grasslands that were larger than 0.5 ha at BONWR to include in our sample. Grasslands at BONWR had a wide variety of management histories with varying fire and herbicide treatments. We defined the boundaries for each of our grasslands as the grassland area with a unique management history. We did this because we wanted to examine the association between management histories and occupancy by crawfish frogs. Combining adjacent grasslands with different management histories into one sampling unit would have precluded this comparison. Further, our management boundaries always coincided with physical boundaries (i.e., road, creek, forest) because physical boundaries were used as fire breaks for prescribed burns. We named adjacent grasslands with different management histories a grassland complex. After we selected our sample, we selected monitoring points next to grasslands to listen for crawfish frogs. We selected monitoring points in areas we thought would 1) maximize our detection rate (i.e., areas near the center of grasslands or near ponds and other wetlands), and 2) would provide the most complete aural coverage of grasslands. Monitoring points were located on minimal-use gravel roads that were closed to the public during our surveys. We placed monitoring points >1 km apart from each other; this was twice the distance at which we thought we could reliably identify a crawfish frog call (although their calls can be heard from greater distances in favorable conditions; Swanson 1939, Minton 2001). We monitored >1 grassland from monitoring points when possible (i.e., when >1 grassland were adjacent to monitoring points). This resulted in us being able to monitor our preselected, random 45 grasslands from 38 monitoring points. We established 12 routes, each route included 3 monitoring points; with the exception that 2 routes included 4 points. Each of 6 observers monitored 1 route per night. Each point within a route was monitored for 20 minutes before observers moved to the next point. We randomly assigned observers to routes, and the time the observer started each route (30 min, 90 min, or 150 min after sunset). Additionally, each night we randomized the order in which monitoring points were surveyed within a route. Thus, the observer, start time, and call-point order were all random. All routes had to be completed by 0100 hours to be included in the analysis.

Each call point was monitored 5 times/year between 14 and 29 March, 2010 and 2011, which we estimated to be the peak calling period. During previous years (2001–2009) of opportunistic monitoring, we rarely heard crawfish frogs calling outside this period (but see Busby and Brecheisen [1997] and Engbrecht [2010] for chorusing in other areas). Prior to conducting surveys, all observers underwent extensive training, including passing the U.S. Geological Survey, Patuxent Wildlife Research Center, Public Frog Quiz for Indiana (http://www.pwrc.usgs.gov/frogquiz, accessed 24 Jun 2010), and a field test.

At each call point, observers recorded the presence or absence of calling crawfish frogs, the azimuths to calling frogs, and in 2011, they recorded the time they first heard crawfish frogs. In addition, observers collected data on the following sample-specific metrics that we thought might be associated with detection probability: date, start time, temperature, wind (Beaufort scale), cloud coverage, precipitation, and a noise index. We collected data on site-specific covariates including: the size of the grasslands being surveyed, the size of all the grasslands adjacent to, and including our monitored grassland (but with different management histories; i.e., the grassland complex), the burn frequency in each of the grasslands, and whether the grassland was burned or sprayed with herbicide during the year of the survey. We calculated the burn frequency as the number of prescribed fires between 1998 and the sampling period. Grasslands burned during the year of surveys were burned within 1 month prior to surveys. Grassland herbicide treatments consisted of a mixture of Imazapyr, Fosamine, and metsulfuron-methyl (i.e., Habitat®, Krenite®, Lineage®, and Escort® [DuPont, Wilmington, DE]) and surfactants. They were applied using a helicopter during August 2009 and 2010.

Model Development and Analysis

We developed a suite of a priori hypotheses describing the relationship between environmental covariates, detection, and occupancy. We developed these hypotheses from published literature on crawfish frogs, and other amphibians when applicable. We included 13 hypotheses for detection and 7 hypotheses for occupancy.

