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Population Decline and Landscape-Scale Occupancy of the Crawfish Frog (*Lithobates areolatus*) in Northwest Arkansas

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***Lithobates areolatus* (Crawfish Frog) is an imperiled amphibian, unique among ranid frogs due to its obligate use of crayfish burrows, highly terrestrial behavior, and reliance on open-canopy habitats within the central USA. Currently listed as near-threatened by the IUCN, and as state endangered, threatened, or of greatest conservation need in every state where it occurs, *L. areolatus* could potentially serve as an umbrella species for biodiversity conservation in the region. However, few studies have sought to identify site characteristics most strongly associated with the occupancy of *L. areolatus* or rigorously assessed the status of populations across core areas of the species' range in Arkansas, Oklahoma, and Kansas. Within northwest Arkansas, we used an occupancy-modeling framework to 1) determine landscape characteristics that could serve as predictors of the occupancy of *L. areolatus* and 2) assess the status of current and historical populations. We completed 405 time-constrained auditory surveys across 81 potential and historical breeding wetlands of *L. areolatus* over two breeding seasons (March–April 2016 and 2017). Estimated occupancy and detection were 0.26 and 0.32, respectively. We did not detect *L. areolatus* at 37.5% (6/16) of historic breeding wetlands during our study, indicating these populations are likely extirpated. Occupancy probability was strongly related to density of prairie mounds within 1 km of breeding wetlands and was weakly related to clay and chert/gravel loam soil. Our results suggest that: 1) *L. areolatus* is widespread throughout northwest Arkansas but is threatened by the expanding human population, 2) detection probability is high under optimal conditions (cool temperatures [9–12°C] and recent rain [within 24 hr]), and 3) prairie mound density is a useful proxy for upland habitat quality, likely reflecting minimal soil disturbance and presence of crayfish burrows.**

LITHOBATES areolatus (Crawfish Frog) is currently experiencing precipitous declines throughout its range in the eastern Great Plains of the central United States (Parris and Redmer, 2005; Lannoo and Stiles, 2020). *Lithobates areolatus* is unique among North American amphibian species because adults are obligate crayfish burrow commensals and have been documented to migrate over a kilometer to and from their breeding wetlands (Heemeyer and Lannoo, 2012; Heemeyer et al., 2012). Adult *L. areolatus* are highly terrestrial, spending all but the brief (1–4 week) breeding season at crayfish burrows in open-canopy upland habitat, and larval *L. areolatus* require fish-free ephemeral wetlands with limited competitors for optimal survival (Parris and Semlitsch, 1998; but see Palis, 2009; McKnight and Ligon, 2016). Due to the species' unique habitat requirements, habitat loss and degradation are thought to be the primary cause of decline. The IUCN (Hammerson and Parris, 2004) has listed *L. areolatus* as near-threatened; the species is listed as endangered, threatened, or a species of greatest conservation need in all of the states in which it occurs. As such, *L. areolatus* may serve as an umbrella species for biodiversity conservation in grassland ecosystems throughout its range.

Due to the declining status of *L. areolatus*, an understanding of both range-wide patterns of habitat use and probability of detection are important for developing effective conservation and management strategies. Telemetry studies have shown that adult *L. areolatus* select open-canopy grassland habitat with a high density of crayfish burrows (Heemeyer et al., 2012; Williams et al., 2012a). Crayfish burrows serve as an important refugia from predation, desiccation, and high daytime temperatures (Engbrecht and Lannoo, 2012; Heemeyer and Lannoo, 2012; Kwiatkowski et al., 2017); however, assessing the availability of this critical habitat element involves on-the-ground surveys which can be time-consuming and often require access to private property if evaluating availability at large spatial scales. Some studies have used auditory recording systems and call-surveys during the breeding season to determine patterns of occupancy and detection (Williams et al., 2012b, 2013), and multiple inventory and monitoring studies have been completed, aimed at documenting populations across the range of *L. areolatus* (i.e., Illinois [Palis, 2018], Indiana [Engbrecht and Lannoo, 2010], Kansas [Busby and Brecheisen, 1997]). Few studies have focused on Arkansas populations or used an occupancy framework to assess factors affecting occupancy across a human-altered landscape, while accounting for imperfect detection (but see Williams et al., 2013).

