

# USING CALL SURVEYS AND ECOLOGICAL NICHE MODELING TO ASSESS THE DISTRIBUTION AND STATUS OF CRAWFISH FROGS (*LITHOBATES AREOLATUS*) IN LOUISIANA, USA

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**Abstract.**—Crawfish Frog (*Lithobates areolatus*) occupancy has declined by 35% throughout much of its historic range primarily due to conversion of habitat to agriculture. In Louisiana, USA, most records date prior to the 1970s, and more recently the species has been documented at only a few locations. This study aimed to assess the current distribution and status of *L. areolatus* in Louisiana and determine the climatic and habitat associations of the species. In Spring 2019, we conducted nighttime call surveys along roads near historic locations for *L. areolatus* in areas where potentially suitable habitat remains. Despite considerable effort, we encountered no individuals. To identify suitable areas for subsequent surveys, we developed an Ecological Niche Model using locality information from 1990–present from Louisiana, Texas, and Oklahoma, and bioclimatic, land cover, and soil hydrology variables. Only six of the 12 parishes with historic records of *L. areolatus* were predicted to have appreciable areas of suitability for the species. We established five new routes based on the model and surveyed them along with our 2019 routes during 2020 and 2021. We also deployed 12 automated audio recorders in 2020 and seven in 2021. Despite these additional efforts, no *L. areolatus* were found, indicating the species may be extirpated or extremely rare in Louisiana. Nonetheless, our study identified climatic and habitat associations for the species across its southern range, as well as areas that could be evaluated for potential reintroduction sites.

**Key Words.**—acoustic monitoring; amphibian; Cajun Prairie; crayfish burrow; Maxent; species distribution modeling

## INTRODUCTION

Global biodiversity has decreased significantly in the last few centuries (Butchart et al. 2010). Of the five major vertebrate taxonomic groups, amphibians are the most threatened, with one-third of species experiencing population declines (Cunnington and Fahrig 2010; Hoffmann et al. 2010; Luedtke et al. 2023). Alarm over the past 25 y about worldwide amphibian declines has motivated biological research of this group (Williams et al. 2013). Despite this, status assessments and characterization of threats have been conducted unevenly across amphibian species (Stuart et al. 2004; Williams et al. 2013; Luedtke et al. 2023) and some taxa require further attention.

Many amphibian populations are threatened because of continued land use changes that impact critical habitat and lead to fragmentation and isolation (Brooks et al. 2002; Stuart et al. 2004; Becker et al. 2007). To counter this, quick and accurate habitat assessments are required to safeguard remaining habitat (Peterman et al. 2013). Accurate knowledge of the geographic distribution of a species is crucial

but can be challenging to obtain because species detection is positively related to abundance (Groff et al. 2014). Distribution and occupancy modeling using presence/absence data have become useful tools to direct survey efforts and identify important environmental covariates for species persistence (Peterman et al. 2013).

One effective approach is to use Ecological Niche Modeling to predict species distributions and then employ surveys to determine occupancy in particular habitats. Ecological Niche Modeling uses abiotic and biotic variables from known georeferenced occurrence points for a species to produce a spatial niche envelope that predicts geographic areas in which that species could occur (Costa et al. 2010). This method has been useful in guiding surveys for rare amphibians aimed at identifying unknown populations. For example, Groff et al. (2014) used Ecological Niche Modeling to select 44 sites in Oregon predicted to be suitable for the Oregon Spotted Frog (*Rana pretiosa*) and then found two new records for the species via field surveys at those sites. In another study, Peterman et al. (2013) found Ecological Niche Modeling accurately distinguished



**FIGURE 1.** The Crawfish Frog (*Lithobates areolatus*) photographed from Atoka County, Oklahoma, USA. (Photographed by Donald B. Shepard).

occupied from unoccupied ponds for Jefferson's Salamander (*Ambystoma jeffersonianum*), increasing the number of known breeding ponds in Illinois, USA, from six to 33.

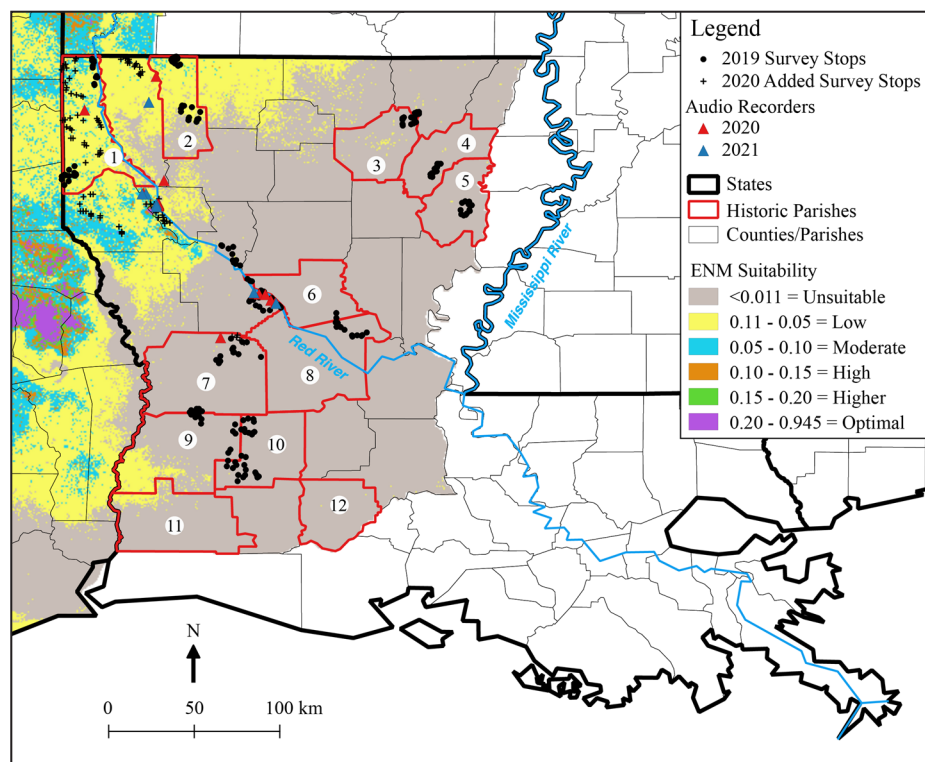
The ranid frog subgenus *Nenirana* contains four species, the majority of which are imperiled (Hillis and Wilcox 2005): Pickerel Frog (*Lithobates palustris*), Gopher Frog (*Lithobates capito*), Dusky Gopher Frog (*Lithobates sevosus*), and Crawfish Frog (*Lithobates areolatus*). Some researchers consider *L. areolatus* (Fig. 1) to be the most secretive of the four species because they spend little time away from crayfish burrows and have small home ranges except during their seasonal breeding migrations (Heemeyer and Lannoo 2012; Lannoo et al. 2017). Consequently, *L. areolatus* are difficult to sample and a considerable amount of their biology remains unknown (Lannoo et al. 2018). The distribution of *L. areolatus* spans 13 U.S. states from southeastern Texas and west-central Alabama northward to southern Iowa and western Indiana (Powell et al. 2016). In a recent assessment by Lannoo et al. (2017), however, the 243 counties/parishes with historic locations have seen a 35% decline in occupancy. Six of 13 states list *L. areolatus* as S1-Critically Imperiled or S2-Imperiled with another four states listing them as S3-Vulnerable ([https://explorer.natureserve.org/Taxon/ELEMENT\\_GLOBAL.2.106291/Lithobates\\_areolatus](https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.106291/Lithobates_areolatus)). In Texas, *L. areolatus* were once found across the eastern half of the state, but in the last 20 y evidence indicates pronounced population extirpation (Matthew Kwiatkowski et al., unpubl. report). Reasons for declines of *L. areolatus* can be attributed to several factors including habitat loss and degradation due to urban development, the spread of agriculture, strip

