Trend estimation and effects of landscape composition on the distribution of Illinois chorus frogs (*Pseudacris illinoensis*) in Illinois

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Executive summary

Illinois chorus frogs (*Pseudacris illinoensis*) occur as a genetically distinct population in Illinois and are threatened by the loss of sand prairie habitat and ephemeral wetlands. The Illinois Department of Natural Resources initiated a long-term monitoring plan in 2015 at 95 sites (sampled at least once annually) to track changes in the distribution of *P. illinoensis*. In this report, I examine spatial and temporal variation in occupancy and detection probability from the first eight years of monitoring data (2015–2022). I used a multi-season occupancy model with Bayesian inference to make the conclusions and recommendations below. It is important to stress that monitoring sites were chosen within areas identified as having suitable habitat for *P. illinoensis*. Thus, all conclusions and recommendations based on my analyses are generalizable only to the statistical population encompassing suitable habitat for *P. illinoensis*.

- Analysis of the eight years of detection data shows it is unlikely that the distribution of *P. illinoensis* is decreasing within the sampled area. Occupancy estimates were around 60% when surveys started in 2015, and occupancy estimates have been >70% since 2019. Statistically there was weak support for an increase in *P. illinoensis* occupancy over the eight years of sampling ($beta_{year}$ = 0.49, 95% credible interval = 0.00 – 1.04). Changes in occupancy may be due to true extinctions and colonizations or annual variation in breeding activity.

- *P. illinoensis* occupancy was related to landscape composition. Occupancy was positively related to the proportion of pond cover intersecting with sandy soils in the surveyed area. Construction of ephemeral ponds in sandy soils may be a useful target for habitat restoration. Pond cover at the section scale was more important for explaining variation in occupancy than pond cover at larger spatial scales (including areas surrounding the site of interest).

- Overall detection probability was 0.57 (95% credible interval = 0.37 – 0.76) when holding all detection covariates at their mean.

- Detection probability depended strongly on the observer conducting chorus breeding surveys, with observer-specific detection probabilities ranging from 0.12 to 0.92. Observer variation in detection probability was not related to performance on a quiz on identifying *P. illinoensis* calls. Some of the observer variation may be due to spatial variation in abundance (which affects chorusing) or conditions that interfere with hearing *P. illinoensis* calls.

- Detection probability was greatest early in the breeding season and sharply declined as the breeding season progressed.

- Rainfall one day prior to surveys was more important for explaining variation in detection probability than rainfall measured on the day of surveys or two days prior to surveys.

- Detection probability was positively related rainfall, but only when evening temperatures were moderately warm. For example, there was no relationship between detection probability and rainfall when temperature was 45 F, but detection probability increased with rainfall when temperature was 60 F.

- As a default strategy I recommend that two surveys continue to be performed at each site annually. However, given that detection probability declines with date, observers should consider starting surveys earlier than in the past, potentially as early as mid-February at some sites. When starting surveys early in the season, observers should try to target evenings with temperature above freezing and when there have been recent rains. I recommend encouraging observers to perform a third survey when *P. illinoensis* is not detected during the first two surveys, and particularly if observers start surveys earlier than in the past, or if initial surveys are conducted during suboptimal conditions (low temperature, little rainfall).

- I recommend observers record two additional variables during surveys: 1) the number of vehicles that pass by the listening post during the survey, and 2) the observer's opinion on whether noise interfered with detecting *P. illinoensis* during the survey.

1. Introduction

Illinois chorus frogs (*Pseudacris streckeri illinoensis*, hereafter "*P. illinoensis*") occur as isolated populations in Missouri, Arkansas, and west-central and southwestern Illinois (Conant and Collins 1991). Phylogeographic evidence based on nuclear and mitochondrial DNA indicates that a historical refugium existed for *P. streckeri/illinoensis* in central Texas, whereas *P. illinoensis* diverged from *P. streckeri* more recently (Barrow et al. 2015). The Integrated Taxonomic Information System recognizes *P. illinoensis* as a distinct species.

P. illinoensis occurs in sandy soils in sand prairies and agricultural fields (Brown and Rose 1998). Adults are terrestrial and migrate to ephemeral, fishless wetlands to breed in early winter and spring. *P. illinoensis* population declines are related to the loss and fragmentation of sand prairies and breeding wetlands associated with agriculture (Tucker 1998, Trauth et al. 2006, Illinois Natural History Survey 2017). *P. illinoensis* is listed as "threatened" in Illinois and "rare" in Missouri, and it is under review by the U.S. Fish and Wildlife Service for federal listing under the Endangered Species Act (Department of the Interior, Fish and Wildlife Service 2015).

In Illinois *P. illinoensis* is known to occur in sandy soils along the Illinois River corridor, near the Mississippi River in Madison county, and near the junction of the Ohio and Mississippi rivers in southern Illinois (Illinois Natural History Survey 2017). Genetic evidence shows the northern and southernmost populations are strongly diverged, indicating little ongoing gene flow (Barrow et al. 2015). Most populations on record occur in the northernmost region, and these populations tend to have low genetic diversity, suggesting ongoing declines (Illinois Natural History Survey 2017).