Occupancy analysis has emerged as a powerful tool for understanding distributions and habitat use of many amphibian species across landscapes (Weir et al., 2005; Gould et al., 2019; Guzy et al., 2019), and northwest Arkansas (NWA) offers a unique opportunity for completing a landscape-scale assessment of the occupancy of *L. areolatus*. Populations of *Lithobates areolatus* have been documented throughout Arkansas, with most records within the northwestern region and Arkansas River Valley (Fowler and Anderson, 2015; Roberts, 2020). Historically, tallgrass prairie habitat was common throughout NWA (Transeau, 1935), but prairies were among the first habitats to be converted to agriculture and little intact prairie habitat currently exists in the region. Presently, degraded prairies in the form of low-intensity agriculture (i.e., hayfields and cattle pastures) and rural habitats are being replaced by urban development to accommodate growing city centers. The NWA region is one of the fastest growing areas within the state, and the human

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population within Benton and Washington Counties grew over 25% and 17%, respectively, between 2010 and 2019 (UScensus, 2019. "Population Estimates." United States Census Bureau. https://www.census.gov [accessed 16 March 2020]). As the population continues to grow, natural and rural lands will continue to be converted for suburban and urban development, leading to an increasingly patchy landscape.

Northwest Arkansas is centrally located within the range of *L. areolatus*, but little work has been done to rigorously assess their status in NWA. Although populations of *L. areolatus* have been documented throughout the NWA region for over 20 years (e.g., Trauth et al., 2004), monitoring has not been consistent, standardized, or comprehensive across potential habitat for *L. areolatus*. We used an occupancy modeling framework to 1) determine landscape characteristics that are the most important predictors of populations of *L. areolatus*, 2) assess the status of current and historical populations, and 3) identify potential areas for habitat conservation to support population persistence. We had two primary hypotheses: 1) occupancy of *L. areolatus* would be negatively associated with urban land cover and positively associated with historic prairie and prairie mound density, and 2) most loss of historical populations (i.e., extirpations) would occur near urban centers, in areas of expanding residential and commercial development. Documenting status and occupancy patterns of *L. areolatus* across NWA provides baseline data for long-term monitoring and helps identify potential conservation priorities for this species.

MATERIALS AND METHODS

Occupancy sampling.—We completed five time-constrained auditory surveys at each of 81 open-canopy ephemeral wetland sites spanning Benton and Washington Counties in northwest Arkansas (Fig. 1). In 2016, we surveyed 60 sites three times and those same sites twice in 2017. In 2017, we added an additional 21 sites, which we surveyed five times. We completed surveys between 9 March and 18 April in 2016 and between 9 March and 6 May 2017. We began surveys immediately following the first heavy rain event in March, and all sites were visited within six days of a rain event. We rotated through all sites before resampling. Sites were centered on potentially suitable breeding wetlands and were selected based on historical records ($n = 16$ sites), proximity to historical prairie habitat, and known habitat preferences for *L. areolatus* (i.e., open-canopy upland habitat and shallow or ephemeral wetlands isolated from larger water bodies) identified using aerial imagery and remote-sensing data. After identifying potential breeding sites, we ground-truthed sites in February 2016 and 2017 to ensure remote-sensing data were accurate. All sites were located along or near roads, and the majority of sites were on private property. Sites included remnant and restored prairies, low- and high-intensity agriculture fields (hayfields, cattle pastures, and row crops), as well as urban areas (e.g., urban preserves, urbanized historic prairie). The combination of limited historic prairie extent, an extensive network of paved and unpaved roads, and the high detectability of a chorus from *L. areolatus* (i.e., calls heard over 1 km away; Lannoo and Stiles, 2020), allowed us to survey most of the suitable breeding wetlands in the region. Thus, our 81 sites represent a majority of the potentially suitable breeding wetlands of *L. areolatus* within Washington and Benton Counties.

We completed surveys following the North American Amphibian Monitoring Program (NAAMP; Weir and Mossman, 2005) protocol. In short, we began surveys 30 minutes after sunset and listened at each site for five minutes. Longer listening periods for *L. areolatus* have been shown to increase detection (Williams et al., 2012b, 2013); however, the large number of sites and geographic area monitored in our study combined with the brief breeding season made longer survey periods untenable. We recorded all species present and scored calling intensity on a 1 to 3 scale (1 = individuals calling with little to no overlap, 2 = calling overlaps, but individuals are still identifiable, 3 = full chorus); intensity scores were collapsed to 0 (non-detection) or 1 (detection) for analysis. During each survey, we recorded temperature and determined the number of days since the last rain event. Both temperature and rain have been shown to be important for the detection of *L. areolatus* (Williams et al., 2012b).