mining, and predatory fish introductions to breeding sites (Palis 2014). The species occurs in open, relatively flat and grassy habitats, such as prairie and pasture, and sometimes in open woodland (Williams et al. 2012; Boundy and Carr 2017). Given their decline, it is vital to better understand the biology of *L. areolatus* and where they occur on the landscape to allow for effective conservation and management of their remaining populations.

In Louisiana, *L. areolatus* are known historically from 15 scattered sites in 12 parishes with most records occurring prior to the 1970s (Boundy and Carr 2017; Fig. 2). More recently (2010s), the species has been documented from a single location in Caddo Parish in northwestern Louisiana (Brad Glorioso, pers. comm.) and from three southern locations in Acadia and Lafayette parishes during the 2007–2010 Louisiana Amphibian and Monitoring Program (LAMP) surveys (Carter et al. 2021). Due to the lack of recent reports and because there no longer is suitable habitat in Acadia and Lafayette parishes (Jacoby Carter, pers. comm.), *L. areolatus* is considered a species of Conservation Concern in Louisiana (Boundy and Carr 2017); however, its current distribution and status are unknown. We assessed the current distribution and status of *L. areolatus* in Louisiana and determined the climatic and habitat associations for the species. This was accomplished through: (1) nighttime call surveys near historic localities during the breeding season of the species (January–April); (2) building a GIS-based Ecological Niche Model (ENM) to predict the distribution of *L. areolatus* in Louisiana; and (3) surveying potentially suitable areas predicted by the ENM for the presence of *L. areolatus* through nighttime call surveys and the placement of automated audio recorders.

## MATERIALS AND METHODS

**Call surveys of historic locations.**—Standardized call surveys are commonly used to detect and monitor frog populations during their breeding season because most anurans can be identified by their species-specific vocalizations (Gooch et al. 2006; Williams et al. 2013; Weir et al. 2014). Breeding in *L. areolatus* begins after heavy rainfall when temperatures are 9°–13° C (Smith 1961; Busby and Brecheisen 1997; Matthew Kwiatkowski et al., unpubl. report). In the southern U.S., the breeding period of *L. areolatus* can start earlier and last longer than in the northern portion of the range, depending on weather (Palis 2014; Matthew Kwiatkowski et



**FIGURE 2.** Louisiana, USA, parishes with historic records for the Crawfish Frog (*Lithobates areolatus*), 2019 and 2020 call survey locations, 2020 and 2021 automated audio recorder locations, and suitability value classes from the preliminary Ecological Niche Model (ENM). Historic parishes are labeled: (1) Caddo; (2) Webster; (3) Ouachita; (4) Richland; (5) Franklin; (6) Grant; (7) Vernon; (8) Rapides; (9) Beaugard; (10) Allen; (11) Calcasieu; and (12) Acadia.

al., unpubl. report). In Texas, *L. areolatus* has begun calling as early as January and continuing until early May, likely because of the warmer climate of coastal Texas prairies (Matthew Kwiatkowski et al., unpubl. report). Due to uncertainty in the timing of the breeding season in Louisiana, we conducted call surveys during a wide period from January to May, following Palis (2014) and Matthew Kwiatkowski et al. (unpubl. report). Efforts to document *L. areolatus* in Louisiana since the 1960s have been irregular geographically and temporally. From 2002–2003, surveys were conducted in Ouachita Parish at a location of historic abundance (Prairie Road) and from which most museum specimens from Louisiana were collected (Smith 2003; VertNet.org. 2019. Amphibia: *Rana/Lithobates areolatus*. Available from <http://portal.vertnet.org/search?q=crawfish+frog> [Accessed 25 February 2019]). Additionally, citizen scientists conducted frog call surveys in Calcasieu, Lafayette, Red River, and Acadia parishes from 1997 to 2017 as part of the Louisiana Amphibian Monitoring Program (Carter et al. 2021; <https://doi.org/10.5066/F7G44NG0>). Two routes surveyed

within these parishes (Rayne in Acadia Parish and Ossun in Lafayette Parish) detected *L. areolatus* between 2007 and 2010 (Carter et al. 2021). Because these parishes were intensively surveyed for multiple years, we focused our survey efforts on other parishes and locations with historic records, including Allen, Beaugard, Caddo, Franklin, Grant, Ouachita, Rapides, Richland, Vernon, and Webster parishes. For the 2019 breeding season, we used satellite images through Google Earth to identify potentially suitable habitat near each historic record. We focused on areas with prairie, grassland, pasture, or other non-row crop vegetation with open canopy and shallow, ephemeral ponds and wetlands. We then ground-truthed these locations to ensure habitat was still present and to find safe locations along roads where we could stop and listen. Near each historic locality, we established a call survey route comprising 12–20 stops, with each stop being spaced about 1 km apart or more. The calls of *L. areolatus* can be heard up to 0.8 km away (Busby and Brecheisen 1997). We established 14 routes (Fig. 2) primarily along quiet, secondary, and tertiary roads consisting of a total of

207 stops. We recorded GPS coordinates for each stop and estimated the total area sampled using buffer analysis in ArcGIS (Esri, Redlands, California, USA), assuming a listening radius of 0.8 km (Busby and Brecheisen 1997) around each of our stops.

