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# Species Distribution Modeling and Niche Overlap for the Louisiana Pine Snake (*Pituophis ruthveni*) and Baird's Pocket Gopher (*Geomys breviceps*)

*Katie Cantrelle, Justin D. Hoffman, and Eddie K. Lyons*

## Abstract

The Louisiana pine snake (*Pituophis ruthveni*) is one of the least studied snakes in North America and recently was listed as Threatened under the United States Endangered Species Act. They often are associated with longleaf pine (*Pinus palustris*) savanna and rely on the Baird's pocket gopher (*Geomys breviceps*) as a major part of their diet, as well as using their burrows for hibernacula. A comparison of geographic ranges, however, show that Baird's pocket gopher is more widespread than the Louisiana pine snake. This suggests that factors other than prey availability limit the overall distribution of the Louisiana pine snake. Our objectives were to generate species distribution models, identify environmental variables that best predicted occupancy, and perform tests of niche overlap between species. Maxent was used to build the species distribution models and tests of niche overlap were performed using ENMTools. Measures of precipitation were most important for predicting occupancy for the Baird's pocket gopher, whereas precipitation and temperature were most important for the Louisiana pine snake. Tests of niche overlap between the Baird's pocket gopher and the Louisiana pine snake were significantly different than the null distribution, which indicate different niche requirements for each species. The Red River in Louisiana appears to have separated regions of habitat for the Louisiana pine snake, creating potential conservation concerns if populations are isolated. Finally, predictions of distribution for the Louisiana pine snake closely resemble the historical distribution of longleaf pine savanna, which is indicative of their close association.

Key words: Baird's pocket gopher, environmental predictors, fundamental niche, *Geomys breviceps*, habitat preferences, Louisiana pine snake, *Pituophis ruthveni*, species distribution modeling

## Introduction

Large-scale research on the distribution and habitat requirements of endangered and threatened species is difficult because of their often limited distributions and small population sizes. Advances in distribution modeling over the past two decades have aided in the monitoring and restoration of rare species by providing a better understanding of their habitat preferences and requirements (Hamilton et al. 2015; McCune 2016; Eaton et al. 2018), assisting in the discovery of new populations by guiding field surveys (Mizsei et al. 2016; Fois et al. 2018), and identifying areas that are suitable for reintroductions (Borthakur et al. 2018; Maes et al. 2019). The Louisiana pine snake (*Pituophis ruthveni*) is among the rarest and least studied snakes in North America (Adams et al. 2017) and currently is categorized as Endangered according to the International Union for the Conservation of Nature (IUCN) and recently was listed as Threatened under the United States Endangered Species Act (USFWS 2018). The Louisiana pine snake is fossorial, only spending short periods of time on the surface (Ealy et al. 2004), and is endemic to western Louisiana and eastern Texas (Conant 1956). It is closely associated with open pine forests, especially longleaf pine (*Pinus palustris*) savannas that possess sandy, well drained soils and an understory that is dominated by grasses (Himes et al. 2006; Wagner et al. 2014).

Longleaf pine savanna once stretched across 90 million acres in the southeastern United States but has been reduced to approximately 5% of its native range (Frost 1993). The significant loss of longleaf pine savanna can be attributed to changes in land use and silvicultural practices, as well as alteration of fire regimes (Landers et al. 1995). Much of this native ecosystem has been replaced with other species of coniferous trees, such as loblolly pine (*Pinus taeda*) or slash pine (*Pinus elliotti*; Outcalt 1997). These shifts in land use and vegetation are thought to have resulted in population declines of the Louisiana pine snake throughout its native range (Reichling 1995; Rudolph et al. 2006).

Within the longleaf pine forest ecosystem, the Louisiana pine snake is closely associated with the Baird's pocket gopher (*Geomys breviceps*). These subterranean rodents represent 75% of the diet biomass for the Louisiana pine snake (Rudolph et al. 2012), and their burrows are used as hibernacula and for fire avoidance (Himes 2000; Rudolph et al. 2007). Baird's pocket gopher is found in areas with sandy, well drained soils (Davis et al. 1938; Wagner et al. 2017), but unlike the Louisiana pine snake, they are not restricted to the longleaf pine savanna ecosystem (Sulentich et al. 1991). The range of the Baird's pocket gopher extends beyond Texas and Louisiana into Oklahoma and Arkansas (Honeycutt and Schmidly 1979) where they often occur in disturbed areas such as roadside rights-of-way, manicured lawns, and pine forests that were recently logged.

Rudolph and Burgdorf (1997) hypothesized that the loss of herbaceous vegetation in the longleaf pine ecosystem due to fire suppression has caused pocket gopher densities to decline and, as a result, populations of the Louisiana pine snake have further declined. Most data on habitat use of the Louisiana pine snake and its preferred prey, Baird's pocket gopher, have been collected in small areas that do not capture landscape-scale habitat preferences (Himes et al. 2006; Wagner et al. 2014; Wagner et al. 2017). Understanding how environmental factors affect the presence of these species and where potential habitat exists at landscape scales will aid in conservation planning. For instance, Rudolph et al. (2018) concluded that one of the most crucial management issues needed for the recovery of the Louisiana pine snake is the identification of additional reintroduction sites. For this to happen, a better understanding of the relationship between the Louisiana pine snake and the environment at both small and large spatial scales is needed. Our objectives were to 1) generate landscape-scale occupancy models for the Louisiana pine snake and Baird's pocket gopher, 2) determine which environmental predictors are most important and limiting to each species, and 3) use measures of niche similarity and overlap to compare the niche requirements for the Louisiana pine snake and Baird's pocket gopher.