Landscape data collection and analysis.—We measured a variety of variables at each of our sites using a GIS (ArcMap v.10.7.1 ESRI, Redlands, CA) with the Aerial Imagery base map, as well as a soil raster file (Arkansas GIS, 2013. gSSURGO MapUnit FY 2013. https://gis.arkansas.gov [accessed 15 January 2020]) and historic prairie extent layer acquired from the Arkansas Natural Heritage Commission, and 2016 landcover data from the National Land Cover Database (NLCD, 2016. CONUS Landcover. https://www.mrlc.gov/ [accessed 15 January 2020]). Within ArcGIS, we created a 1.2 km buffer surrounding each breeding wetland, representing the core upland habitat used by populations of *L. areolatus* (Heemeyer et al., 2012), and counted the number of prairie mounds and wetlands within that buffer using aerial imagery. Prairie mounds, also known as pimple mounds or mima mounds, are small dome-shaped hillocks that can be found throughout native prairies and river valleys of the southern mid-continent of North America (Melton, 1954; Seifert et al., 2009). Prairie mounds are micro-relief features that are thought to be formed through a combination of erosion and upwelling of soil from biotic ecosystem components (e.g., prairie dogs, pocket gophers, ant species; Johnson and Horwath Burnham, 2012). Due to an inability to gain access at many of our private property sites ($n = 73$), we were unable to measure potentially important habitat variables, such as vegetation and crayfish burrow density. Instead, we used presence of prairie mounds, which are easily identified from aerial imagery, as an indication of both historic prairie habitat presence and lack of plowing or other intensive habitat alteration. We also tabulated the percent urban land cover within the buffer at each site using the tabulate area tool within the Spatial Analyst ArcGIS extension. We did not include agricultural land cover due to an inability to differentiate intact or restored prairie habitats from pasture, and due to the low prevalence of high-intensity (i.e., row crop) agriculture in our region. Using the historic prairie extent layer, we determined the percentage of each buffer within the historic prairie extent using the tabulate area tool. Finally, we tabulated percent soil type within each site buffer. The soil layer contained over 70 soil types, which we lumped into 14 broader categories (e.g., silt loam, clay, silty clay, etc.) based on Harper et al. (1969). To reduce the number of soil covariates, we ran a principal component