We conducted call surveys similarly to the North American Amphibian Monitoring Program (NAAMP) protocol (Weir and Mossman 2005; Weir et al. 2014). As large rain events that saturate the soil usually initiate breeding migrations for *L. areolatus*, we focused surveys on the 1–3 nights after significant rainfall (> 1 cm) when temperatures were > 7.2°C (Busby and Brecheisen 1997). Each call survey started approximately 30 min after sunset, and we recorded the sky code (0–5 with 0 as no clouds to 5 as drizzle/light rain), moon visibility, and recent rain (hours passed and amount in mm; Weir and Mossman 2005). At each stop, two people listened for 5 min and recorded all frog species heard vocalizing. Detection probability is high during peak breeding (mean = 0.97, range of values 0.87–1.0) but generally low and unpredictable during the early season (mean = 0.26, range of values 0–0.8) for 5-min surveys of known populations of *L. areolatus* (Williams et al. 2013). Although Williams et al. (2013) recommended 15-min surveys should be employed for unknown or small populations of *L. areolatus* during early- or late-season calling, the gain in detection probability beyond 5 min during these times is modest (5.5% gain on average for 10 min, 11% gain on average for 20 min) and comes at a cost in the number of sites that can be visited during a night. Therefore, we used 5 min, as this sufficed in other studies for detecting *L. areolatus* during peak breeding (e.g., Busby and Brecheisen 1997) and allowed us to survey more sites per night. For each frog species heard, we assigned a calling index value of: 1 = individuals can be counted/space between calls; 2 = individuals can be distinguished but some calls overlap; or 3 = full chorus, which were continuous, constant, and overlapping calls (Weir and Mossman 2005). We also recorded air temperature (°C), humidity (%), and maximum wind speed (m/s) at each stop and counted the number of cars that passed during the 5-min period to assign a noise index from 0 (no appreciable effect) to 4 (profoundly affecting hearing of calls) to account for any interference with detection.

**Modeling strategy.**—To guide 2020 survey efforts, we built a preliminary ENM for *L. areolatus* in late 2019 using 124 occurrence points from Texas, Oklahoma, and Louisiana, and a subset of

environmental data layers (see below). In summer 2020, we then built a final ENM with additional environmental data layers and following best-practice recommendations by Merow et al. (2013) and Araújo et al. (2019).

**Species occurrence records.**—For our ENMs, we gathered occurrence locations for *L. areolatus* from VertNet (VertNet.org. 2019. op. cit.), Herpetological Review, iNaturalist, HerpMapper, and from personal communication with professional herpetologists. These occurrence coordinates were based on museum specimens, photographs, recorded calls, road kills, and eDNA surveys for the species. For the ENM, we restricted occurrence data to what is considered the southern subspecies (*L. areolatus areolatus*), which is the portion of the range of the species in Texas, Louisiana, southwestern Arkansas, and Oklahoma south of the Arkansas River (see Goin and Netting 1940; Bragg 1953; Parris and Redmer 2005; Powell et al. 2016). We also only used records from 1990 to the present to best match recent land use and climate with presence of *L. areolatus*. After removing duplicate records and those with missing coordinates, we were left with 124 occurrence points in Texas, Oklahoma, and Louisiana. To alleviate effects of sampling bias and spatial autocorrelation in our final model, we thinned our 124 occurrence points through spatial filtering such that all points were at least 5 km apart (Fourcade et al. 2014). After doing this, we were left with 55 occurrence points. To quantify geographic sampling bias, we calculated a Kernel Density Estimate of the sampling points using the S-PLUS 6.0 MASS package in R 1.5.0 (Venables and Ripley 2002; R Development Core Team 2020) and used it to generate a bias file for downstream use in the final ENM. Carter et al. (2021) reported two detections of *L. areolatus* in Acadia and Lafayette parishes in Louisiana, but this information was published after our modeling and call surveys, so we did not include them.

**Environmental variables.**—For environmental data, we used several climate, land cover, and soil hydrology variables (Table 1). We included climate variables because precipitation and temperature are critical for initiating and maintaining breeding activity, for determining hydroperiods of breeding ponds, and because they are often determinants of species range limits (Costa et al. 2008, 2010). Because habitat for *L. areolatus* is tallgrass or outlier prairie, wooded regions along streams associated with grasslands,

**TABLE 1.** Environmental variables used in Ecological Niche Modeling of the Crawfish Frog (*Lithobates areolatus*) in Louisiana, USA, and their original spatial resolution and source. Isothermality (Bio 3) is mean diurnal temperature range/annual temperature range.

Environmental variables	Resolution	Source
Soil hydrology:		
Hydrologic soil group	10 m	Gridded Soil Survey Geographic (gSSURGO) Database – 2016 <a href="https://gdg.sc.egov.usda.gov/">https://gdg.sc.egov.usda.gov/</a>
Topographic wetness index	1 km	Hydro1k – 2018 <a href="https://doi.org/10.5066/F77P8WN0">https://doi.org/10.5066/F77P8WN0</a>
Land cover	1 arc-sec	2016 National Land Cover Database (Homer et al. 2020)
Climate:		
Annual mean temperature (Bio 1)	30 arc-sec	WorldClim2.0 (Fick and Hijmans 2017)
Mean diurnal range (Bio 2)		
Isothermality (Bio3)		
Max. temp. warmest month (Bio 5)		
Mean temp. wettest quarter (Bio 8)		
Mean temp. driest quarter (Bio 9)		
Annual precipitation (Bio 12)		
Precip. wettest month (Bio 13)		
Precipitation seasonality (Bio 15)		