A rangewide pilot study was conducted to examine strategies for long-term monitoring of the *P. illinoensis* distribution in Illinois based on chorus breeding surveys (Hulin et al. 2015). Based on occupancy data from the pilot study, Cosentino (2014) showed annual sampling of 75-90 sites would lead to high statistical power to detect 30-50% declines in occupancy. In 2015, the Illinois Department of Natural Resources initiated a program to monitor occupancy at 95 locations across the range of suitable habitat for *P. illinoensis* in Illinois. Using the first three years of monitoring data (2015-2017), Cosentino (2018) showed average detection probability during surveys was 0.6 and varied significantly among observers. Detection probability also varied with conditions during surveys and was greatest early in the breeding season during warm, wet nights with low winds. After accounting for imperfect detection probability, Cosentino (2018) found *P. illinoensis* occupancy was stable with 61-63% of sites occupied during 2015-2017.

In this study I expand the analysis of occupancy and detection probability to include eight years of monitoring data from 2015 to 2022 and to explore additional sources of spatial and temporal variation in occupancy and detection. My specific objectives were to:

1) Test for a linear trend in *P. illinoensis* occupancy across the 8 years of sampling.
2) Test whether *P. illinoensis* occupancy is related to landscape composition, specifically the extent of depressions, hydric soils, ponds, and forest at different spatial scales.
3) Identify predictors of detection probability during surveys.

2. Methods

2.1. Data source

All data used in this report was supplied by the Illinois Department of Natural Resources.

2.2. Study area and surveys

The statistical population of interest for monitoring *P. illinoensis* was suitable habitat within the following counties in Illinois: Alexander, Cass, Mason, Menard, Morgan, Scott, and Tazewell. A GIS-based habitat model was generated for *P. illinoensis* based on the presence of hydric soils, sandy soils, and wetlands for breeding (Hinz et al. 2011, Hulin et al. 2015). Survey sections (1.6 x 1.6 km; 2.59 km^2) were randomly selected within suitable habitat resulting in 95 sections clustered within 10 survey routes (Fig. 1).

Each section was surveyed annually between 2015 and 2022. Sections were surveyed up to two times in each year between February 26 and May 2. Surveys were performed between 5:03 PM and 1:06 AM. During each survey, observers drove along roads along the perimeter of each section and make at least one stop to listen for chorusing *P. illinoensis* within the section (i.e. "listening posts"). Observers conducted chorus surveys for five minutes at each listening post. If *P. illinoensis* is detected at the first post, no further posts are surveyed. Additional posts may be surveyed if *P. illinoensis* is not detected at the first post. There were 15 total observers. Of the 1214 total surveys performed across the eight years, 1172 were performed by a single observer and 42 were performed by two observers working together. Observers recorded the date and time of the survey, number of listening posts at each section, as well as air temperature, humidity, wind level, and moonlight presence during each survey. Wind was recorded on an ordinal scale from 1 (calm) to 5 (fresh breed; >18 mph). Rainfall was recorded for each section from nearby weather stations. Rainfall was recorded separately for the day of each survey, one day before each survey, and two days before each survey.

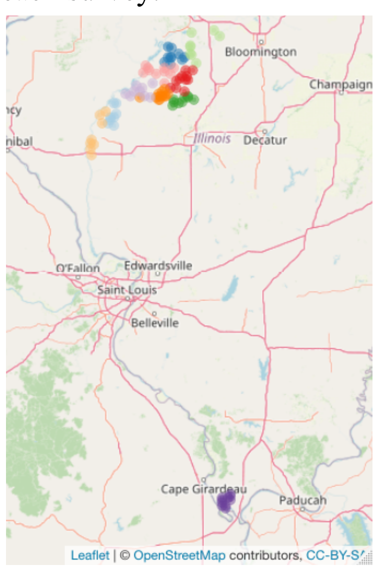

Figure 1. Map of sections surveyed for Illinois chorus frogs (*Pseudacris illinoensis*) between 2015 and 2022. Colors represent different routes assigned to observers.

2.3. Spatial covariates

The proportional cover of four land cover variables was quantified for each section: depressions, hydric soils, standing water, and forest. Depressions were classified from LiDAR-based terrain models as sinks with no surface water flow. Hydric soils were identified from the Illinois chorus frog habitat model as hydric soils within 90 m of sandy soils (Hinz et al. 2011, Hulin et al. 2015). Ponds were also identified from the Illinois chorus frog habitat model as areas of standing water up to 2.5 acres and with a 90-m buffer intersecting sandy soils. Forest cover was classified from LiDAR-based digital terrain and surface models. These land cover variables were quantified at three spatial scales (Fig. 2): 1) each section, 2) each section plus sections immediately adjacent to each surveyed section (hereafter "Buffer1"), and 3) the area encompassing Buffer1 plus the sections immediately adjacent to sections included in Buffer1 (hereafter "Buffer2"). Buffer1 encompasses a square buffer 2.41 km from each section's centroid, and Buffer2 encompasses a square buffer 4.02 km from each section's centroid.