Detection hypotheses.—We believed that detection probabilities were influenced by 2 categories: temporal variables and weather variables. In addition to these categories, we examined 2 hypotheses presented by previous research. The temporal variables we examined were date, the quadratic form of date (i.e., date^2), and time of night. We hypothesized that calling rates (and thus detection probabilities) were not constant across the breeding season, and that detection probability would have either a positive linear relationship with the date or a quadratic relationship with the date (i.e., gradually increase to a peak, then decrease). We also hypothesized that, during the hours of our surveys (30 min after sunset to 0100 hours), detection probability would increase later at night. Additionally, we hypothesized that all of the temporal metrics could contribute to detection probability, and we included a temporal model with additive combinations of the date, date^2, and time covariates (Oseen and Wassersug 2002, Weir et al. 2005, Saenz et al. 2006, Cook et al. 2011).

Our weather category included models with one covariate for each of the following metrics: precipitation during the survey (Busby and Brecheisen 1997, Saenz et al. 2006, Engbrecht 2010), amount of precipitation 24 hours preceding the survey (Busby and Brecheisen 1997), and temperature (Bragg 1953, Busby and Brecheisen 1997, Minton 2001, Saenz et al. 2006, Engbrecht 2010). In addition to these metrics, we initially considered noise, wind speed, and cloud cover, but because these metrics were highly correlated with rain (0.70, 0.74, and 0.82, respectively) we removed them from the analysis. We hypothesized that detection probability was positively correlated with temperature (Busby and Brecheisen 1997, Oseen and Wassersug 2002, Engbrecht 2010), and positively correlated with the amount of rain in the 24 hours preceding the survey (Busby and Brecheisen 1997, Saenz et al. 2006). We also hypothesized that rain during surveys would affect detection probabilities; however, we were unsure whether rain would have a positive or negative effect. For example, Engbrecht (2010) found that rain during crawfish frog surveys decreased detection probabilities, whereas Busby and Brecheisen (1997) found that rain during surveys increased detection probabilities. Thus, although we examined the correlation between detection probability and rain during surveys, we did not make an a priori prediction on the effect of rain during surveys on detection probabilities, and thus considered this analysis exploratory. We hypothesized that all our weather metrics could be associated with detection probability, and we therefore included a model for the additive combination of all the weather metrics. Finally, we included a global model that included all of our temporal and weather metrics.

Our models examining hypotheses presented in previous research included 2 studies, Busby and Brecheisen (1997) and Engbrecht (2010). Busby and Brecheisen (1997) examined chorusing phenology of crawfish frogs in east-central Kansas, USA, and they found that once chorusing had begun it was positively correlated with rainfall and temperature. Engbrecht (2010) examined detection probability of crawfish frogs in southwestern Indiana, and found that detection was optimized when surveys occurred early in the night, temperatures were $>13^\circ$ C, it was not raining, and there were not any disturbances. Thus, we included models to represent each of these hypotheses. Our last detection model was a no-effects (null) model.

Occupancy hypotheses.—We believed that occupancy by crawfish frogs could be associated with physical characteristics of sites (i.e., grassland size, grassland complex size, topological relief), or management characteristics of sites (i.e., fire or herbicide history). Because crawfish frogs migrate up to 1,020 m between their burrows and breeding sites, we hypothesized that large grasslands provide better habitat (Heemeyer et al. 2012). Thus, we predicted that occupancy probability would be positively correlated with grassland size and that this correlation would be larger than expected based on complete spatial randomness (i.e., a Poisson process in which $Pr[z = 1] = 1 - e^{-\lambda A}$. Similarly, we hypothesized that grassland-complex size would be positively correlated with occupancy. Busby and

Brecheisen (1997) found that crawfish frog occupancy was higher in flatter areas in east-central Kansas. Thus, we hypothesized that variation in elevation would be negatively correlated with occupancy probability. In southeastern Indiana, prescribed fire occurs concurrently with the crawfish frog-breeding season, yet the effect of prescribed fire on crawfish frog occupancy has not been assessed. Thus, we examined the correlation between prescribed fire and occupancy probability. We developed 2 alternative hypotheses for this correlation. First, if prescribed fire caused significant mortality to migrating crawfish frogs, then we expected occupancy probability to be lower in grasslands with higher burn frequencies. Second, if prescribed fire caused negligible amounts of mortalities, then we hypothesized that high burn frequencies would be positively correlated with occupancy probability because prescribed fire prevents woody encroachment in grasslands, resulting in better crawfish frog habitat (Williams et al., in press). Similarly, we wanted to examine whether burning grasslands within 1 month prior to breeding season negatively affected occupancy. Finally, we wanted to examine whether herbicides applied to the growing season before the breeding season reduced occupancy by crawfish frogs.