pastures, and in some cases, flooded agricultural fields (Bragg 1953; Smith 1961; Johnson 1987; Busby and Brecheisen 1997; Kory Roberts, pers. comm.), we included land cover to consider how vegetation and land use influence the distribution of the species. Additionally, we included soil hydrology variables to identify areas where shallow bodies of water (i.e., breeding sites) may form during large rains and where burrows of terrestrial burrowing crayfish (e.g., Devil Crayfish, *Lacunicambarus diogenes*, and Painted Devil Crayfish, *Lacunicambarus ludovicianus*; Chris Bonvillain, pers. comm.) may be present. Some environmental data layers were initially at different resolutions (Table 1), so we resampled the land cover and soil hydrology layers to 30 arc-sec (about 1 km<sup>2</sup>) to align with the climate layers. All layers were clipped in ArcGIS to a spatial extent that encompassed all known historic localities of the southern subspecies in Texas, Arkansas, Louisiana, and Oklahoma. Multicollinearity among variables can be a problem for Ecological Niche Modeling (Merow et al. 2013) and some of the 19 bioclim variables from WorldClim (Fick and Hijmans 2017) are highly correlated. To reduce multicollinearity, we ran a correlation analysis in ArcGIS on all 19 bioclim variables across our spatial extent. Using the correlation matrix, we identified groups of variables that were correlated at  $-0.75 > r > 0.75$  and retained just one variable from each group. We opted to retain variables representing minimums or maximums over averages because extremes are more likely to limit ranges of species (Costa et al. 2008). This reduced the number of climate variables to be used in modeling to

nine (Table 1).

**Preliminary ENM.**—We constructed ENMs for *L. areolatus* using a maximum entropy method implemented in Maxent (Phillips et al. 2006). Maxent uses environmental covariate data from occurrence records and a background sample to estimate presence sites in a focal area (Elith et al. 2011). Maxent also allows comparison of suitability estimates among regions because of its ability to generate a probability distribution for habitat suitability based on an index across the study area (Elith et al. 2011; Groff et al. 2014). In late 2019, we created a preliminary ENM for southern *L. areolatus* using the nine bioclim variables and land cover with our 124 localities from 1990 to the present (Table 1). We used the auto features and default settings of Maxent, including a regularization multiplier of 1 and 10,000 random background points sampled from the historic range of the southern subspecies of *L. areolatus*. To evaluate the model, we set aside 25% of our sample records for testing (Phillips et al. 2006). We imported the resulting suitability map in logistic output format into ArcGIS for viewing. A grid cell is considered to be unsuitable if its suitability value was less than the minimum training presence, which is the lowest predicted suitability value among all occurrence points in the training data set. Given this, we manually set classification breaks as  $< 0.011$  (unsuitable), 0.011–0.05 (low), 0.05–0.10 (moderate), 0.10–0.15 (high), 0.15–0.20 (higher), and  $> 0.20$  (optimal).

**Final ENM.**—Parameter settings of niche models can have large effects on model outcomes so species-specific tuning is recommended to improve model performance (Elith et al. 2011; Petford et al. 2019; Zurell et al. 2020). To aid in this for our final ENM, we used the R package ENMeval 0.3.0 (Muscarella et al. 2014) to construct ENMs under different parameter settings and perform model evaluation to identify the optimal settings for our data set. We built models with six combinations of feature classes and explored regularization multiplier values from 0.5 to 10 in 0.5 increments. Feature classes (linear, quadratic, product, threshold, hinge, categorical) are different mathematical transformations that can be applied to environmental variables to allow modeling of complex relationships whereas the regularization multiplier aims to penalize model complexity to prevent over-fitting (Merow et al. 2013; Morales et al. 2017). We used our thinned set of 55 occurrence points and our complete set of climate, land cover, and soil hydrology environmental variables (Table 1). We used the randomkfold method of cross-validation with five folds and 10,000 background points sampled from the historic range of the southern subspecies of *L. areolatus* with sampling density weighted based on our bias file (see above). We then chose the best model using the Akaike Information Criterion corrected for small sample sizes (AICc), which reflects both model goodness-of-fit and complexity (Burnham and Anderson 2004; Warren and Seifert 2011; Muscarella et al. 2014). The model with the lowest AICc value (i.e.,  $\Delta\text{AICc} = 0$ ) is considered the best, which in our case was the model with a regularization multiplier of 5 and linear (L) and quadratic (Q) feature classes. Using the optimal settings determined by ENMeval, we ran Maxent with the thinned set of 55 occurrence points and full set of 12 environmental variables (Table 1). We used the raw output format, as recommended by Merow et al. (2013), and incorporated our bias file so that the 10,000 background points were sampled based on sampling density (Fourcade et al. 2014). We used permutation and the jackknife method to estimate variable importance and set the maximum number of iterations to 5,000 (Rhoden et al. 2017) to allow more opportunity for model convergence. We imported the average suitability map of the five replicate folds into ArcGIS for viewing and rescaled the raw values to range from 0–1 by dividing by the maximum value. Cells with predicted suitability values below the minimum training presence (< 0.159) were considered unsuitable and we manually

set other classification breaks as 0.159–0.35 (low), 0.35–0.55 (moderate), 0.55–0.75 (high), and > 0.75 (optimal).

**Model evaluation.**—Visual inspection establishes an important plausibility check for spatial models (Zurell et al. 2020); however, we also assessed the accuracy of our model quantitatively using several methods including through Receiver Operating Characteristic (ROC) plots (Baldwin 2009). These plots graph sensitivity, which is how well the data correctly predict presence, and 1 - specificity, which is a measure of correctly predicted absences (Fielding and Bell 1997; Baldwin 2009). The significance of this curve is quantified by the Area Under the Curve (AUC) with values ranging from 0.5, indicating a fit no better than random, to 1.0, indicating a perfect fit (Baldwin 2009). A model with an AUC of 0.7 is considered informative and an AUC > 0.9 is a very strong model (Baldwin 2009). To evaluate the accuracy of our models, we used the AUC of training and test data for our preliminary ENM and the mean AUC of training and test data of our five replicates for our final ENM.

The use of AUC in ENM has been criticized, especially with presence-only data, and it may not be a good indicator of model accuracy (Lobo et al. 2007). Furthermore, methods to correct for sampling bias have been shown to produce models with lower AUC values (Fourcade et al. 2014), further questioning the utility of AUC in this context. Given these issues, we also used a null model approach to assess the performance of our final ENM following Raes and Ter Steege (2007). We created 100 data sets of 55 points each (the number of presence locations for *L. areolatus*) from the 10,000 background points sampled using our bias file. We then ran Maxent on the 100 data sets treating each as a set of occurrences of the species under the same settings as our final ENM above, minus the jackknife for variable importance. We compared both training and test AUC of our final model against the distribution of training and test AUCs of the 100 replicates. If the AUC of our model is in the top 5% of AUCs in the null distribution, then our model is considered significantly better than random.