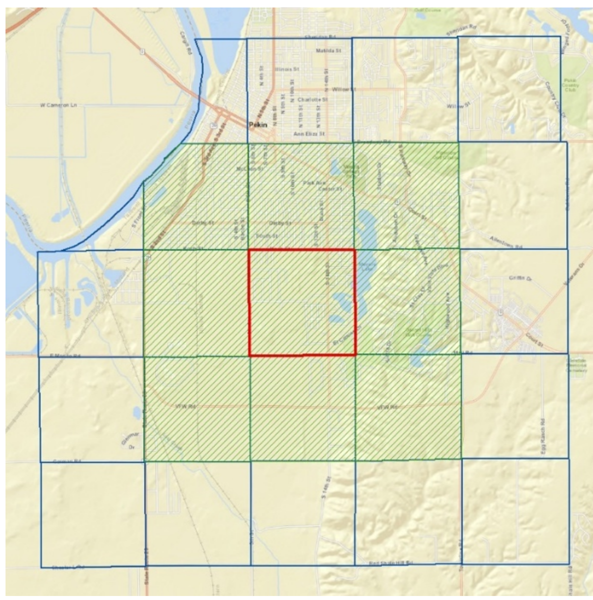

Figure 2. Example map of a 1.6 x 1.6-km survey section (red) and surrounding sections used to quantify land cover at different spatial scales. Hatched sections represent Buffer1, and open and hatched sections together represent Buffer2. Buffers were cut off at rivers. Map supplied by the Illinois Department of Natural Resources.

2.4. Statistical analysis

I used single-species, multi-season occupancy models to accomplish three goals: 1) estimate occupancy of survey sections by *P. illinoensis* each year and test for a linear trend in occupancy over time, 2) test whether occupancy is related to land cover covariates at different spatial scales (Section, Buffer1, Buffer2), and 3) identify predictors of detection probability during surveys. The multi-season occupancy model is used to jointly estimate latent occupancy (z_{ik}) and detection probability (p_{ijk}) based on repeated detections j in each year k at each section i (y_{ijk}). I defined the latent occupancy as $z_{ik} \sim Bernouilli(\psi_{ik})$, where ψ_{ik} is the probability of occurrence at site i during year k. To test how *P. illinoensis* occupancy varies over time and with land cover variables, I fit a submodel defined as:

$$\text{logit}(\psi_{ik}) = \beta 0_{ik} + \beta 1_i{*}\text{depression}_i + \beta 2_i{*}\text{hydric}_i + \beta 3_i{*}\text{pond}_i + \beta 4_i{*}\text{forest}_i + \beta 5_i{*}\text{year}_{ik} + w_i{*}\text{route}_i + \eta_k{*}\text{year}_k,$$

where $\beta 0$ represents the intercept, $\beta 1\text{-}4$ represent slopes for the effects of land cover variables, β_5 represents the linear trend, w_i represents a zero-mean random effect of route (to account for the clustering of sections within routes), and η_k represents a zero-mean temporal random effect of year.

I described the repeated detections of chorus frogs as $y_{ijk} \sim Bernouilli(z_{ik}p_{ijk})$. I fit a submodel of detection probability defined as

$$\text{logit}(p_{ijk}) = \alpha 0_k + \alpha 1_{ijk}{*}\text{temperature}_{ijk} + \alpha 2_{ijk}{*}\text{rain}_{ijk} + \alpha 3_k{*}\text{temperature}_{ijk}{*}\text{rain}_{ijk} + \alpha 4_k{*}\text{date}_{ijk} + \alpha 5_{ijk}{*}\text{wind}_{ijk} + \alpha 6_{ijk}{*}\text{posts}_{ijk} + w_{ijk}{*}\text{observer}_{ijk},$$

where $\alpha 0$ represents the intercept, $\alpha 1\text{-}6$ represent fixed effects of conditions during survey (temperature, rain, wind), Julian date, and number of listening posts, and w represents a zero-mean random effect of observer. I included an interaction effect between temperature and rain to test whether the effect of rain on detection probability depended on temperature. I used a binary classification for wind, distinguishing between nights with low wind (1-4 on the ordinal scale) and high wind (fresh breeze, category 5 on the ordinal scale). Number of listening posts was also defined categorically as one versus more than one listening post. Observer was defined as either the single individual or pair of individuals conducting surveys. There were $n = 14$ observer categories using this classification.

I fit three occupancy submodels using land cover variables quantified from either the section, Buffer1 or Buffer2 spatial scales. I also fit three detection submodels using either rainfall quantified on the day of each survey, one day before surveys, or two days before surveys. I fit all combinations of these occupancy and detection submodels for a total of nine occupancy models.