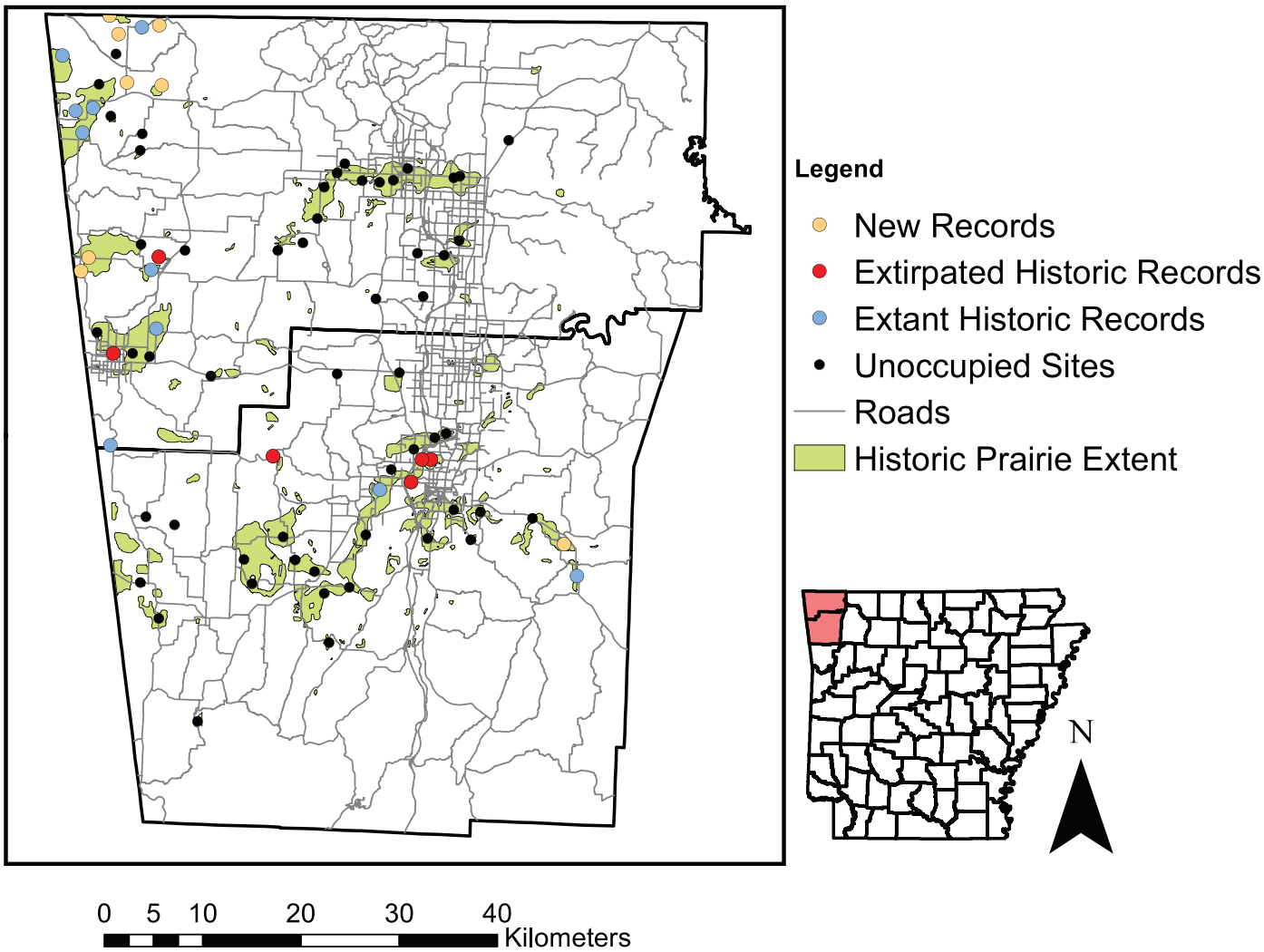

Fig. 1. Sites ($n = 81$) surveyed for populations of *Lithobates areolatus* (Crawfish Frog) in northwest Arkansas during the spring 2016 and 2017 breeding seasons. Sites were located within Benton and Washington Counties (shaded area of state inset). Historic and current occupancy records are indicated and in relation to historic prairie extent. Roads are included to portray urbanization.

analysis (PCA) to identify patterns in soil composition across sites. We included soil PC1, soil PC2, and soil PC5 as covariates for model selection. We included soil PC1 and PC2, which explained 17.5% and 12.8% of the variation across sites, respectively. Soil PC1 was characterized by a strong positive association with sandy and stony loam soils. Soil PC2 was characterized by a strong negative association with silt loam and strong positive association with chert loam and gravelly silt loam. We also included soil PC5, which explained 10% of the variation, because it had strong positive associations with Silty Clay and Silty Clay Loam soils, which did not weigh heavily on other principal components, but we suspected clay soils might be important in mediating occupancy (Williams et al., 2013). The three soil principal components cumulatively explained 40% of the variation in soil types among sites.

Occupancy analysis.—We used a static occupancy model to estimate the occupancy of *L. areolatus* at wetland breeding sites, and to explore the influence of seven site-specific covariates (prairie mound density, number of wetlands, percent buffer within historic prairie, percent urban land cover, soil PC1, soil PC2, soil PC5), while accounting for imperfect detection (MacKenzie et al., 2002). We included days since last rain, and temperature as sampling covariates, as well as year, due to some sites being sampled over two years. We constructed our models using the 'unmarked' package (Fiske and Chandler, 2011) within R v. 4.0.0 (R Core Team, 2020) and used an information-theoretic approach to model selection (Burnham and Anderson, 2002). Prior to running all models, we confirmed that covariates were not strongly correlated (all $R^2 < 0.50$) and standardized each covariate using a *z* transformation.

To determine occupancy of *L. areolatus* at breeding wetlands, we used a two-step approach (similar to Peterman et al., 2013). First, we modeled combinations of our detection covariates (rain, temperature, and year), while holding site occupancy constant. All detection models that were used in selection included year as a covariate, except the null model (Table 1). We then modeled occupancy using the best supported parameterization for detection probability (MacKenzie et al., 2018). For occupancy probability estimation, we modeled all possible covariate combinations ($2^7 = 128$ possible models). We performed a goodness-of-fit test with

Table 1. Model selection based on QAIC for covariates influencing detection probability (p_i) of *Lithobates areolatus* at 81 sites across historic prairie regions of northwest Arkansas, USA, 2016–2017. With the exception of the null model, all models included an effect of year on detection.

Model	K	QAIC	ΔQAIC	QAIC wt	Cum. Wt	Quasi-LL
ψ(.) p(rain + temp + year)	6	99.03	0	0.54	0.55	−43.52
ψ(.) p(rain + year)	5	99.4	0.45	0.45	0.99	−44.7
ψ(.) p(year)	4	108.1	9.09	0.01	1	−50.06
ψ(.) p(temp + year)	5	109	10.01	0	1	−49.52
ψ(.) p(.)	3	111.7	12.67	0	1	−52.85

parametric bootstrapping and calculated an overdispersion parameter (ĉ) based on our global model to adjust parameter standard errors and for model selection (MacKenzie and Bailey, 2004). We used the MuMIn package (Bartoń, 2020) to calculate Akaike's Information Criterion (AIC) and quasi-Akaike's Information Criterion (QAIC) values for model selection. QAIC adjusts for overdispersion by incorporating ĉ, and models with QAIC weights ≤2 were used for model averaging (Hamer and Mahoney, 2010). We also calculated relative covariate importance (w+), which is the sum of QAIC weights that included a given covariate (Burnham and Anderson, 2002; Fuller et al., 2016). For our occupancy model selection table, we removed parameters with 85% confidence intervals that included zero, which was suggested by Arnold (2010), as a method for reducing the effect of additional covariates on ΔQAIC values. However, all covariates were included for model averaging and relative importance estimation.