## Methods

Occurrence records of the Louisiana pine snake were compiled from data provided by the Louisiana Department of Wildlife and Fisheries (LDWF). Prior to 1993, there were fewer than 60 known records of the Louisiana pine snake. These records were obtained primarily through targeted surveys of certain areas (Conant 1956; Thomas et al. 1976; Young and Vandeventer 1988). Due to the paucity of information on the Louisiana pine snake's distribution, an extensive trapping survey was conducted from 1993 to 2001 (Rudolph et al. 2006). The trapping protocol consisted of setting funnel traps in areas of Texas and Louisiana where historical records existed, and then trapping in areas with no prior records. In all, 14 sites across 10 counties in Texas and 9 sites across 5 parishes in Louisiana were surveyed. Six of 23 sites yielded captures of the Louisiana pine snake. All snakes were released at the point of capture. Since these surveys, additional occurrence data were added through continued trapping efforts by the United States Forest Service, Texas Parks and Wildlife, Louisiana Department of Wildlife and Fisheries, and United States Fish and Wildlife Service. In total, 187 *P. ruthveni* have been captured in seven Louisiana parishes and 45 individuals have been captured in 11 Texas counties (Appendix I). Exact capture localities are not provided for this species given its conservation status. Occurrence data for the Baird's pocket gopher from Texas and Louisiana (Appendix II) was downloaded using the online database VertNet (http://vertnet.org). This site provides access to biodiversity data from various museum collections.

Duplicate records were removed from the occurrence data and only records collected from 1960 to 2010 were retained. This range of collection dates was chosen because it generally aligns (+/- 10 years) with the temporal scale of the climate data (1970–2000) and allowed us to maximize the number of records for modelling (Phillips et al. 2017). Sampling bias is a common problem in occurrence data and can lead to environmental bias and inaccurate model predictions (Phillips et al. 2009; Kramer-Schadt et al. 2013; Syfert et al. 2013). Occurrence data were filtered so that no occurrence point (within each species) was < 10 km apart to limit sample selection bias (Boria et al. 2014). This distance was chosen because there is a paucity of information on the maximum dispersal distances of each species and 10 km between occurrences should sufficiently limit sample selection bias. The Geographic Distance Matrix Generator v. 1.2.3 (Ersts 2020) was used to determine distances between points. One point was randomly removed from a cluster of localities and the matrix was rerun. This process was repeated until all points were > 10 km from each other. Temporal and spatial filtering reduced the initial number of occurrences from 142 to 47 for the Louisiana pine snake and from 502 to 241 for the Baird's pocket gopher.

Digitized climate and soil layers were imported into ArcGIS (version 10.5.1) and overlaid on localities of the Baird's pocket gopher and the Louisiana pine snake. These environmental predictors were chosen because climate variables, such as temperature and precipitation, strongly influence the distribution of species (Andrewartha and Birch 1954). Also, fine scale studies have shown that soil characteristics strongly influence the occurrence of the Louisiana pine snake and Baird's pocket gopher (Himes et al. 2006; Wagner et al. 2014, Wagner et al. 2017). Both species, especially the Louisiana pine snake, is notably associated with longleaf pine forests; however, the distribution of vegetative communities is ultimately determined by the underlying substrate and climate (i.e., temperature and precipitation) of the region. Because these layers are included in the analysis, vegetative data was not used so that a clear relationship between each species and the environment could be determined. Climate layers were downloaded from the North America WorldClim database (version 2.1; http://www.worldclim.org/; Fick and Hijmans 2017). WorldClim data are a set of 19 bioclimatic variables (BIO 1–19) that are based on climate conditions from 1970 to 2000. These data were derived from monthly temperature and precipitation values from a global network of 4,000 climate stations. Temperature was recorded in degrees Celsius × 10 and precipitation in millimeters. Data on soil permeability, porosity, rock fragment volume, and soil texture (percent sand, percent silt, and percent clay) were obtained from the Earth System Science Center at The Pennsylvania State University's Soil Information for Environmental Modeling and Ecosystem Management effort (http://www.soilinfo.psu.edu). All climate and soil data possess a 1 $km^2$ spatial resolution. Each layer was transformed with an Albers equal area projection.

Maxent (3.3.3k) was used to model the distributions of the Louisiana pine snake and Baird's pocket gopher because it is designed to make predictions from incomplete or sparse data (Phillips et al. 2006). Maxent predictions were produced with the raw output and interpreted as the relative occurrence rate, which is the probability that a given cell on the landscape is included in a collection of presence records (Merow et al. 2013). Maxent often has outperformed other presence-absence and presence-only models (Elith et al. 2006; Hoffman et al. 2010) and has been used to model the distribution of endangered species such as the flat-headed cat *Prionailurus planiceps* (Wilting et al. 2010) and the critically endangered Himalayan soap pod tree *Gymnocladus assamicus* (Menon et al. 2010). Maxent has produced high-quality models with little sensitivity to sample size (Wisz et al. 2008). In addition to producing estimates of occurrence, results from Maxent have been combined with tests of niche similarity and overlap (Warren et al. 2010; Warren and Seifert 2011) to better understand the role of environmental factors in limiting species ranges at large spatial scales (Glor and Warren 2010; Trumbo et al. 2016; Coxen et al. 2017; Hu and Jiang 2018).