I used the *spOccupancy* package (Doser et al. 2022) in *R* (R Core Team 2020) to fit the models with a Bayesian approach with Markov chain Monte Carlo. All continuous covariates were standardized prior to fitting the models, and missing observations for detection covariates were mean-imputed. I fit the models with noninformative prior distributions for all regression coefficients (mean = 0, variance = 2.72) and an inverse-Gamma function with shape = 1 and scale = 1 for the random effects. For each model, I ran three chains, each with 1000 batches of 100 iterations (100,000 total iterations), discarding the first 80,000 iterations as burn-in. I thinned the remaining iterations by 20. This resulted in 3000 iterations to describe the posterior distribution of each parameter. I used the Gelman-Rubin statistic to examine convergence of parameter estimates (R-hat < 1.1; Gelman and Hill 2007).

I first used WAIC to compare the relative support of the nine models with different versions of rainfall as a detection covariate and spatial scales for occupancy covariates. I selected the most-supported model (lowest WAIC) and assessed goodness of fit with a Freeman-Tukey test and

Bayesian p-value. I quantified 95% credible intervals (CI) for each parameter and focused my discussion on parameters with CIs that excluded zero.

3. Results and Discussion

The total number of sections surveyed in each year ranged from 10 in 2020 to 93 in 2021 and 2022 (median = 81.5 sections surveyed per year). When sections were surveyed in a given year, they were generally surveyed twice. The number of sections surveyed only once each year ranged from 0 2021 and 2022 to 35 in 2019 (mean = 7.5 sections surveyed only once). The mean naïve occupancy probability (not adjusted for imperfect detection) across years was 0.41 and ranged from 0.26 in 2016 to 0.75 in 2020.

The most supported occupancy model included land cover covariates measured at the section scale and rainfall measured one day prior to surveys (Table 1). Models using rainfall one day before surveys represented the three-most supported models, and models using landscape variables at the section scale were either more supported or competitive with models with landscape variables at larger spatial scales. The most supported model with landscape covariates at the section scale and rainfall measured one day prior to surveys had good model fit (Bayesian p-value = 0.30) and was selected for all further analysis and interpretation.

Table 1. Model selection statistics for nine occupancy models of *Pseudacris illinoensis* that varied in spatial scale for land cover covariates (section, Buffer1, Buffer2) and timing of rainfall data (day of survey, one day prior, two day prior).

Land cover spatial scale	Rainfall	WAIC	deltaWAIC
Section	One day prior	1145.10	0.00
Buffer2	One day prior	1149.33	4.23
Buffer1	One day prior	1151.32	6.22
Buffer2	Day of survey	1153.70	8.60
Section	Day of survey	1153.92	8.82
Buffer1	Day of survey	1154.24	9.14
Section	Two days prior	1159.73	14.63
Buffer2	Two days prior	1160.44	15.34
Buffer1	Two days prior	1162.22	17.12

The occupancy submodel showed there was a marginally significant increase in overall occupancy between 2015 and 2022 (Fig. 3). Although the trend estimate was not quite significant at the 95% confidence level, it is very likely that the distribution of Illinois chorus frogs is either stable or increasing, and is unlikely to be decreasing within the sampled population. It is important to note that changes in distribution do not necessarily represent true extinction and colonization events, as some annual changes in occupancy status may represent local populations skipping breeding seasons or resuming breeding after a skipped season. Notably the annual estimates in occupancy were substantially greater than naïve estimates, demonstrating the importance of using models that account for imperfect detection to estimate occupancy.

The occupancy model showed *P. illinoensis* occupancy was positively related to pond cover (Fig. 4) but not to cover of depressions, hydric soils, or forest cover at the section scale (Table 2). This finding suggests that restoration of small, temporary pools that intersect with sandy soils may be particularly advantageous for facilitating *P. illinoensis* recovery. I suggest conducting breeding surveys in areas that would be considered for restoration (e.g., sections with low coverage of ponds that intersect with sandy soils) prior to pond construction to establish baseline conditions for long-term monitoring of restoration success.

Table 2. Parameter estimates and 95% Bayesian credible intervals (CI) for fixed effects on *Pseudacris illinoensis* occupancy and detection probability. Includes estimated means, lower 95% CI bound (95% LCI), and upper 95% CI bound (95% UCI) across 3,000 iterations of the Bayesian occupancy model.

Response variable	Parameter	Mean	95% LCI	95% UCI
Occupancy	Intercept	1.03	-0.56	2.71
	Depression	-0.28	-0.69	0.08
	Hydric	-0.31	-0.75	0.17
	Pond	1.18	0.53	1.98
	Forest	0.12	-0.36	0.75
	Year	0.49	0.00	1.04
Detection	Intercept	1.17	0.32	2.03
	Temperature	0.26	0.06	0.47
	Rainfall	0.31	0.04	0.62
	Temperature*Rainfall	0.42	0.20	0.67
	Date	-0.68	-0.96	-0.40
	Wind	-0.64	-1.39	0.07
	Listening posts	-1.90	-2.39	-1.40