We combined each of the 13 detection hypotheses with each of the 7 occupancy hypotheses for 91 models. We examined each model using the multi-season occupancy model parameterization in Program PRESENCE (MacKenzie et al. 2006). We approximated the parsimony of each of these models using Akaike's Information Criterion for small samples (AIC_c) and weighed the support of each model using AIC_c weights (ω; Burnham and Anderson 2002). We estimated detection probability (P), occupancy probability (ψ), colonization probability (γ), and covariate values from our top model. We calculated the odds ratios and corresponding 95% confidence intervals for each metric from our top model. If the 95% confidence interval for the odds ratio overlapped 1, we concluded that the metric did not influence occupancy or detection probability. We plotted the metrics that we concluded influenced occupancy and detection probability.

RESULTS

We surveyed grasslands 5 times/year between 14 and 29 March, in 2010 and 2011. We detected crawfish frogs at 22 of the 45 potential grasslands in 2010 and 24 of the 45 grasslands in 2011. Thus, the naïve estimate of occupancy was 0.49 in 2010 and 0.53 in 2011. During pre-monitoring sampling in 2010, crawfish frogs were first detected 4 days before sampling began at one location, and 3 days before at another, but were not detected anywhere else until after surveys started. In 2011, 1 frog was captured in a minnow trap 5 days before sampling began, and 1 frog was captured 1 day before sampling began. We did not hear any frogs calling before our surveys in 2011. In both years, all telemetered frogs left their breeding ponds before the conclusion of the surveys. Thus, we feel the number of days and timing of our surveys reasonably covered the breeding season at BONWR.

The most supported model for crawfish frog occupancy and detection included the site metric grassland size and the sample metrics: date^2, time of night, precipitation during the survey, precipitation in the previous 24 hours, and temperature (Table 1; Fig. 1). This model contained nearly all the Akaike weight (ω; Table 1). Based on this model, detection probability peaked on 19 March, and there was a positive relationship between detection and the following metrics: precipitation during the survey, precipitation in the previous 24 hours, temperature, and time (Fig. 1). The 95% confidence interval for the odds ratio for rain during the survey overlapped 1, and therefore we concluded it did not influence detection probability (Table 2). Given our top model, the mean occupancy estimate for BONWR was 0.50. Occupancy appeared to be highly correlated with grassland size. The odds ratio for grassland size was 1.05 (95% CI = 1.02–1.08). Thus, the probability of occupancy increased by a factor of 1.05 for each 1-ha increase in grassland size (Fig. 2). Mean size for occupied grasslands was 57 ha (range = 11–133 ha), and mean size for unoccupied grasslands was 24 ha (range = 0.5–81 ha). To examine whether the increase in probability associated with larger grassland size was consistent with a Poisson process, we plotted the predicted occupancy probability related to grassland size from our model, and the expected values given a Poisson process (Fig. 2). Relative to grassland size, the occupancy probability from our top model increased at a faster rate than a Poisson process (Fig. 2). However, the confidence intervals for grassland size overlapped the expected values of a Poisson process, and thus our data were insufficiently precise to detect a difference, if a difference existed.

At all sites at which we detected frogs in 2010, we also detected them in 2011. Additionally, at 2 sites where we did not detect frogs in 2010, we did detect them in 2011. The estimated growth rate of occupied grasslands (λ) between 2010 and 2011 was 1.06. The colonization probability (γ) = 0.08 (95% CI = 0.02–0.32), and the persistence ($1 - \varepsilon$) = 1. Based on our modeling procedures, there was no support that detection probability varied between years. In 2011, 66% of crawfish frog calls were heard in $\leq$5 minutes of a survey, 83% were heard in $\leq$10 minutes, and 96% were heard in $\leq$15 minutes of our 20-minute survey.