Maxent does not require data on species absence; rather, it uses a set of background points to characterize the surrounding environment. The area where background points are drawn from is called the background extent. This area can significantly impact model results and should be determined based on some ecological justification (Elith et al. 2011; Barbet-Massin et al. 2012; Merow et al. 2013). Several methods have been used to set the background extent and choose background points. Phillips et al. (2009) used background points taken from a set of target species that possess the same sampling bias as the occurrence data. Other studies have generated background points from a pre-defined buffer around each occurrence point (Coxen et al. 2017; Jarnevich et al. 2017). This buffer is meant to reflect the dispersal distance or home range of the target species. Both approaches presented challenges in defining the background extent for the two species in this study. For instance, little is known about the dispersal abilities or home range size for either species (Himes et al. 2006; Wagner et al. 2017), especially the Baird's pocket gopher. Due to this paucity of information, it was not possible to assign a pre-defined buffer around each point that was ecologically justifiable. The problem with using a set of target species for background points is that they must have the same sampling bias as the occurrence data to be meaningful (Phillips et al. 2009). Pocket gophers present a challenge to this because their movements are restricted to underground burrows and require different survey and trapping methods compared to terrestrial small mammals. Given these issues and in order to be consistent in our methodology between species, the background extent was set to the counties/parishes with species occurrence data. This limits the background data to areas where surveys have been conducted and that are accessible to each species (Barve et al. 2011). For each species 10,000 background points were generated.

Twenty-six (19 climate, 7 soil) predictor variables were included with the occurrence data in Maxent. An initial investigation was conducted to determine the impact of model complexity and variable selection on Maxent predictions. Model complexity in Maxent is determined by two modifiable parameters (Elith et al. 2011). The first is feature class, which transforms the environment variables and includes linear, quadratic, product, threshold, and hinge features. The default feature class setting (Auto features) allows all feature types to be used. The second parameter is the regularization multiplier (beta parameter), which balances model fit with model complexity. The default value for the regularization multiplier is 1 (Phillips and Dudik 2008). Several studies have found that the default settings in Maxent do not always provide the best prediction (Merow et al. 2013; Muscarella et al. 2014; Morales et al. 2017). To determine which combination of feature class(es) and regularization multiplier provided the best model, a similar approach to the one recently developed by Perkins-Taylor and Frey (2020) was used. This approach incorporates variable selection by objectively removing highly correlated variables in addition to tuning measures of model complexity.

First, a Pearson's correlation matrix was generated for climate and soil data to identify highly correlated variables ($r > 0.99$). None of the variables for either species possessed this level of correlation so we proceeded to tune the regularization multiplier and feature classes using all 26 predictor variables. Candidate models were generated using all possible feature class combinations and regularization multipliers from 0.5 to 5 in increments of 0.5. ENMTools 1.3 (Warren et al. 2010) was used to calculate Akaike's Information Criteria with a small sample size correction (AICc) to determine which feature class(es) and regularization multiplier provided the best fit model (Burnham and Anderson 2002). A model was considered best fit if it had the lowest AICc value.

Next, these settings were used to produce a Maxent model using all environmental variables. Any variable with less than 5% contribution was removed from the analysis. Then, any variable(s) that were highly correlated ($r > 0.7$) with the variable that had the highest percent contribution was removed and the model was rerun using the reduced set of predictor variables. This process was repeated until all variables were either retained or removed. Finally, the model regularization multiplier and feature class(es) were retuned using the reduced set of environmental variables and we selected the final model as the one with the lowest AICc value.

Additional metrics of model fit are provided for the final model (as determined by AICc), including the minimum training presence (MTP) and 10% training presence omission rates, as well as the area under the receiver operating characteristic curve (AUC). Previous studies have noted that AUC can falsely inflate model fit due to spatial autocorrelation (Lobo et al. 2008; Veloz 2009). Model accuracy is dependent on the data chosen to test the model results. To address this issue, omission rates and AUC were calculated using a k-fold cross-validation. This method splits the data into folds/sections, where one fold is used to train the model and the rest are used for testing. The process repeats itself until all folds are used for testing. A 5-fold cross-validation was used for the Louisiana pine snake because it had a relatively small sample size ($n = 47$) and a 10-fold cross-validation was used for the Baird's pocket gopher ($n = 241$). Other model settings included a convergence threshold of $10^{-5}$ and 5,000 maximum iterations. Variable importance was determined by its percent contribution to the model's prediction and a jackknife analysis. Finally, Maxent was directed to produce response curves for the variable with the highest percent contribution showing how the probability of presence changes over a range of values.

Niche requirements for the Louisiana pine snake and the Baird's pocket gopher were compared by calculating measures of niche overlap and niche breadth using ENMTools 1.3 (Warren et al. 2010). Niche overlap is a measure of similarity between the predicted occurrence (those produced from Maxent) of two or more species. Three similarity statistics were used to compare the predictions: Schoener's D, I statistic, and relative rank. Schoener's D statistic (Schoener 1968) compares measures of niche similarity based on microhabitat or diet. However, Warren et al. (2008) warns that the D metric could imply an unjustified biological interpretation of cell values because the assumptions of the metric may not align with the output of the species distribution model. The I metric is a similarity statistic that treats the value of each cell on a map as a probability distribution (Warren et al. 2008). Finally, the relative rank statistic estimates the probability that the ranking of any two patches of habitat are the same. Ultimately it measures the model's ability to determine the relative rank of two randomly chosen patches of habitat regardless of their exact habitat suitability statistic (Warren and Seifert 2011). The metrics I and D are determined by comparing the probability of occupancy between species at each grid cell. Each statistic ranges from 0 (no overlap) to 1 (complete overlap). Niche identity and background similarity tests were performed in ENMTools 1.3 to determine the significance of these measures. The niche identity test determines if a species ecological niche differs more than expected from the same underlying distribution, and the background similarity test is used to establish if the ecological niches from species with overlapping ranges are different from one another. Each test was performed for both I and D metrics using 1,000 replicates to generate a psuedoreplicated null distribution. Significance between the I and D values with the null distribution was determined using a paired T-test. Niche breadth is determined in ENMTools 1.3 using the threshold independent inverse of Levin's index (Levins 1968) and is a measure of how much of the study area is suitable for each species. This index uses the occupancy scores from Maxent and then standardizes them so that they range from 0 to 1 with higher numbers indicating that more of the landscape is being used.