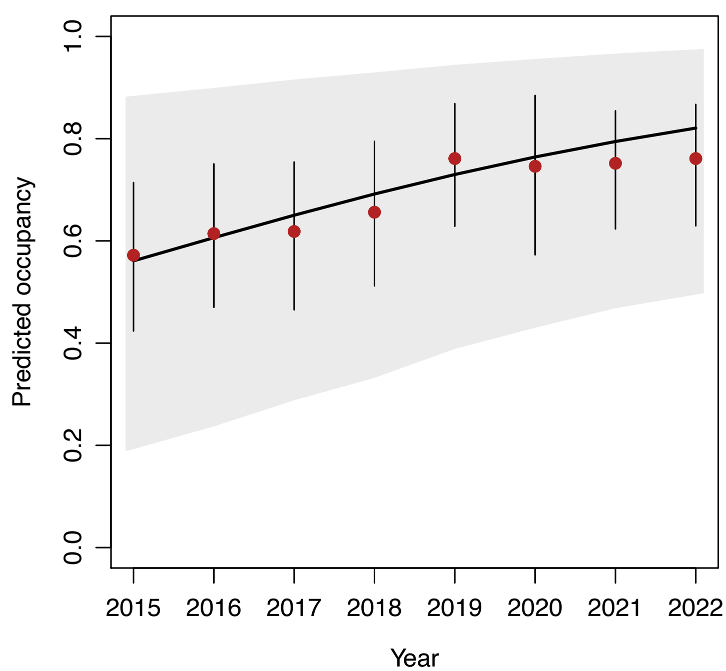

Figure 3. Relationship of *Pseudacris illinoensis* occupancy across all sections to year of sampling. Red circles represent point estimates of occupancy in each year, vertical error bars represent 95% credible intervals for the estimate of occupancy in each year, and shaded area represents the 95% credible interval for the linear trend.

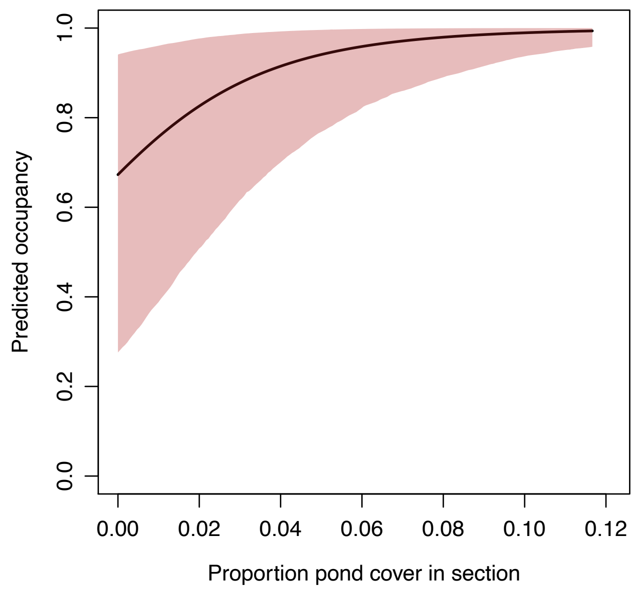

Figure 4. Relationship of *Pseudacris illinoensis* occupancy to the proportion of pond cover in each section. Shaded area represents the 95% credible interval for the linear trend.

In addition to the fixed effects of year and pond cover on occupancy, there was a strongly significant random effect of route (mean = 6.02, 95% CI = 1.27 – 20.14) and a significant random effect of year (mean = 0.31, CI = 0.04 – 1.33). *P. illinoensis* occupancy was greatest along the Olive Branch, Havana/Easton, and Arenzville routes and lowest along the Greenview route (Fig. 5). Occupancy estimates along the Green Valley/Mackinaw route were highly uncertain, likely because of missing detection data (no surveys in 2018 and 2020 and five of eight sections with no surveys in 2016) and low detection probability (only two detections across 89 total surveys). With respect to variation over time, occupancy was consistently greater in 2019-2022 than 2015-2018 across routes (Figs. 3, 5). Occupancy estimates in 2020 were often high due to most routes not being surveyed (Figs. 3, 5).