**Call and automated audio recorder surveys.**—For the spring 2020 breeding season of *L. areolatus*, we used the preliminary ENM-predicted distribution for *L. areolatus* in Louisiana (Fig. 2) and Google Earth to identify potentially suitable habitat in areas not surveyed in 2019. As in 2019, we then ground-

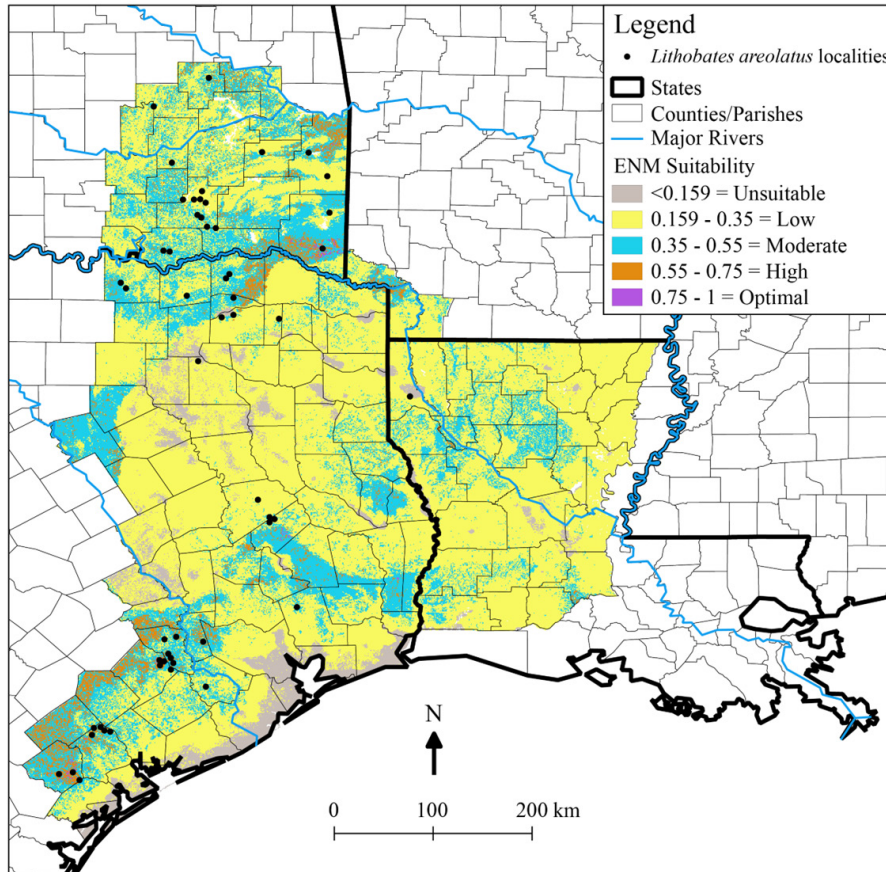
truthed these areas and established five new call survey routes in Red River, De Soto, Caddo, and Bossier parishes (Fig. 2). Adding these five new routes gave us a total of 19 routes and 292 stops for our 2020 surveys. We aimed to survey routes three times during the 2020 season if they occurred in areas predicted to be more suitable; however, due to the COVID-19 pandemic and resulting travel restrictions in late March 2020, we were only able to survey one of the five new routes three times, three routes twice, and one route once. In 2021, we were able to survey three of these new routes in the most suitable areas three additional times each but with only one listener due to social-distancing requirements. Latitude and longitude coordinates for each stop of our 19 routes and the survey dates for each route are provided in Supplemental Information Tables S1 and S2.

Because automated recorders can be used for extended periods and in difficult-to-access areas, they increase detection probability, especially for secretive frog species such as *L. areolatus* (Williams et al. 2013). In 2020 and 2021, we deployed three types of automated audio recorders (SM4 and SM-mini, Wildlife Acoustics Inc., Concord, Massachusetts, USA; Swift, Cornell Ornithology Lab, Ithaca, New York, USA) at sites the preliminary ENM predicted to be suitable for *L. areolatus* (Fig. 2). Recorders were placed on the Red River National Wildlife Refuge (NWR; Red River and Natchitoches parishes), Bayou Pierre Wildlife Management Area (WMA; Red River Parish), and Bodcau WMA (Webster Parish) in both 2020 and 2021, and in Loggy Bayou WMA (Bossier Parish) and Soda Lake WMA (Caddo Parish) in 2020 (Supplemental Information Table S3). The model predicted the Yates unit of the Red River NWR in Red River Parish as most suitable and the Lower Cane and Brake Bottom units in Natchitoches Parish as low suitability. Despite Lower Cane being of low predicted suitability, a U.S. Fish and Wildlife Service intern reported calling *L. areolatus* there and in the Yates unit in 2008, but these records were never confirmed (Carter et al. 2021; Gypsy Hanks, pers. comm.).

We deployed 12 recorders (four Swifts and eight SM4s) in 2020 and seven recorders (four Swifts, one SM4, and two SM-minis) in 2021 (Supplemental Information Table S3). In 2020, we initially deployed recorders from mid-January to mid-February and retrieved in early June. In 2021, we deployed recorders from mid-March to late May. We programmed recorders to record for 5 min every hour from sunset to sunrise (1800 to 0600 CST January to

early March and 1900 to 0700 CST mid-March to late May). We attached the recorders to trees by wetlands or shallow ponds in open grassland or scattered woodland. Flooding of the Red River on the Yates unit in February 2020 forced us to relocate two of the detectors further from the river, one of which was later relocated again to private land near one of our call survey routes in Vernon Parish (Fig. 2). This was because part way through the season some landowners informed us that they had potentially seen *L. areolatus* in June 2019 and claimed they heard their calls in mid-January 2020.