DISCUSSION

The occupancy probability of crawfish frogs at BONWR was high (0.50) considering their patchy distribution across their range (Hammerson and Parris 2004, Engbrecht and Lannoo 2010). Our data best supported our hypothesis that occupancy probability increased in larger grasslands. The average size of occupied grasslands was almost 2.4 times the size of unoccupied grasslands (57 ha and 24 ha, respectively), and the odds of using a grassland increased by a factor of 1.05 for every 1-ha increase in grassland size. Although the increase in occupancy probability in relation to grassland size was larger than was predicted based on a Poisson process (Fig. 2), the confidence interval overlapped the expected values of a

Table 1. The top 6 ranked models from model-selection procedure examining occupancy and detection hypotheses of breeding crawfish frogs during call surveys at 45 grasslands at Big Oaks National Wildlife Refuge, Indiana, USA, 2010–2011.

Model description[a]	K	$-2 \times \log(L)$	ΔAIC_c	$AIC_c\ \omega$
Ψ(Grassland size) P(Date + Date^2 + Time + Rain + Rain$_{24}$ + Temp)	11	285.35	0.00	1.00
Ψ(Complex size) P(Date + Date^2 + Time + Rain + Rain$_{24}$ + Temp)	11	298.59	13.24	0.00
Ψ(.) P(Date + Date^2 + Time + Rain + Rain$_{24}$ + Temp)	10	300.91	13.56	0.00
Ψ(Burn frequency) P(Date + Date^2 + Time + Rain + Rain$_{24}$ + Temp)	11	299.71	14.36	0.00
Ψ(Relief) P(Date + Date^2 + Time + Rain + Rain$_{24}$ + Temp)	11	300.66	15.31	0.00
Ψ(Grassland size) P(Date + Date^2)	7	309.85	16.5	0.00

[a] Occupancy metrics include the size of the sample grassland (grassland size), the size of all grasslands adjacent to the sample grassland (complex size), the burn frequency between 1998 and 2010 (burn frequency), and the SD of elevation of the grassland sample (relief). The detection metrics include: the day of year (date), the quadratic form of day of year (date^2), the time of night (time), the temperature (temp), if it was raining during the survey (rain), and the amount of rain in the 24 hours preceding the survey (rain$_{24}$). K = the no. of parameters, L = the likelihood, AIC_c = Akaike's information criterion for small samples, ΔAIC_c = the relative difference in AIC_c values from the top-ranked model, and $AIC_c\ \omega$ = AIC_c model wt.

Poisson process and it remains unclear whether crawfish frogs occupy large grasslands disproportionately more than would be expected based on complete spatial randomness (Fig. 2). The smallest grassland crawfish frogs occupied at BONWR was 11.3 ha. Thus, although crawfish frogs could be an area-sensitive species and occupancy and detection increased by the size of the grassland, our data were not conclusive because of the wide confidence interval. Crawfish frog movements could be limited by an unsuitable habitat (e.g., forest or agriculture) matrix surrounding grassland patches, as well as the grassland patch size (Prugh et al. 2008; Roznik and Johnson 2009; Williams et al., in press).

The mean detection probability for our sampling in 2010 and 2011 was 0.45. Our sampling occurred while crawfish frogs were at their breeding ponds, and therefore inference from these results only applies to that period. Detection probability would be much lower outside this period (Engbrecht 2010). Assuming independence between surveys, and a 0.45 detection probability for each visit, then the probability of detecting a frog at least once at an occupied site in 2 surveys = 0.70, in 3 surveys = 0.83, in 4 surveys = 0.91, in 5 surveys = 0.95, and in 6 surveys = 0.97 (Fig. 3). However, our results suggest that these detection probabilities increase when temperatures are >8° C, when it rains >0.3 cm in the previous 24 hours, and when sampling near the peak of the calling season, which was 19 March at BONWR.