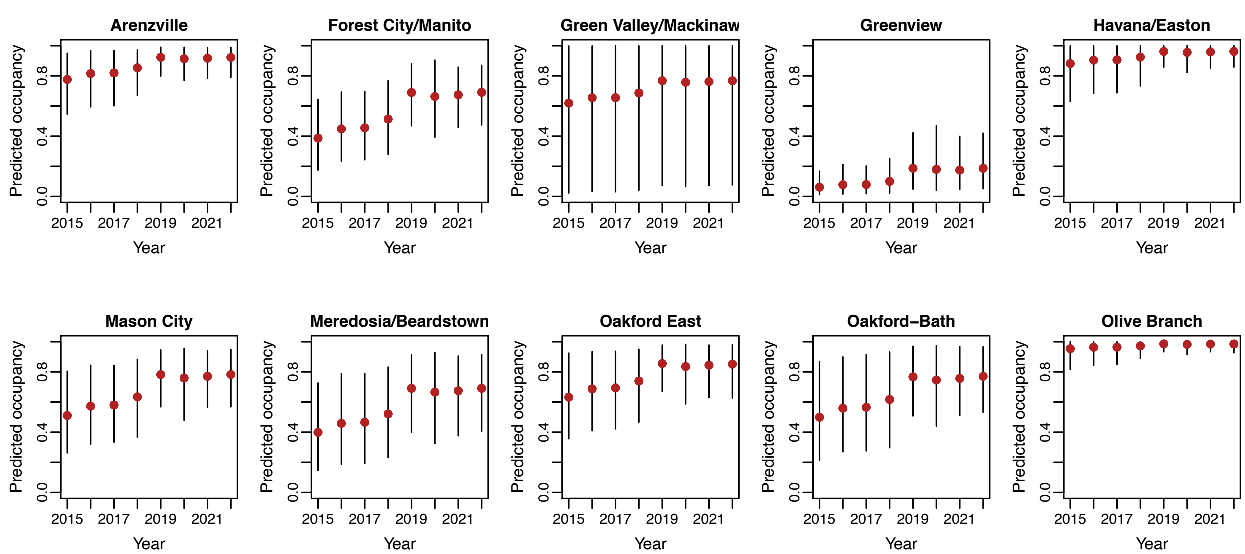

Figure 5. Yearly occupancy estimates of *Pseudacris illinoensis* for each sampled route. Error bars represent 95% credible intervals.

The mean detection probability when holding all detection covariates at their mean and ignoring variation due to observer was 0.57 (95% CI: 0.37 – 0.76). This is consistent with the overall detection probability estimated after the first three years of monitoring data (0.60, Cosentino 2018). However, there was substantial variation in detection probability among surveys. First, there was a significant random effect of observer (mean = 2.33, 95% CI: 0.68 – 5.68), indicating that detection probability varied among observers (Fig. 6). Some of the variation among observers may reflect variation in intrinsic ability to detect chorus frogs, although there was no relationship between the estimated detection probability for each observer and score on a quiz to assess ability to accurately identify Illinois chorus frog calls (Fig. 7). Observers are assigned to routes that vary in spatial location, so any component of the detection process that varies spatially can contribute to observer variation in detection probability. For example, spatial variation in *P. illinoensis* abundance (that affects strength of chorus) or conditions that affect observer's ability to hear chorusing (e.g., vehicular traffic) likely contribute to observer variation in detection probability. To distinguish among these hypotheses, I recommend observers record the following for each survey: 1) number of cars that pass by during surveys, and 2) whether or not noise significantly interfered with the observer's ability to hear a chorus (e.g., Cosentino et al. 2014).

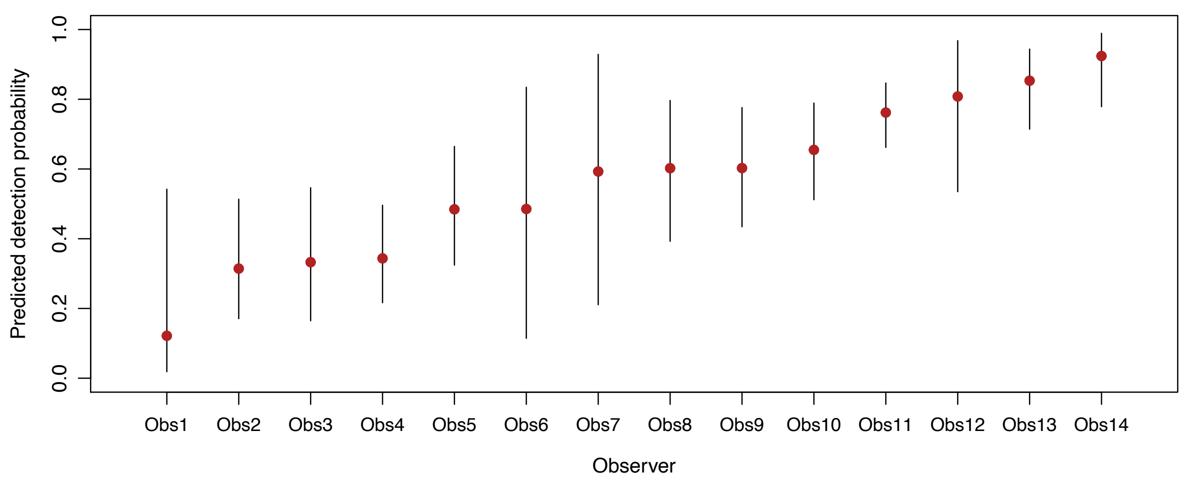

Figure 6. Estimated detection probability of *Pseudacris illinoensis* during surveys for each observer. Observers are indicated with generic codes. Error bars represent 95% credible intervals.