## RESULTS

The Maxent model with the lowest AICc value for the Louisiana pine snake had a regularization multiplier of 1.5, used linear and quadratic features, and had an AUC value = 0.85. This model had omission rates of 0.11 (10% training) and 0.07 (MTP). The occupancy models from Maxent show that probability of occurrence for the Louisiana pine snake is found in parts of northern and western Louisiana and eastern Texas (Fig. 1). Areas with high probability of occurrence are not continuous, however, with regions in northern

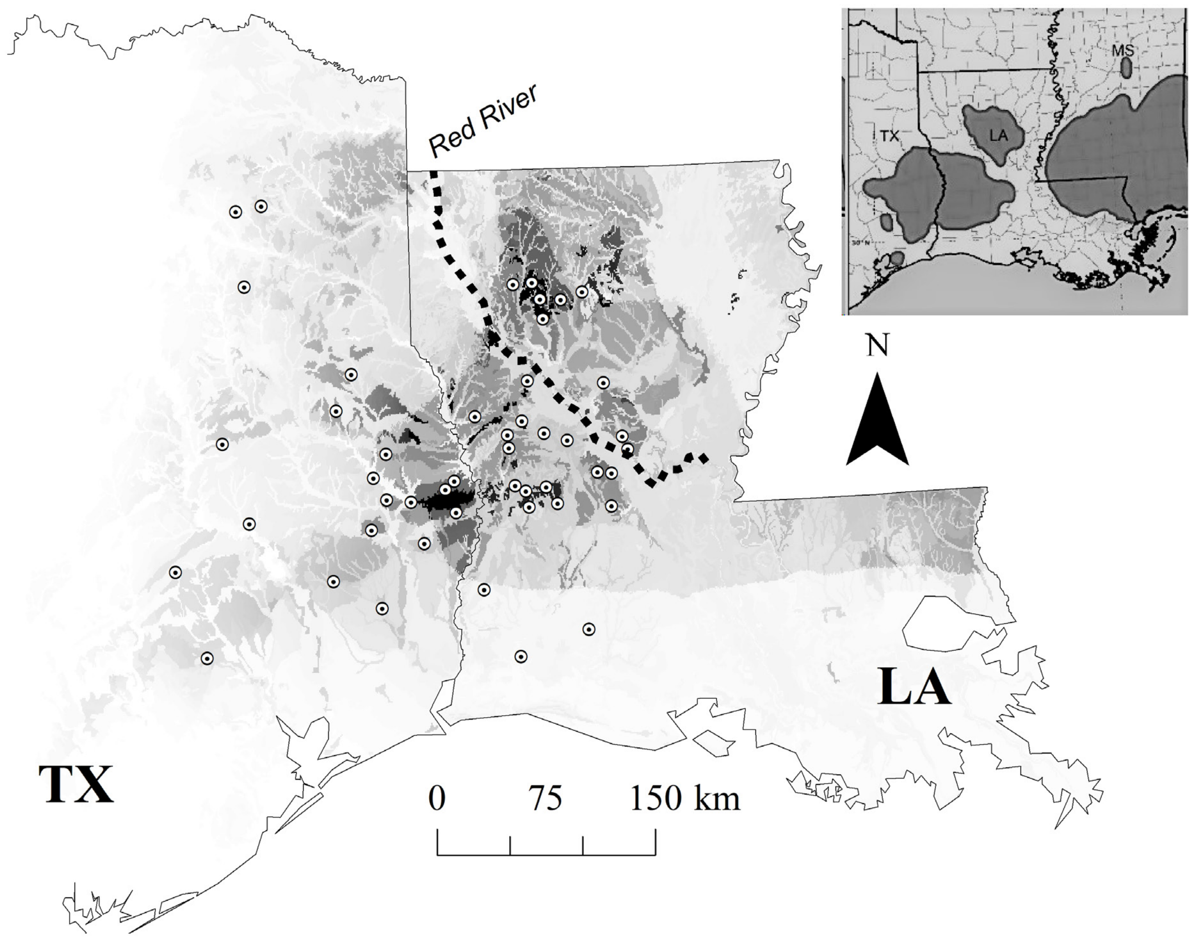


Figure 1. Predicted occupancy for the Louisiana pine snake (*Pituophis ruthveni*) in Louisiana and Texas. Darker shading indicates higher occupancy rates. Enclosed circles represent spatially and temporally selected species occurrences. Map inset shows the historical range of longleaf pine savanna in Louisiana, Texas, and Mississippi as drawn by United States Department of Agriculture.

Louisiana being separated by the Red River from those in western Louisiana and eastern Texas. Results of the jackknife analysis for variable importance show a mix of precipitation and temperature related variables as most important (Table 1). Precipitation of the Coldest Quarter was the highest ranked variable in training gain and AUC, whereas Precipitation of the Driest Quarter was highest ranked for testing gain. Similarly, Precipitation of the Coldest Quarter had the highest percent contribution (40.8 %) to the model (Table 2). The response curve shows that probability of occurrence in the Louisiana pine snake is highest in areas where the precipitation during the coldest quarter was approximately 250 mm and declined as precipitation levels decreased (Fig. 2).