Audio recorders collected over 1,000 hours of recordings in 2020. To analyze recordings for the presence of *L. areolatus*, we developed a series of simple classifiers using Kaleidoscope Pro (Wildlife Acoustics Inc., Concord, Massachusetts, USA). We first obtained sound files with known *L. areolatus* from Texas (provided by Dan Saenz) and the Caddo Parish, Louisiana locations (provided by Brad Glorioso). For each site in each year, we created a training dataset by haphazardly selecting two nights of recordings from each month and combining those recordings with the known *L. areolatus* calls. A separate training data set and analysis was performed for each site because background noises are often site-specific and can affect the analysis (Knight and Bayne 2019). To identify sounds similar to *L. areolatus*, we tuned Kaleidoscope Pro to settings most likely to identify *L. areolatus* calls based on calls in the training data and known information on call characteristics (Lannoo et al. 2018). The signal parameters were set to 50–2500 Hz, duration of 0.3–0.7 s, and 0.5 s maximum inter-syllable gap. We performed a Cluster Analysis on each training dataset, *L. areolatus* calls were identified, and then a classifier was created. Cluster parameters were 2.0 maximum distance from cluster center to include in output, an FFT window of 21.33, which is best for lower frequency calls like owls and *L. areolatus*, 12 maximum states, 0.5 maximum distance to cluster center for building clusters (recommended by manufacturer), and 500 maximum clusters. The classifier was made so that it would label all *L. areolatus* calls and any similar sound as *L. areolatus*. If all *L. areolatus* calls in the training dataset were not correctly labeled in the first classifier, then we further refined the classifier until all *L. areolatus* calls in the training dataset were correctly labeled. Our goal was to minimize false negatives (i.e., accidentally missing a *L. areolatus* call). We then applied the final classifier for each site to the full set of recordings for that site with a



**FIGURE 3.** Potential distribution of the Crawfish Frog (*Lithobates areolatus*) across portions of Oklahoma, Arkansas, Texas, and Louisiana, USA, estimated by the final Ecological Niche Model (ENM) of this study. Species occurrences used in modeling are shown along with suitability value classes.

small number of *L. areolatus* recordings (test data) not used in the training data to evaluate how well the classifier performed on the test data. We then listened to every sound the classifier labeled as an *L. areolatus* and listened to 20 sounds in each of the other clusters to check for any calls that may have been missed by the classifier. If a cluster had *L. areolatus* calls from the test data missed by the classifier, we listened to 40 sounds in that cluster. Analyses resulted in an average of 43.5 clusters per site.

## RESULTS

**Call surveys of historic and ENM-predicted locations.**—From 18 January to 13 May 2019, we surveyed each of our 14 routes two to three times on a total of 34 survey nights (Supplemental Information Table S2). We surveyed approximately 366.1 km<sup>2</sup> within the Louisiana parishes with historic records of *L. areolatus*. We heard 13 frog species but detected no *L. areolatus* (Supplemental Information Table S4).

Notably, we recorded several species known to breed syntopically with *L. areolatus* (e.g., Cope’s Gray Treefrog, *Hyla chrysoscelis*, Cajun Chorus Frog, *Pseudacris fouquettei*, Spring Peeper, *Pseudacris crucifer*, Green Frog, *Lithobates clamitans*, and Southern Leopard Frog, *Lithobates sphenoccephalus*); Wright and Myers 1927; Busby and Brecheisen 1997; Parris and Redmer 2005), which indicated that we were surveying habitats potentially suitable for *L. areolatus*.

From 14 January to 29 March 2020, we surveyed each of our 19 routes one to three times (Supplemental Information Table S2). We were only able to conduct a total of 30 survey nights before we were forced to end surveys prematurely due to COVID-19. We surveyed approximately 528.7 km<sup>2</sup> within the Louisiana parishes with historic records of *L. areolatus* and four preliminary ENM-predicted parishes. We heard 11 frog species, including the same syntopic species listed above but detected no *L. areolatus* (Supplemental Information Table



S4). From 5 March to 30 April 2021, we surveyed three routes three times each for nine survey nights to supplement the 2020 season that was shorter than planned (Supplemental Information Table S2). Optimal weather conditions did not occur prior to March in 2021. The three routes were Mansfield in De Soto Parish, Coushatta in Red River Parish, and Shreveport in Caddo Parish. We heard nine of the same species as in previous years but detected no *L. areolatus* (Supplemental Information Table S4).

**Model predictions.**—Our preliminary ENM predicted sizeable areas of suitable habitat for *L. areolatus* in Louisiana, primarily in the northwestern part of the state in Caddo, Bossier, Webster, Claiborne, Red River, De Soto, Sabine, and Natchitoches parishes (Fig. 2). Much of Louisiana was predicted to be unsuitable (Fig. 2). Given this, we established new survey routes for 2020 in Red River, De Soto, Caddo, and Bossier parishes (Fig. 2). We also deployed our automated audio recorders on public lands (Red River NWR, Louisiana WMAs) located within or near suitable areas predicted by our model (Fig. 2).

Across our four-state spatial extent, our final ENM predicted the most suitable areas for *L. areolatus* are in the prairie regions of southeast Texas, eastern and southeastern Oklahoma into adjacent northeastern Texas, and the southwestern corner of Arkansas (Fig. 3). A large portion of eastern and central Texas was predicted to be unsuitable or of low suitability (Fig. 3). In Louisiana, our final ENM predicted some of the same areas of high suitability as the preliminary ENM such as western Red River and southeastern De Soto parishes (Figs. 2 and 3). The final ENM predicted almost all of Louisiana was suitable, although most was classified as low suitability (Fig. 3 and Supplemental Information Fig. S1). Northern Caddo and southwestern De Soto parishes were considered to be less suitable by the final ENM compared to the preliminary ENM (Figs. 2 and 3). Additionally, our final ENM predicted moderate suitability across much of northern Calcasieu, southern Beauregard, and central Allen parishes (Fig. 3). Our final ENM also identified six parishes (Jackson, Bienville, Winn, Caldwell, La Salle, and St. Landry) that contain sizable areas of moderate to high suitability but no historic records or survey effort for *L. areolatus* (Fig. 3). Given predictions of our final ENM, only half of the 12 parishes with historic records of *L. areolatus* were predicted to have appreciable areas of moderate to high suitability for the species. According to

our final ENM, three of our five new 2020 routes, and nine of our 14 2019 routes were in areas of low suitability for *L. areolatus*. Placement of our twelve audio recorders in 2020 and our six audio recorders in 2021 fell close to, or within, areas predicted to have moderate to high suitability in the final ENM.