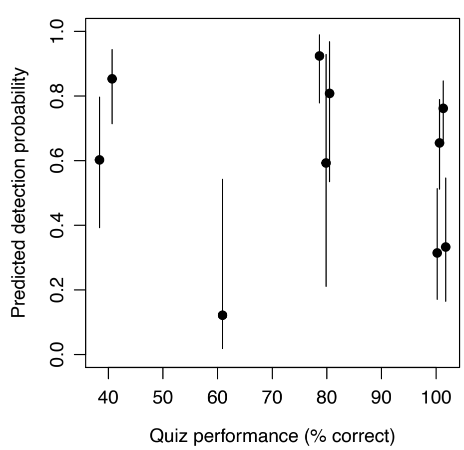

Figure 7. Relationship of predicted detection probability for each observer to performance on a quiz on accuracy of identifying *Pseudacris illinoensis* calls. Quiz performance represents the percent of correct identifications based on five audio recordings of calls. Predicted detection probabilities are from an occupancy model with a random effect of observer (Fig. 6). Error bars represent 95% credible intervals. There was no significant relationship between detection probability and quiz performance based on a simple linear regression not accounting for the uncertainty in detection probability estimates (beta = -0.001, SE = 0.004, t = -0.38, P = 0.72, R^2 = 0.02).

There were three additional findings from the detection submodel. First, there was a significant interaction effect between temperature during surveys and rainfall one day before surveys. Detection probability was generally greatest when temperature was high and rainfall was high, but the positive effect of rainfall on detection probability was only evident when temperature was high (Fig. 8). Rainfall is important for filling breeding pools and likely as a signal to *P. illinoensis* adults to begin breeding in spring, but the effect of rainfall is temperature dependent. Chorusing is likely limited during rainy conditions when temperatures are cool, potentially due to energetic constraints. Rainy conditions on cold nights also likely occur early in the breeding season, potentially before breeding pools have filled, which would lead to low detection probability. In any case, detection probability can be maximized (>0.7) by targeting days with at least 0.2 inches of rain in the previous day and evening temperatures >60 F.

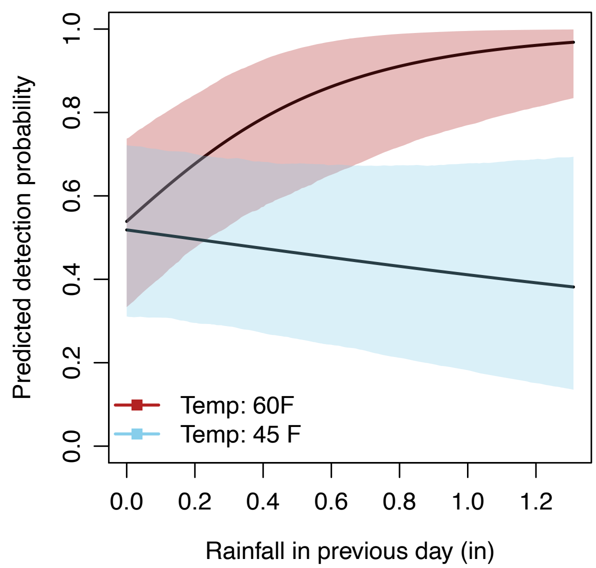

Figure 8. Relationship of detection probability of *Pseudacris illinoensis* during surveys to rainfall in the previous day at warm (60 F) and cool (45) temperatures. Shaded areas represent 95% credible intervals.

Second, detection probability was negatively related to Julian date (Fig. 9). The relationship between detection probability and date was stark, with detection probabilities averaging around 0.8 in late February and early March and <0.4 in April. It may be fruitful to start surveys earlier than in the past, targeting nights that are relatively warm and wet for the time of year. Although temperature is generally lower earlier in the breeding season, it is important to note that the relationship between temperature and survey date is weak ($r = 0.20$), and there are evenings with relatively moderate temperature (>50 F) early in the season (e.g., early March; Fig. 10). Moreover, *P. illinoensis* is known to begin breeding early in the season when temperature is above freezing, and even when some snow remains on the ground (Brown and Rose 1988). *P. illinoensis* chorusing may be starting earlier than expected by observers, and encouragement to begin surveys earlier than in the past may be prudent, potentially as early as mid-February at some sites (Brown and Rose 1988).

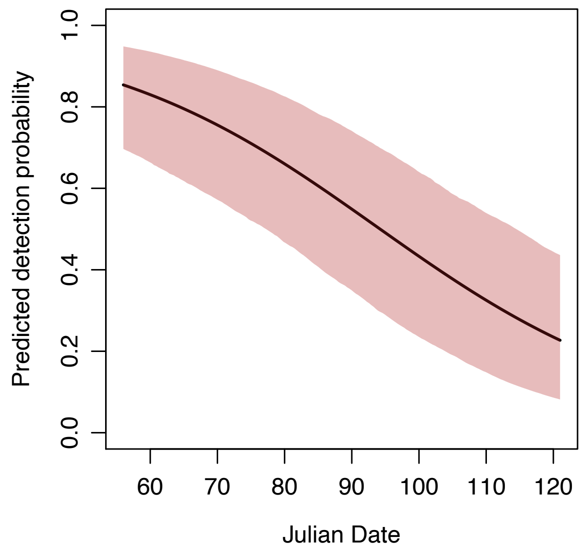

Figure 9. Relationship of detection probability of *Pseudacris illinoensis* during surveys to Julian date. The first Julian date corresponds to February 26. Shaded areas represent 95% credible intervals.