RESULTS

We completed 405 auditory surveys between March 2016 and May 2017 and detected adults of *L. areolatus* at 18 (22%) of the 81 sites. All but two sites occupied by *L. areolatus* were located on private property. We failed to detect breeding *L. areolatus* at six (37.5%) of 16 historic localities (Fig. 1). These sites likely reflect instances of local extirpation; site-specific estimated occupancy probability ranged from 0.04 (0.04 SE) to 0.07 (0.05 SE), with the exception of the northernmost of these sites (0.22 [0.13 SE]), which was close to an occupied site (<1.5 km) and had relatively high prairie mound density (48 per km^2). These sites of apparent extirpation were primarily located near urban centers in Washington County (city of Fayetteville) and Benton County (cities of Siloam Springs and Gentry) and in several cases urban and suburban development had unequivocally destroyed wetland and upland habitats needed by *L. areolatus* (Fig. 1). We documented the breeding activity of *L. areolatus* at eight new localities. Extant populations of *L. areolatus* were predominately located in three large sections of historic prairie in western Benton County, with only three sites in Washington County (Fig. 1). We did not record any *L. areolatus* calling at sites located in a large, but isolated, historic prairie region of central Benton County or in historic prairie regions of western Washington County (Fig. 1).

In our occupancy analysis, the global model fit the data of *L. areolatus* well, but the goodness-of-fit test suggested there was some overdispersion (ĉ = 1.84), so we used QAIC weights for model selection and averaging. Our top detection model included days since rain, temperature, and year (Table 1). The relative importance value (w+) for days since rain was 1.00; temperature had a relative importance of 0.44. Naïve detection probability was 0.32 (0.06 SE). However, when days since rain, year, and temperature were included to inform detection our estimated detection probability was 0.97 (0.05 SE) under optimal conditions after five surveys. Detection probability was highest (>0.60) during cooler temperatures (9–12°C) and within 24 hrs of rainfall (Fig. 2). The lowest temperature with a detection of *L. areolatus* was 8.89°C.

Occupancy model selection and relative importance results indicated that prairie mound density was the most important factor in predicting site occupancy of *L. areolatus*. Mound density, soil PC2, and soil PC5 were the only covariates that had 85% confidence intervals that did not overlap zero. The best supported model for site occupancy included only mound density (Table 2); however, models that included soil covariates were also highly ranked (ΔQAIC < 2). Mound density had a relative importance close to 1 (0.98); all other covariates had a lower relative importance, ranging between 0.28 and 0.37 (Table 3). Estimated occupancy of breeding wetlands included in our study was 0.26 (0.06 SE). Model-averaged estimates of occupancy probability ranged from 0.02 (95% CI 0.00–0.08) when mound density was near zero to 0.99 (95% CI 0.99–1.00) at the highest mound density

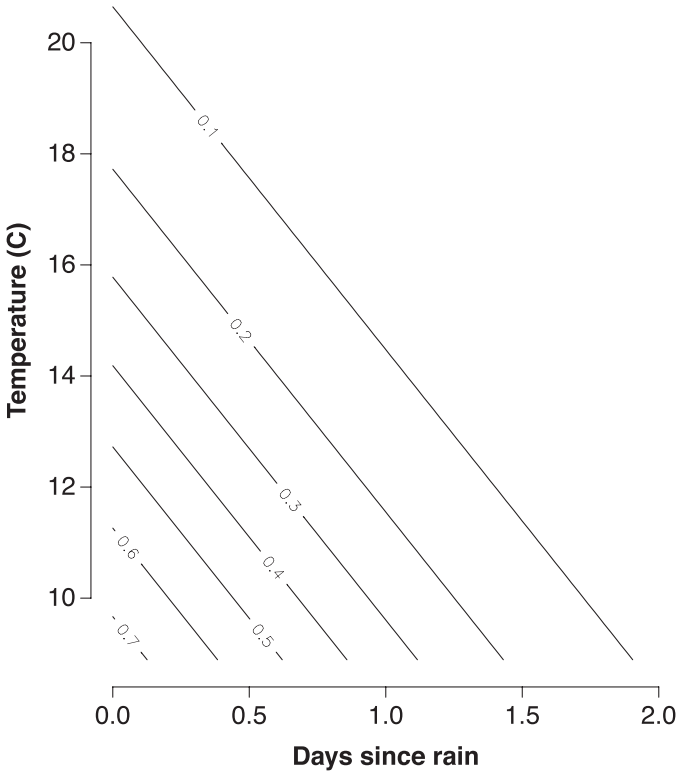

Fig. 2. Mean detection probability of *Lithobates areolatus* (Crawfish Frog), showing a joint effect of temperature and days since rain.