The Maxent model with the lowest AICc value for Baird's pocket gopher had a regularization multiplier of 0.5, used the threshold feature, and had an AUC = 0.71. This model had omission rates of 0.058 (10% training) and 0.012 (MTP). Probability of occupancy for Baird's pocket gopher are highest in the western and northern regions of Louisiana and in eastern and northern central Texas (Fig. 3). The jackknife analysis on training and testing data determined that Precipitation of the Driest Quarter was the most important variable followed by Mean Temperature of the Driest Quarter (Table 1). The ranking of these two variables was inverted for the jackknife analysis on AUC testing data. Precipitation of the Driest Quarter had the highest percent contribution (82.5 %) towards the model (Table 2). Probability of

Table 1. Maxent jackknife results of variable importance for the Baird's pocket gopher (*Geomys breviceps*) and the Louisiana pine snake (*Pituophis ruthveni*). Measures of variable importance include the training gain, testing gain, and AUC values for testing data. Only the three most important variables for each category are listed.

| | Baird's pocket gopher | | Louisiana pine snake | |
|---|---|---|---|---|
| | Variable | Value | Variable | Value |
| Training gain | Precip Driest Qrt | 0.154 | Precip Coldest Qrt | 0.631 |
| | Mean Temp Driest Qrt | 0.015 | Precip Driest Qrt | 0.599 |
| | Clay | 0.014 | Mean Temp Wettest Qrt | 0.493 |
| Test gain | Precip Driest Qrt | 0.211 | Precip Driest Qrt | 0.566 |
| | Mean Temp Driest Qrt | 0.165 | Precip Coldest Qrt | 0.524 |
| | Clay | 0.051 | Mean Temp Wettest Qrt | 0.492 |
| AUC | Mean Temp Driest Qrt | 0.675 | Precip Coldest Qrt | 0.775 |
| | Precip Driest Qrt | 0.632 | Mean Temp Wettest Qrt | 0.748 |
| | Clay | 0.621 | Precip Driest Qrt | 0.741 |

Table 2. Average percent contribution of environmental variables for the Louisiana pine snake (*Pituophis ruthveni*) and Baird's pocket gopher (*Geomys breviceps)* generated in Maxent using a 5-fold cross validation for the pine snake and a 10-fold cross validation for the pocket gopher. The highest average percent contribution is in bold type.

| | Percent contribution | |
|---|---|---|
| Variable | Louisiana pine snake | Baird's pocket gopher |
| Precip Driest Qrt | 25.1 | **82.5** |
| Mean Temp Wettest Qrt | 15.4 | -- |
| Precip Coldest Qrt | **40.8** | -- |
| Sand | 23.7 | -- |
| Clay | -- | 9.0 |
| Mean Temp Driest Qrt | -- | 4.0 |
| Rock Volume | -- | 4.5 |
| Mean Temp Warmest Qrt | -- | 0.0 |