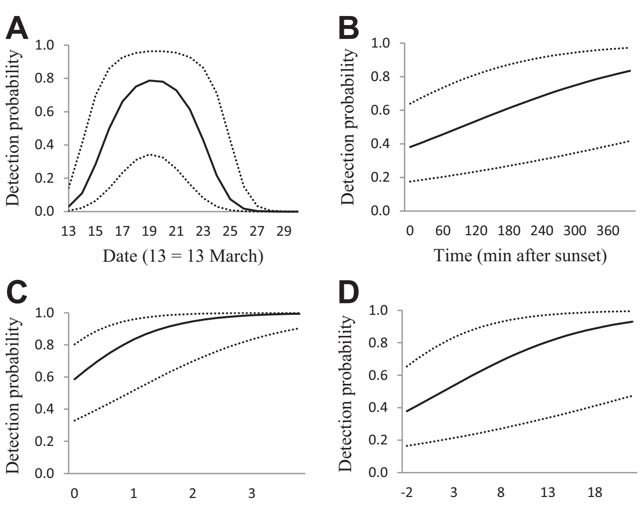

Figure 1. The influence of environmental metrics on detection probabilities of breeding crawfish frogs at Big Oaks National Wildlife Refuge, Indiana, USA, from 2010 to 2011. (A–D) Relationship between detection probability and the following: day of year in March (date), time of night (time), amount of rainfall in the previous 24 hours (rain$_{24}$), and temperature (° C; temp), respectively. The relationships for each variable and detection were calculated with the other 3 variables set at their respective mean values. The mean values were: date = 21 March; time of night = 3 hours 56 minutes after sunset; rain during the past 24 hours = 0.3 cm; temp = 8° C.

Busby and Brecheisen (1997) suggested that the onset of crawfish frog calling behavior was triggered by a combination of appropriate moisture conditions and ambient temperature. Engbrecht (2010) also noted that temperature was associated with calling activity. Although we did not examine factors associated with the onset of breeding, our results also support a positive correlation between chorusing and rain and temperature. Engbrecht (2010) found that rain and disturbances during a survey decrease the detection probability of crawfish frogs. Our data did not support this hypothesis at BONWR. One reason for this difference might be that the frogs Engbrecht (2010) sampled were concentrated into 2 large ponds. Frogs in a concentrated area might be more likely to be affected by a disturbance such as a field crew collecting data nearby (as was the case in Engbrecht [2010]) than frogs with a more scattered distribution (as at BONWR). Further, Engbrecht (2010) noted the correlation between rain and

Table 2. Model estimates for covariates from the function: logit(y) = $\beta_0 + \beta_1, \ldots, \beta_n$ in the best supported model for occupancy and detection of crawfish frogs at Big Oaks National Wildlife Refuge, Indiana, USA, from call surveys conducted in March 14–29, 2010 and 2011.

Covariate	Estimate	SE	Odds ratio (95% CI)
Detection covariates			
Intercept	−45.97	0.54	
Date	4.62	0.02	101.49 (97.11–106.68)
Date^2	−0.12	0.00	0.89 (0.89–0.89)
Time	0.01	0.00	1.37 (1.20–1.57)
Rain	−0.23	−0.23	0.79 (0.27–2.33)
Rain$_{24}$	1.27	0.23	3.56 (2.24–5.60)
Temp	0.13	0.03	3.62 (1.88–6.96)
Occupancy covariates			
Intercept	−1.88	0.68	
Grassland size	0.05	0.02	1.05 (1.02–1.08)