Table 2. Model selection based on QAIC for covariates influencing occupancy probability of *Lithobates areolatus* (ψ_i) at 81 sites across historic prairie regions of northwest Arkansas, USA, 2016–2017. The top-ranked models with a ΔQAIC $\leq$ 2 are listed, after removing covariates with 85% CI that included 0. The covariate set for detection was held constant and included days since rain, temperature, and year.

Model	K	QAIC	ΔQAIC	QAIC wt	Cum. Wt	Quasi-LL
ψ(mound density)	7	92.67	0.00	0.47	0.47	−39.33
ψ(mound density + soilPC5)	8	94.16	1.50	0.22	0.69	−39.08
ψ(mound density + soilPC2)	8	94.50	1.83	0.19	0.88	−39.25

(Fig. 3). The mean model-averaged occupancy probability was 0.73 (95% CI 0.63–0.83). Once mound density reached 50 mounds per km^2, occupancy probability increased dramatically and plateaued near 100% probability when mound density was greater than 150 mounds per km^2 (Fig. 3). Mound density across the 81 sites included in this study ranged from 0 to 244 mounds per km^2. Soil PC2 and soil PC5 were both positively associated with occupancy but had only minor effects on occupancy probability. Specifically, mean model-averaged occupancy probability increased from 0.35 (95% CI 0.07–0.63) to 0.40 (95% CI 0.00–0.89) with increasing soil PC2 scores and increased from 0.33 (95% CI 0.02–0.65) to 0.42 (95% CI 0.00–0.88) with increasing soil PC5 scores. Thus, the occupancy of *L. areolatus* increased slightly with the presence of chert and gravelly silt loam (soil PC2) and with increasing clay content (soil PC5).

DISCUSSION

We conducted a comprehensive landscape-scale occupancy study of populations of *L. areolatus* in an increasingly human-altered region at the core of its historic range, northwest Arkansas. Overall estimated occupancy was 0.26, indicating that much of the apparently suitable habitat was unoccupied. Although we confirmed the continued existence of 62% of historically known breeding populations, six (38%) populations have apparently been extirpated, primarily due to urban expansion within the past 20 years. Detection probability of *L. areolatus* was high (>0.6) under ideal conditions (low temperature and recent rain); thus, we expect that had populations of *L. areolatus* been present at the historic sites, we would have detected them over the course of five surveys. Our results indicate that populations of *L. areolatus* are more likely to be found in areas where upland habitat has remained relatively intact (e.g., little soil disturbance and likely high crayfish burrow density), as indicated by a high density of prairie mounds. The association with prairie mounds shows promise as an integrative proxy for upland habitat suitability that could be used to rapidly assess potentially suitable habitat for *L. areolatus* from remote-sensing data. Weak, but positive associations with soil covariates hinted that soils may have been important in mediating occupancy historically, but these relationships may have been weakened by past and recent extirpations and increased urban development. *Lithobates areolatus* is threatened throughout much of its range due to the loss and degradation of native prairie habitats; our results suggest that trend is no different in NWA.

The overall occupancy rate for *L. areolatus* was low across our study region, with fewer than 25% of sites having at least one detection. Low overall occupancy was driven in part by a lack of detections in large patches of historic prairie in central Benton and western Washington Counties (Fig. 1). These regions are not appreciably more degraded than other historic prairie areas in our study area; the lack of historical or recent records suggests that populations of *L. areolatus* may not have ever occurred in these areas. Reflecting the lack of intact prairie habitat, *L. areolatus* was most commonly found

Table 3. Cumulative QAIC weight of models that included each occupancy covariate. Higher weights indicate higher relative covariate importance (w+). Each covariate was listed in an equal number of candidate models ($n = 64$ out of 128 total models).

Site covariate	w+
Mound density	0.98
Soil PC5	0.37
Historic prairie	0.36
Urban land use	0.35
Soil PC2	0.33
Soil PC1	0.31
Number of wetlands	0.28