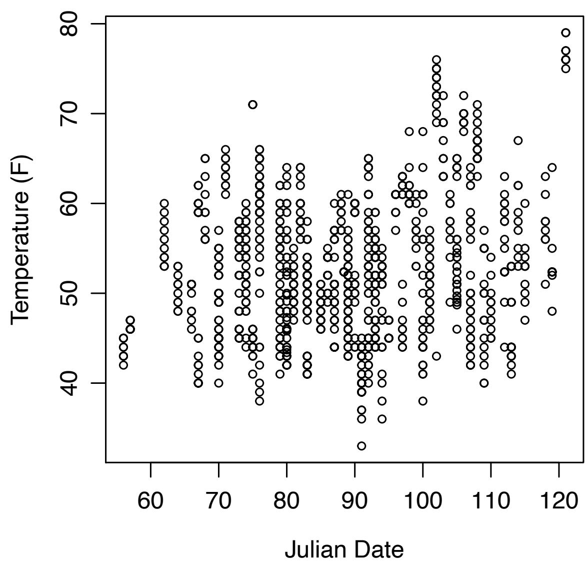

Figure 10. Relationship of temperature during surveys to Julian date.

Third, detection probability was lower at sections with more than one listening post than sections with a single listening post (Fig. 11). This relationship is very likely explained by the "removal" survey design used within each section. If *P. illinoensis* is heard chorusing at the first listening post, no additional listening posts are surveyed. Multiple listening posts are only surveyed if *P. illinoensis* is not detected at the first post. The listening post variable essentially represents whether *P. illinoensis* was detected at the first post or not, so sections with only a single survey almost by definition will have greater detection probability. Multiple listening posts are most likely in sections that have little *P. illinoensis* habitat and therefore low abundance and chorusing level. I recommend observers continue to survey at additional posts when *P. illinoensis* is not detected at the first post, as all additional surveys increase the cumulative probability of detection for the section. It is possible to gain more knowledge about the detection process by recording data at the listening post level rather than at the section level. Occupancy models can accommodate nested designs in which detection histories at each listening post are nested within sections. Observers would record all detection data and detection covariates at each listening post to use this type of nested design for analysis. However, given that data were not collected at the listening post scale in the past, occupancy models would need to be parameterized to accommodate the change in the spatial scale at which detection histories are recorded.

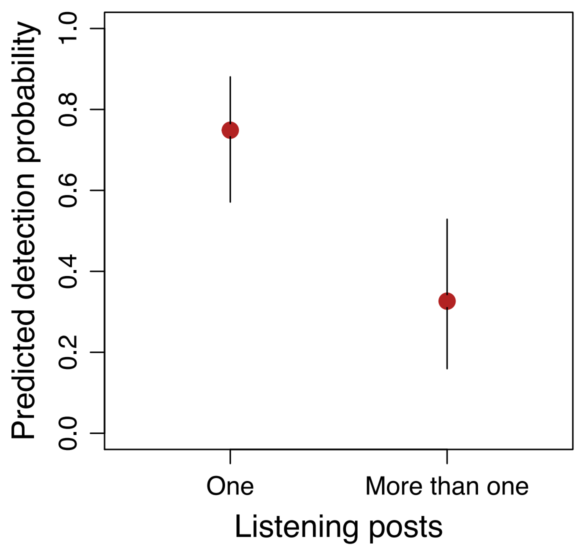

Figure 11. Relationship of detection probability of *Pseudacris illinoensis* during surveys to the number of listening posts in each section. Error bars represent 95% confidence intervals.

It is worth nothing that there was a significant amount of missing data for detection covariates (date: 26 cases, temperature: 30 cases, wind: 22 cases; rainfall on day of survey: 63 cases; rainfall one day prior to surveys: 112 cases; rainfall two days prior to surveys: 111 cases; listening posts: 15 cases). In occupancy models all detection-nondetection observations must have corresponding survey-specific detection covariates to be used to estimate model parameters. In this analysis, missing data in detection covariates were mean-imputed in order to retain the detection data, but these missing observations likely contribute to uncertainty in parameter estimates. Thus, it is important to remind observers to record all detection covariates when conducting surveys.

I remain confident that conducting two surveys per season at each section is generally adequate for obtaining precise estimates of occupancy probability. However, the timing of surveys with adequate conditions is extremely important. My analyses suggest surveys should be conducted relatively early in the breeding season, particularly when there is a combination of relatively warm evenings and rain in the previous day. Many studies have shown that anuran chorusing can start earlier in the season with climate warming, so attempting surveys earlier than usual may be worthwhile. As suggested in Cosentino (2018), I continue to think it would be valuable to add a third survey to sections when *P. illinoensis* is not detected during the first two surveys, particularly if observers believe conditions during the first two surveys were poor. Finally, I recommend observers start recording two additional variables during surveys: a) record the number of vehicles that pass by each listening post during a survey, and b) indicate whether there were conditions that interfered with hearing *P. illinoensis* calls during a survey (binary response: Yes or No). These variables could help identify additional sources of variation in detection probability, potentially explaining variation currently attributed to observer.

4. Literature Cited

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