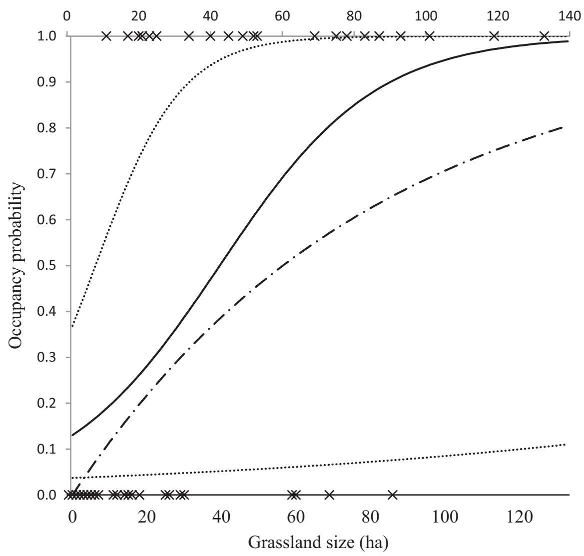

Figure 2. The predicted influence of grassland size on occupancy probability of breeding crawfish frogs, given our model (solid line), and 95% confidence intervals (dotted lines) at Big Oaks National Wildlife Refuge, Indiana, USA, in spring 2010 and 2011. Also shown is the probability that a site was occupied by at least one crawfish frog given a Poisson process ($Pr[z = 1] = 1 - e^{-\lambda A}$; dashed line). The × marks on the 0 and 1 occupancy probability lines are the observed values plotted against grassland size.

disturbance (field crews were often collecting data while it was raining), and thus was unable to determine whether detection was affected by the disturbance, or alternatively, by the rain. Our data suggest that neither of these covariates, relative to other covariates, affected detection probabilities when breeding ponds were scattered within grasslands. That is, although a disturbance at one breeding pond likely affects the calling rates of that pond, other ponds within the same

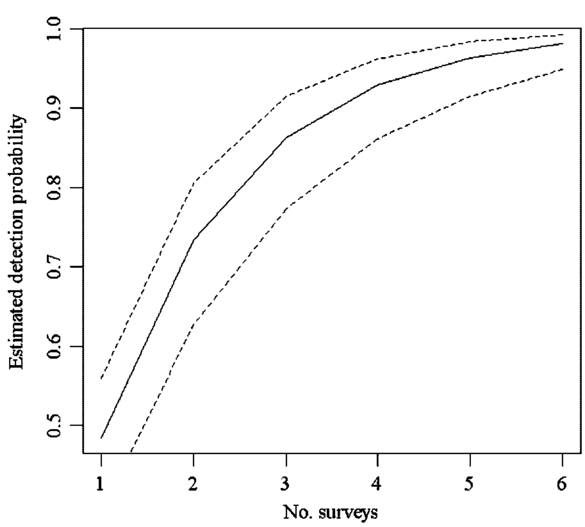

Figure 3. Detection probability and 95% confidence intervals of crawfish frogs in relation to the number of surveys conducted during average conditions at Big Oaks National Wildlife Refuge, Indiana, USA, from 2010 to 2011. The mean values were: date = 21 March; time of night = 3 hours 56 minutes after sunset; rain during the past 24 hours = 0.3 cm; temperature = 8° C.

grassland may not be affected by that disturbance. We note that there may be alternative metrics that we did not measure that contribute to the onset of breeding season. Two possibilities include water temperature and photoperiod.

The onset of chorusing at BONWR began around 14 March, and lasted <2 weeks with the exception of sporadic calling slightly before 14 March. The peak chorusing occurred on 19 March. The breeding-period length estimated from our call surveys was consistent with our trapping data and telemetry data; frogs generally entered and left the breeding ponds between 14 and 28 March. Thus, the crawfish frog-breeding period (as estimated from call surveys, telemetry, and capture histories) was shorter at BONWR in 2010 and 2011 than at other areas where breeding phenology has been examined (Busby and Brecheisen 1997, Engbrecht 2010). Busby and Brecheisen (1997) noted that crawfish frog chorusing occurred between March and early May in east-central Kansas. Engbrecht (2010) noted that it lasted between early March and late April in southwestern Indiana. Intraspecific variation in temporal patterns of breeding is well-documented in other anuran species, and is likely a result of weather conditions, latitude, altitude, and/or habitat aridity (see review in Wells 2007). In general, chorusing was most prevalent in mid- to late-March at all studies that have examined crawfish frog-breeding phenology (Busby and Brecheisen 1997, Engbrecht 2010, this study).