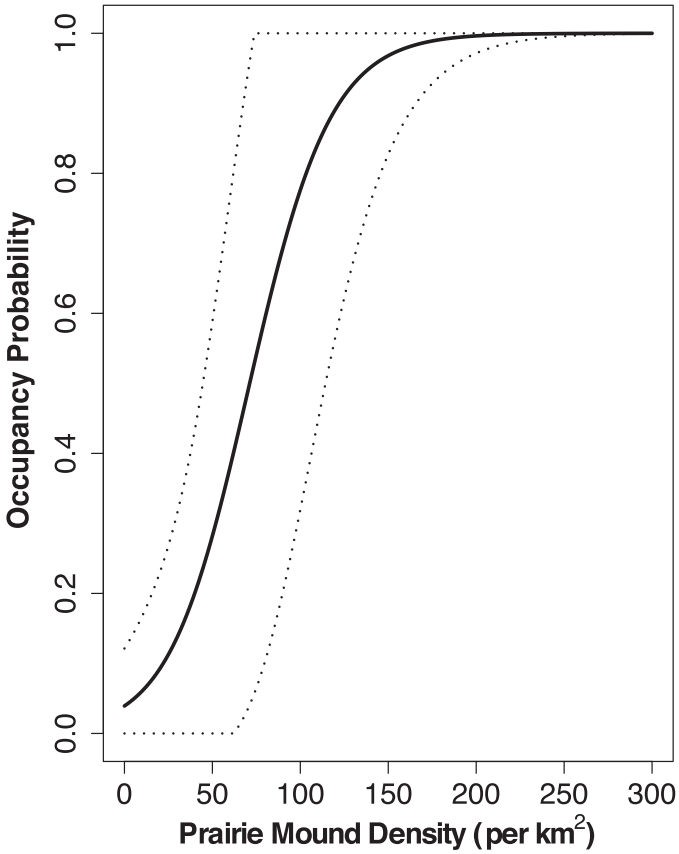

Fig. 3. Model-averaged predictions (based on QAIC weights) of occupancy probability of *Lithobates areolatus* (Crawfish Frog) based on prairie mound density within 1.2 km of a breeding wetland.

in the low-intensity agricultural areas of western Benton and central Washington Counties, where there were large tracts of open-canopy habitat with relatively low-intensity disturbance, similar to habitats where populations of *L. areolatus* were most commonly found in Kansas (Busby and Brecheisen, 1997). In western Benton County, where most of our occupied sites occurred, land cover is primarily pasture and hayfield agriculture, with very little urban development. In contrast, five of the six extirpated populations were in areas with extensive recent urban development in both Benton and Washington Counties, especially around the cities of Fayetteville and Siloam Springs. While some historical populations have likely been lost, our study documented several previously unrecorded breeding populations, suggesting that *L. areolatus* is still widespread throughout the region, but remains rare and patchily distributed. Most of the remaining populations within the NWA region breed at wetlands on private property. Only two of the 18 sites with extant populations of *L. areolatus* are protected, and even those are located within very small preserves that may not protect enough upland habitat to ensure long-term population viability. At both protected sites, much of the calling activity occurred in privately owned agricultural wetlands adjacent to the preserves (C. Kross, pers. obs.), suggesting that primary breeding wetlands may also lack protection. Although NWA contains extensive public/protected land, especially national forest, and state and national park land, the vast majority is in mountainous or historically forested regions. The preservation of larger tracts of grassland habitats is critical for the long-term persistence of populations of *L. areolatus* within NWA.

Our top detection model was the global model, closely followed by a model only incorporating days since rain and year. Detection probability was highest (~70%) immediately following rain. Our results were similar to Williams et al. (2012b), a two-year occupancy study that found detection probability for *L. areolatus* increased when temperatures were >8°C and within 24 hours of a rain event. In contrast, a follow-up to Williams et al. (2012b) recorded calling activity over a two-month period at two known breeding wetlands of *L. areolatus* and found that rain within 24 hours negatively affected the detection of *L. areolatus* (Williams et al., 2013). These contrasting effects of rain on detection might reflect the short duration of our call surveys, which might be biased toward detecting calling individuals early during migration to their breeding wetlands (Williams et al., 2013). In our study, *Lithobates areolatus* was detected calling between 9 March and 13 March 2016 and between 26 March and 21 April 2017. As a result, we did not include a date parameter in our models, instead focusing on a year effect. The difference in timing and length of the calling window between years, driven by the timing of spring rains, likely had a significant effect on detection probability. Our results indicate that call surveys immediately following a rain event and early in the breeding season are optimal for locating occupied sites with the least amount of survey effort.

In accordance with our hypotheses, occupancy probability of *L. areolatus* increased with density of prairie mounds. Prairie mounds are dome-shaped soil structures that were likely formed by the selective erosion of soil deposits in Arkansas (Quinn, 1961; Durre et al., 2019), or upwellings by biotic ecosystem components (Horwath and Johnson, 2006). Prairie mounds are indicative of historic prairie habitat that has not been degraded by intensive agriculture (i.e., plowing; Horwath and Johnson, 2006), thus serving as a proxy for multiple aspects of prairie habitat quality, especially lack of soil disturbance. Habitat composition is important for *L. areolatus* due to its unique need for suitable breeding wetlands connected to terrestrial uplands containing crayfish burrows (Heemeyer and Lannoo, 2012; Williams et al., 2012a; Lannoo et al., 2017). Potentially suitable breeding wetlands for *L. areolatus* can be identified relatively easily based on aerial imagery and vegetation composition that indicates hydroperiod. However, assessing upland habitats conducive to crayfish burrows and juvenile dispersal can be difficult, often requiring on-the-ground data collection to assess soil disturbance and crayfish burrow presence on property that might be hard to access. Areas with the highest mound densities in our study were also the least modified, primarily low-intensity agriculture (i.e., pasture and hayfields) and protected and/or restored conservation properties. One of our protected areas with high mound density and a population of *L. areolatus*, Woolsey Wet Prairie Sanctuary, was also a recent restoration and currently supports a diverse amphibian and reptile community, as well as an abundance of burrowing crayfish (Baecher et al., 2018). Thus, our results suggest that presence of prairie mounds can serve as a useful integrative proxy for upland habitat quality (i.e., low soil disturbance and crayfish burrow presence) in parts of the range of *L. areolatus* where prairie mounds occur and can easily be used to identify potential locations for *L. areolatus* using remotely sensed data.