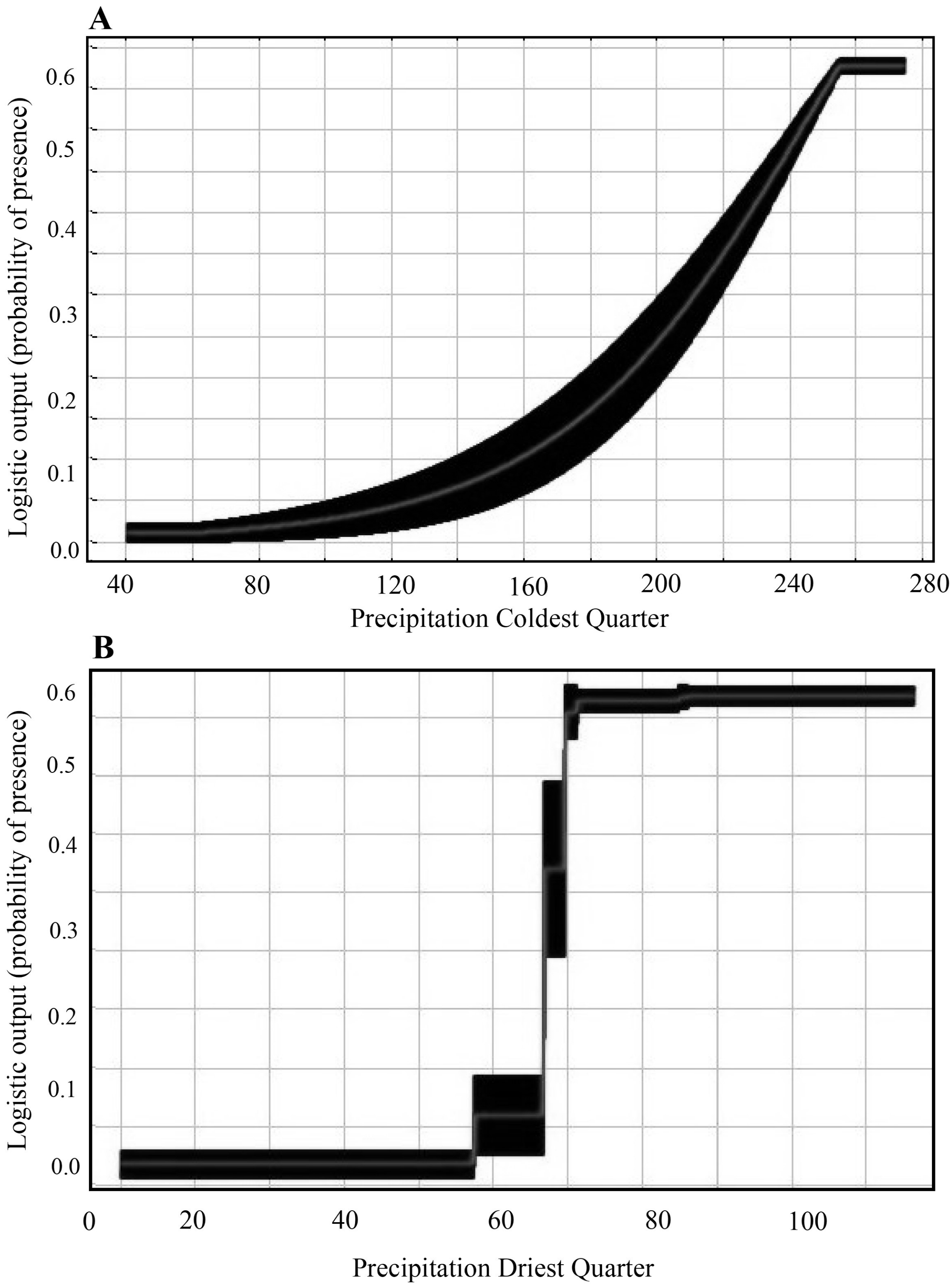


Figure 2. Species response curves showing how the probability of occurrence for the A) Louisiana pine snake (*Pituophis ruthveni*) and B) Baird's pocket gopher (*Geomys breviceps*) varies over different values of the most important predictor variable (as determined the percent contribution to the best fit Maxent model). Shaded areas represent +/- one standard deviation.

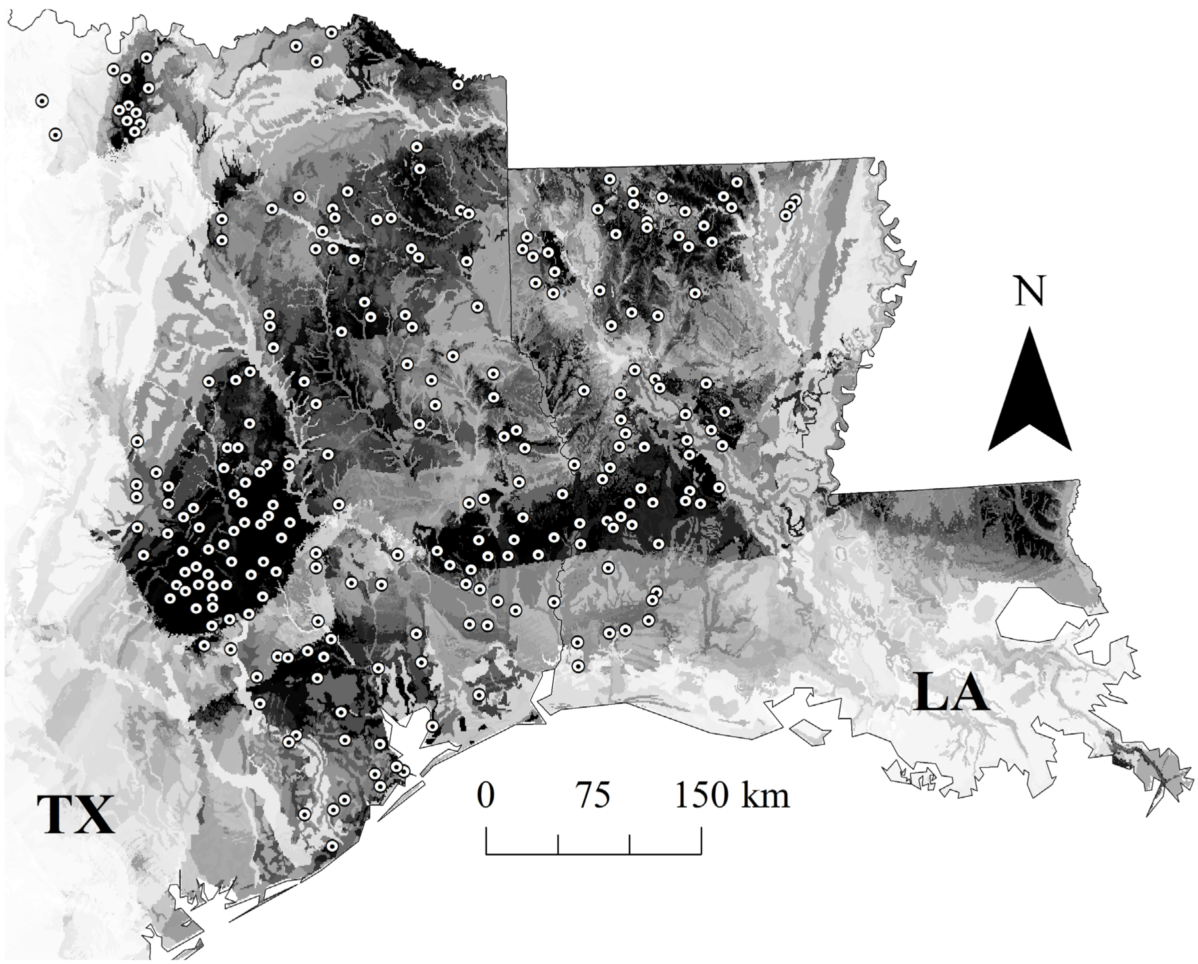


Figure 3. Predicted occupancy for the Baird's pocket gopher (*Geomys breviceps*) in Louisiana and Texas. Darker shading indicate higher occupancy rates. Enclosed circles represent spatially and temporally selected species occurrences.

presence for Baird's pocket gopher is highest in areas that received > 70 mm of precipitation during the driest quarter of the year (Fig. 3).