**Environmental variable importance.**—Seven of the 12 environmental variables contributed to the final ENM in some capacity with the top five variables accounting for 99.7% of model fit (Table 2). Based on permutation and jack-knife analyses of variable importance, the most important variables were mean temperature of driest quarter (Bio 9), land cover, mean diurnal range (Bio 2), and Hydrologic Soil Group, with mean temperature of driest quarter being the single most important variable (Table 2). The probability of species presence was negatively related with the mean temperature of the driest quarter and positively related with mean diurnal range. Furthermore, *L. areolatus* showed a marked increase in the probability of presence when land cover is pasture/hay and/or when Hydrologic Soil Group is B/D (clay soils with a very slow infiltration rate and a high water table but that will have a moderate rate of infiltration and runoff if drained).

**Model evaluation.**—For our preliminary ENM, the AUC for training data was 0.91 and the AUC for test data was 0.92, indicating the model was

**TABLE 2.** Percentage contribution and permutation importance of each environmental variable analyzed in the final Ecological Niche Model (ENM) for the Crawfish Frog (*Lithobates areolatus*) across portions of Oklahoma, Arkansas, Texas, and Louisiana, USA. Abbreviations PC = percentage contribution and PI = permutation importance.

Variable	PC	PI
Mean temperature driest quarter (Bio 9)	39.7	54.5
Land cover	28.5	23
Mean diurnal range (Bio 2)	16	16.7
Hydrologic soil group	8.6	3.5
Isothermality (Bio 3)	7	0
Precipitation seasonality (Bio 15)	0.2	1.9
Topographic wetness index	0.1	0.3
Precipitation wettest month (Bio 13)	0	0
Annual precipitation (Bio 12)	0	0
Mean temperature wettest quarter (Bio 8)	0	0
Maximum temperature warmest month (Bio 5)	0	0
Annual mean temperature (Bio 1)	0	0

very strong. For our final ENM, the mean AUC for training data was 0.76 and the mean AUC for test data was 0.67, indicating the model was marginally informative. Using the null-model approach, both the mean training and test AUCs of our final ENM were significantly better than random ( $P = 0.03$  and  $0.01$ , respectively).

**Automated audio recorder surveys of ENM-predicted locations.**—Our classifiers for *L. areolatus* performed moderately well, correctly identifying 63.3–87.3% (mean = 73.6%) of test calls. Because classifiers were designed to minimize false negatives in the training data, many sounds were incorrectly identified as *L. areolatus*, including some calls of other frog species (e.g., American Bullfrog, *Lithobates catesbeianus*, *L. clamitans*, *L. sphenoccephalus*), Coyotes (*Canis latrans*), crows (*Corvus* spp.), owls (Strigidae, Tytonidae), and trains. All of these have a component of their call/sound that overlaps the frequency of *L. areolatus* calls. No *L. areolatus* calls were detected in any of the recordings from our sites in either year.

## DISCUSSION

We found no extant populations of *L. areolatus* at our survey sites in Louisiana despite considerable effort and a multifaceted approach that included nighttime call surveys near historic localities during the breeding season (January–April), Ecological Niche Modeling to predict where suitable conditions exist, and automated audio recorders in areas identified as being suitable for the species. These results indicate the species is either extirpated from most of the state or incredibly rare. Our findings add to a growing concern about the status and conservation of *L. areolatus* across its geographic range. Declines have been documented in many of the 13 states in which they occur, leading to conservation ranks of S1-Critically Imperiled or S2-Imperiled in six states with another four states listing them as S3-Vulnerable ([https://explorer.natureserve.org/Taxon/ELEMENT\\_GLOBAL.2.106291/Lithobates\\_areolatus](https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.106291/Lithobates_areolatus)). Our results and recent information from northwest Arkansas (Kross and Willson 2022) show that declines and local extirpations appear to be range wide. Conservation efforts for *L. areolatus* should be undertaken in Louisiana to avoid or reverse extirpation from the state. Efforts should include conducting additional surveys in areas not covered well by our study (see below), restoring habitat, and

reintroducing the species.

Even though we did not detect *L. areolatus*, our final ENM still provided novel insight into regional suitability, identifying areas of high suitability in eastern and southeastern Oklahoma, southeastern Texas, and the southwestern corner of Arkansas. With regard to Louisiana, the largest areas of highest suitability occurred in western Red River, southeastern De Soto, and southern St. Landry parishes. The 12 parishes with historic records of *L. areolatus* were predicted to be of predominately low to moderate suitability. Several parishes (e.g., Jackson, Winn, and St. Landry) with no historic records or survey effort for *L. areolatus* were predicted to contain sizable areas of moderate to high suitability. These parishes should be explored through nighttime call surveys and automated audio recorders in the future.

We found climatic, hydrologic, and land use variables were all important in predicting the distribution of *L. areolatus*. Our final ENM showed mean temperature of the driest quarter was the most important variable associated with the presence of *L. areolatus*, with the species showing a steady decline in occurrence probability with increased temperature. Higher temperatures in the driest quarter could increase the rate that ponds dry, leading to shorter hydroperiods, which in turn could mean low to no recruitment of *L. areolatus*. Low survivorship of tadpoles and juveniles would be detrimental to populations (Kinney 2011; Stiles et al. 2016; Terrell et al. 2023). Additionally, high temperatures when it is dry could increase desiccation rates when *L. areolatus* are active on the surface. As *L. areolatus* are known to occupy deep crayfish burrows and descend to the chamber in the water table to avoid desiccation (Heemeyer et al. 2012), individuals could stay safe (moist) in their burrows during the day, but low humidity at night could restrict surface activity such that they cannot feed to meet their metabolic demands. As smaller individuals (juveniles) are generally more vulnerable to desiccation (Child et al. 2006; Rittenhouse et al. 2008) and have higher metabolic rates than larger individuals (Prokić et al. 2019), juvenile *L. areolatus* could be most impacted by dry conditions. Increased temperature and aridity with climate change may lead to additional loss of suitable habitat for *L. areolatus* (Lannoo and Stiles 2020) and this may already be happening in the western part of the distribution (Seager et al. 2018). A better understanding of how temperature and precipitation patterns influence the distribution, population demography, and activity patterns of *L.*

*areolatus* is needed to predict how the species will respond to future climatic changes.