Clay soils have been proposed as a potentially important predictor of the occupancy of *L. areolatus* (Busby and Brecheisen, 1997). Our results lend some support to this idea, as soil PC5 had the second highest relative importance value of the covariates examined in our study. We also found some evidence for an occupancy relationship with chert loam and gravelly silt loam soils, as reflected by the positive effect of soil PC2 on occupancy. Prairie mounds most commonly contain a claypan or compacted gravel layer (Cox, 1984; Horwath and Johnson, 2006), and our prairie mound covariate may have also been an indicator of these soil conditions. However, the effects of soil covariates were weak, with wide confidence intervals. The lack of strong associations between occupancy and our soil covariates may in part reflect sites with suitable soils where populations have been extirpated by anthropogenic factors, such as urbanization, or where populations never occurred historically due to natural barriers or isolation of prairie remnants that prevented colonization. We also might have missed a key soil type association when we binned soil types into broader categories. However, Kwiatkowski et al. (2017) completed a fine-scale analysis of the soils that made up crayfish burrows used by adult *L. areolatus* and observed that individuals used whatever crayfish burrows were available, irrespective of soil composition. Regardless, a more thorough evaluation of soil conditions preferred by adult *L. areolatus* would prove a valuable contribution toward understanding occupancy patterns.

Contrary to our hypotheses, historic prairie extent and urban land cover were not important predictors of occupancy by *L. areolatus*. Much of the NWA landscape, especially large sections of the historic prairie, has been altered for human use, rendering that habitat unsuitable for populations of *L. areolatus*. Our site selection criteria might also have weakened

the ability to detect effects of land cover covariates; we focused on open-canopy habitats that were in proximity to historic prairie, and high-intensity agricultural land use (i.e., row cropping) was rare in the region. Additionally, our exclusion of some covariates due to an inability to differentiate between restored prairie habitat and low-intensity agriculture in the GIS land use analysis likely limited our ability to detect relationships with land cover. Finally, lack of an effect of urban land cover might have been driven by low overall occupancy probability and the presence of populations of *L. areolatus* in a few protected areas near urban edges. Nonetheless, the loss of historic populations of *L. areolatus* in urban areas suggests increasing urbanization throughout the NWA region is a threat to population persistence.

Lithobates areolatus is an imperiled amphibian throughout its range. We documented 18 breeding locations spread across two counties in NWA and found that occupancy by *L. areolatus* was near 100% at sites with high densities of prairie mounds. However, we also documented extirpation of several populations near urban centers. Our research revealed that presence of prairie mounds can serve as an easily assessed proxy for upland habitat suitability and that detectability of *L. areolatus* is high shortly after early spring rains. Thus, we recommend inventory and monitoring initiatives that employ auditory surveys following early spring rain events and that use prairie mound density to identify sites with a high potential for occupancy by *L. areolatus*. We also recommend future research that includes collection of on-the-ground covariates, such as fine-scale vegetation, soil, and crayfish burrow measurements, to fully understand the factors that are most strongly related to occupancy by *L. areolatus* (Cruickshank et al., 2020). For improving detection, we recommend the use of song meters at random breeding wetlands to verify the effectiveness of the five-minute calling window. Finally, continued monitoring and concerted conservation efforts will be needed to ensure long-term persistence of populations of *L. areolatus* within NWA. Given that most populations currently occur on private property, establishing strong and mutually beneficial relationships with landowners is a critical aspect towards the conservation of *L. areolatus*. Moreover, the species would greatly benefit from larger protected areas, centered on current metapopulations in western Benton County. Active habitat restoration has been shown to preserve and enhance populations of *L. areolatus* (Lannoo et al., 2009; Baecher et al., 2018), and captive-rearing has been used to augment populations in Indiana (Stiles et al., 2016). With low overall occupancy indicating ample availability of apparently suitable habitat, restoration and reintroduction could help to secure population persistence of *L. areolatus* within the NWA region.

DATA ACCESSIBILITY

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