Estimates of niche overlap were variable between Baird's pocket gopher and Louisiana pine snake (Schoener's D index = 0.443; $I = 0.747$, Relative rank = 0.821). However, identity tests of niche equivalency showed that these values of niche overlap fell significantly ($P < 0.0001$) below the pseudoreplicated null distribution (Fig. 4). Similarly, background similarity tests showed that observed overlap between the two species were significantly ($P < 0.0001$) lower than expected (Fig. 4). Estimates of niche breadth were noticeably different between species with Baird's pocket gopher possessing a higher inverse concentration value (0.225) compared to Louisiana pine snake (0.112), indicating the pocket gopher has broader niche requirements.

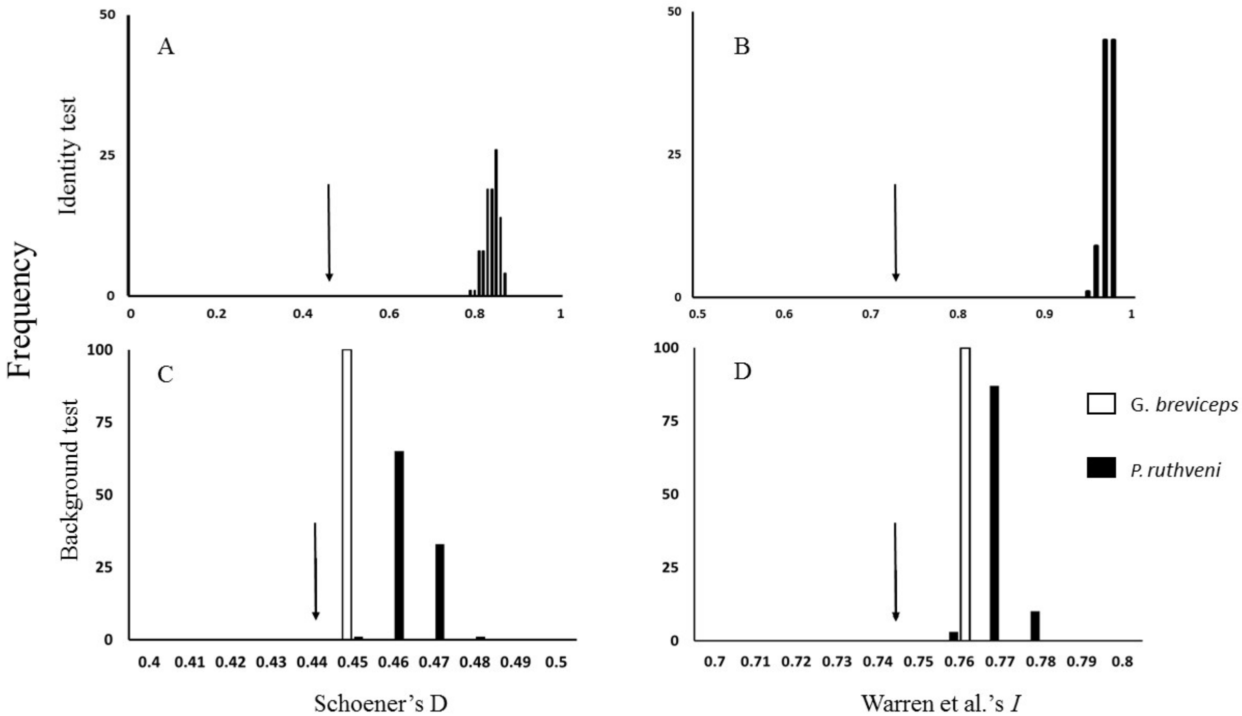


Figure 4. Results of ENMTools tests of niche equivalency and background similarity for the Baird's pocket gopher (*Geomys breviceps*) and Louisiana pine snake (*Pituophis ruthveni*). Histograms show the distribution of overlap scores from the pseudoreplicated null distribution from identity tests of niche equivalency (A, B) and background similarity (C, D). Arrows identify the values of niche-overlap for the Schoener's D and Warren et al.'s *I* matrices.

## DISCUSSION

Areas of predicted occurrence for the Louisiana pine snake are more concentrated (Fig. 1) than those of the Baird's pocket gopher (Fig. 3) in Texas and Louisiana. The Louisiana pine snake's distribution is fragmented into two general areas, with boundaries coinciding with the Red River in central Louisiana. The Louisiana pine snake prefers longleaf pine savanna (Himes et al. 2006; Wagner et al. 2014), and areas predicted to have high probability of occurrence closely resemble the historic distribution of longleaf pine savanna in Louisiana and Texas (Fig. 1). This is especially apparent in north-central Louisiana, where a pocket of longleaf pine was isolated from similar regions in Louisiana and Texas by the Red River.

Environmental variables important to predicting occupancy varied between the Louisiana pine snake and Baird's pocket gopher. For the Louisiana pine snake, Precipitation of the Coldest Quarter (January to March) had the highest contribution when predicting occurrence (Table 1) where probability of occurrence decreases in areas receiving less precipitation (Fig. 2). This suggests both precipitation and temperature are important when defining this species geographic range. The importance of temperature is not surprising given that ectotherms are more physiologically sensitive to changes in ambient temperature than endotherms (Aragón et al. 2010). Variation in the thermal environment can have a strong impact on distribution, habitat selection, and physiology of snakes and lizards (Grant and Dunahm 1988; Blouin-Demers and Whitehead 2002; Bashey and Dunham 1997; Harvey and Weatherhead 2011). The climate of east Texas and western Louisiana can be considered humid subtropical with long, hot summers and short mild winters. Because these areas do not experience large declines in winter temperatures like northern latitudes, reptiles and amphibians can be active year-round. Pierce et al. (2014)

detected winter movements in Louisiana pine snakes with some moving substantial distances (> 100 m). All winter locations were in burrows of Baird's pocket gopher, which suggests the Louisiana pine snake would need to excavate soil while leaving and entering the different burrow systems. Areas with more precipitation increases soil moisture and makes burrowing easier (Andersen and MacMahon 1981).