Our ENM showed a marked increase in the probability of presence of *L. areolatus* when land cover was pasture/hay and for Hydrologic Soil Group B/D, which are clay soils with a very slow infiltration rate and a high water table. The importance of pasture/hay is consistent with the ecology of the species and a key feature we used when establishing call survey routes. The presence of Hydrologic Soil Group B/D would allow for the accumulation of shallow, temporary, fishless bodies of water for *L. areolatus* to breed (e.g., Bragg 1953; Busby and Brecheisen 1997; Williams et al. 2012). This soil type would also promote the persistence of moisture in terrestrial crayfish burrows throughout the dry season, providing refuge for *L. areolatus*. The terrestrial crayfish species *Lacunicambarus diogenes* is widely distributed throughout eastern North America and is known to dig elaborate and deep burrows in clay-dominated soils to a depth of 0.15 to 5 m that contain hypoxic/anoxic water (Grow and Merchant 1980; Helms et al. 2013). *Lithobates areolatus* preferentially occupies deep burrows by descending to the chamber in the water table to avoid desiccation in summer and to seek warmer temperatures in winter (Heemeyer et al. 2012). Terrestrial burrowing crayfish species such as *L. diogenes* therefore provide suitable burrows for *L. areolatus* and are likely important determinants of occupancy.

Because *L. areolatus* lives most of the year in crayfish burrows in terrestrial uplands and migrate an average of 400–500 m, and occasionally > 1 km, to nearby ponds for breeding (Heemeyer and Lannoo 2012; Matthew Kwiatkowski et al., unpubl. report), our approximately 1-km spatial scale for variables used in modeling captured variation in both of these important habitat components. In the future, however, ensemble modeling could be incorporated to explore the range of predictions given different uncertainties (i.e., initial conditions, model classes, etc.) and direct future survey efforts (Araújo and New 2007; Thuiller et al. 2009; Breiner et al. 2015, 2018; Hao et al. 2019; Zurell et al. 2020). Additionally, given the importance of climatic variables in our model, another future step might be to look at how the distribution of *L. areolatus* is projected to change under different climate change scenarios.

Because *L. areolatus* rely on crayfish burrows and undisturbed soil, they are threatened by terrestrial upland habitat loss or modification in addition to any loss or modification of aquatic breeding habitats.

With respect to the southern range of *L. areolatus*, Lannoo and Stiles (2020) speculated declines were not as severe because much of the land area in Texas was used for cattle grazing (pasture) rather than row crop agriculture, which required tilling of soil. Texas Tallgrass Prairie, however, declined by 90% from 1830 to 1994 with most of the loss occurring in coastal prairie due to conversion to farmland (Samson and Knopf 1994; Matthew Kwiatkowski et al., unpubl. report). In Louisiana, the historic Cajun Prairie declined from an overall 1 M ha in the late 1800s to about 40 ha of remnant prairie in 2000 (Fontenot and Freeland 1976; Vidrine et al. 2001). This eastern extension of the Gulf coastal prairie (Allen and Vidrine 1989; Smeins et al. 1992; Vidrine et al. 1995; Allain and Johnson 1997; Allain et al. 2000) comprised tallgrass vegetation and associated swamps, marshes, and pine forests with savannas (Vidrine et al. 2001). Cajun Prairie received an average annual rainfall of > 1.25 m, which commonly flooded its marais (marshes) and platins (circular ponds) for long periods of time (Vidrine et al. 2001). These would have been ideal habitats for *L. areolatus* to breed but as early as the late 1800s, many of the marais and platins were developed into rice patties (Fontenot and Freeland 1976; Vidrine et al. 2001) and by the mid-1900s, the remaining prairie had been plowed and widespread erosion led to a stream-dredging program across the area (Vidrine et al. 2001).

In a land use assessment of the USA, Louisiana was one of the states with the most land use change over a 10-y period (2001–2011) in the form of forest harvesting, urbanization, and agricultural conversion (Homer et al. 2015). Given changes of this magnitude, it is no surprise most historic records of *L. areolatus* date prior to the 1970s, and the species is now either extirpated or extremely rare. Several factors may explain why we did not record any *L. areolatus* in our surveys despite potentially suitable habitat for the species. First, many areas, including NWR units, were historically disked, which would have killed *L. areolatus* living underground in burrows (Heemeyer et al. 2012). Studies of *L. areolatus* in prairie habitats of western Arkansas found occupancy was positively associated with indicators of a historic lack of human disturbance and current site conditions were a poor predictor (Royal et al. 2023). Second, many areas, such as the NWR units and WMAs, are bordered by either the Red River and/or surrounded by agricultural fields or timber forests, which are likely obstacles to any potential dispersal by *L. areolatus* into these

areas. In recent surveys for *L. areolatus* in central Arkansas, however, individuals have been observed calling in flooded agricultural fields and ditches (Kory Roberts, pers. comm.), and scientists in other parts of its range have reported similar observations (see Bragg 1953; Smith 1961; Johnson 1987; Busby and Brecheisen 1997). As breeding in *L. areolatus* is short-duration and depends on optimal habitat and climatic conditions, it is logistically impossible to survey all possible locations in one or two seasons. We encourage additional surveys and suggest protected areas (NWRs, WMAs) be examined in more detail as potential reintroduction sites for the species should such efforts be pursued in Louisiana. Captive-rearing (i.e., head starting) projects to supplement existing populations or establish frogs in formerly occupied or restored sites are underway for *L. areolatus*, *L. capito*, and *L. sevosus* in other states so protocols are well established (U.S. Fish and Wildlife Service 2015; Stiles et al. 2016; Nelson et al. 2024).

Our study represents the most comprehensive survey to date for *L. areolatus* within Louisiana. Based on our results of no individuals or remnant populations being found over the course of 3 y, and because the potential remains for the species to persist within the state, we concur with the current S1-Critically Imperiled rank for the species in Louisiana. We further suggest the species be added to the list of Prohibited Species of Louisiana to protect them from harvest/collection. We have also demonstrated how call surveys and Ecological Niche Modeling can be used to assess the distribution and status of a rare amphibian species. Our ENM-estimated climatic and habitat associations for *L. areolatus* can serve as a tool for ongoing survey efforts for the species in Louisiana. Focused surveys should continue through the combined effort of call surveys and audio recorders on both private and public land, where possible. Moreover, we suggest the reintroduction of *L. areolatus* into Louisiana be actively pursued.

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