Pierce and Gutzwiller (2004) assessed the effects of survey duration on the detection probabilities of a suite of frog species and found that 94% of calls were detected in the first 15 minutes of a 30-minute survey. Our results that 96% of detections were heard within 15 minutes were similar to their findings. Other studies (e.g., Shirose et al. 1997, Crouch and Paton 2002, Gooch et al. 2006, Engbrecht 2010) have found that detection probabilities have not increased significantly in surveys >5 minutes in length. We found that 30% of detections were heard between 5 minutes and 15 minutes. We believe that this difference may have been due to differing population sizes and distributions at study sites. Calling frogs in ponds with large populations are likely to be detected sooner because there are more of them. The breeding ponds at BONWR were small, widely dispersed, and had as few as one frog detected during our surveys. Thus, a 5-minute sampling period is probably appropriate at sites with large populations, but we would have only detected 66% of calling at our study site, had we used a 5-minute sampling period.

The 2,480 ha of grasslands at BONWR had a history of severe disturbance, including fire, persistent herbicides, disking, mowing, and exploding ordnance. This study quantifies Engbrecht and Lannoo's (2010:71) statement that "crawfish frogs appear to be doing well in areas where, paradoxically, ecosystems were severely degraded in the recent past." It supports their hypothesis that populations can be successful if introduced to areas with a history of severe ecological destruction, provided the habitat includes grasslands, crayfish burrows, and suitable breeding sites. Although neither the fire nor the herbicide history of grasslands was a top model for predicting occupancy, they were indirectly related to occupancy because they affect grassland size. Fire, herbicide, and other disturbances are necessary to suppress or prevent woody-plant succession and maintain crawfish frog habitat (Bragg and Hulbert 1976; Briggs et al. 2002, 2005; Heisler et al. 2003; Williams et al., in press). This is true in a mixed grassland–woodland habitat, with a standing seed source of woody plants surrounding grasslands, as at BONWR (Williams et al., in press). Although it was not a top model, there was a positive correlation between prescribed fire and occupancy and aerially applied herbicides and occupancy. Grasslands at BONWR are burned every 3 years on average, often when crawfish frogs were breeding. Although we did not examine mortality related to prescribed fire, the population appeared to be stable, despite the concurrence of crawfish frog breeding and prescribed fire for >10 years at BONWR. Further, there did not appear to be a negative correlation between herbicide application and crawfish frog occupancy. However, it is important to note that herbicides, such as glyphosate, 2,4-D, and atrazine and their associated surfactants have been shown to affect tadpole survival, diversity, productivity, postmetamorphic juvenile survival, and impair sexual development (Hayes et al. 2002, Relyea 2005*a*, *b*). Thus, the long-term effects of herbicide application on crawfish frogs need to be examined, and managers should use caution when determining the timing and selection of herbicides.

Our data were consistent with Busby and Brecheisen's (1997) observation that populations appear stable where suitable habitat exists. The annual growth rate ($\lambda = 1.06$) was >1, which indicates that the BONWR population was slightly increasing. However, our inference is based on 2 years of data, and we suggest that these results be interpreted with caution. Crawfish frogs can live up to 7 years (Williams et al., in press), so populations might persist for up to that time even with no juvenile recruitment. Thus, if recruitment = 0, population declines would not be detected, potentially, for several years. Likewise, because it takes crawfish frogs ≥1 year to become sexually mature, populations may appear to become extinct although juvenile frogs occur. Our study examined the occupancy and detection of adult, male frogs, and did not consider juveniles or females.

MANAGEMENT IMPLICATIONS

Based on our results, we recommend that crawfish frog call surveys be conducted in mid- to late-March and that detection probability will increase when temperatures are >8° C and it has rained during the previous 24 hours. We recommend that surveys be conducted for 15 minutes to increase the probability of detecting small populations. Our results suggest that large grasslands had higher occupancy rates, and we recommend increasing grassland size for crawfish frog management. Further, areas with a high degree of disturbance that have large grasslands and suitable breeding sites and crayfish burrows would likely be good candidate sites for repatriation. There did not appear to be a negative trend in occupancy and prescribed fire, despite a 70-year history of prescribed fire at BONWR and we recommend its use for preventing woody succession in crawfish frog habitat. Likewise, herbicide application did not appear to be correlated with reduced occupancy. However, the use of aerial–herbicide application is not as well-documented and should be used with caution, or under an adaptive-management framework in which timing and the type of chemicals are carefully selected.

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