Precipitation of the Driest Quarter was the most important variable to predicting occupancy of the Baird's pocket gopher (Table 1). As shown by the response curve (Fig. 2), probability of the Baird's pocket gopher occurrence is low until precipitation levels exceed 70 mm during the driest quarter of the year (October to December). Precipitation catalyzes pocket gopher activity by loosening the soil, making it more pliable for digging (Andersen and MacMahon 1981). The energetic cost of burrow excavation is significantly higher than equidistant terrestrial movements (Vleck 1979) and soil that is dry and hardened becomes too energetically expensive to maintain (Romañach et al. 2005a). Also, precipitation will invigorate plant growth and increase food availability. Romañach et al. (2005b) found that length and area of pocket gopher burrows decreased as above ground biomass increased, suggesting that increased food abundance results in decreased digging activity.

Some similarities in environmental variable importance existed between the two species. Precipitation of the Driest Quarter was the most important variable for the Baird's pocket gopher and was among the top three most important variables for the Louisiana pine snake in each measure of the jackknife analysis (Table 2). However, when all predictor variables are considered, our results show differences in niche requirements for the Louisiana pine snake and Baird's pocket gopher at this scale. Tests of niche equivalency found that predicted niches of both species were dissimilar. Background similarity tests showed that niche overlap was significantly lower than expected indicating that the niches of both species are more divergent based on the habitat available to both. The lack of similarity in niche requirements between the Louisiana pine snake and Baird's pocket gopher suggests that prey availability is not a factor restricting the overall geographic range of the Louisiana pine snake. Conversely, predictions of habitat suitability for the Louisiana pine snake closely align with the historical distribution of longleaf pine savanna (Fig. 1).

A surprising result was the lack of contribution that soil variables had in the final models. Pocket gophers in the genus *Geomys* have been well documented as preferring sandy, well drained soils (Miller 1964; Best 1973; Lovell et al. 2004; Hoffman and Choate 2008; Connior et al. 2010). Given that Baird's pocket gopher is the main prey item of the Louisiana pine snake, it is assumed that the Louisiana pine snake would also show preference to areas with these soil characteristics. A recent study by Wagner et al. (2014) found that percent sand and depth to ground water most influenced Louisiana pine snake occurrence. However, our results indicate that soil characteristics had little to no influence on predicting occurrence for either species. We suggest the lack of importance in soil variables at large spatial scales is due to the lower spatial resolution in the data.

Our study used environmental data with a spatial resolution of 1 km, whereas Wagner et al. (2014) used soil data from the Soil Survey Geographic database (SSURGO) which possesses a resolution of 30 m. Processes that influence species distributions are scale dependent (Sexton et al. 2009; Gotelli et al. 2010). Dispersal and habitat are more likely to influence species occurrence at fine spatial scales within their geographic range; however at larger spatial scales climate becomes more important at defining species range boundaries (McGill 2010). By using finer resolution data, Wagner et al. (2014) was able to better explain the unique habitat characteristics (i.e., soil) preferred by the Louisiana pine snake. Conversely, the coarser data used in this study characterized conditions favorable to each species across their geographic range. Duncan et al. (2020) found similar results when they modeled the distribution of the Southeastern pocket gopher *Geomys pinetis*. Although finer scale studies showed the Southeastern pocket gopher was found in sandy soils with low clay content (Bennet et al. 2020), soil variables lacked importance when coarser scale data were used. It is possible these species do not show a tendency to select sandy soils in large scale modeling analyses because the study area lacks an abundance of this soil type. However, both this study and the study by Duncan et al. (2020) used background or absence points from areas reasonably accessible to the target species. It appears that this approach provides a realistic range of soil values for the model to compare to occurrence points.

This study represents the first landscape scale analysis for the Louisiana pine snake and Baird's pocket gopher. We provide evidence that regions with high probability of occurrence for the Louisiana pine snake are isolated from one another by a major river system (Red River). Geographical barriers, such as rivers, can often limit the distribution of a species and naturally fragment populations (Brandley et al. 2010; Naka et al. 2012; Boubli et al. 2015). The longleaf pine savanna ecosystem is dominated by longleaf pine (Outcalt 1997) and an abundance of grasses and forbs which comprise the understory (Rudolph et al. 2006). The soil type is composed mostly of moderately well-drained sandy loams divided by clay bottom ravines (Marks and Harcombe 1981; Himes et al. 2006). Conversely, the Red River floodplain mostly is composed of silty clay soils and oak hardwood forests (Marks and Harcombe 1981). Movement studies show that populations of Louisiana pine snakes are absent from areas dominated with hardwoods or closed canopies (Himes 2000; Himes et al. 2006). This suggests the Red River in Louisiana may act as a dispersal barrier for the Louisiana pine snake leading to greater conservation concerns by preventing gene flow between populations. Finally, the occupancy maps presented in this study could help in the management of land use around existing Louisiana pine snake populations, assist in discovering new populations, identify top-priority survey and reintroduction sites, and set priorities to restore natural habitat for more effective conservation (Kumar and Stohlgren 2009).

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## LITERATURE CITED

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*Addresses of authors:*

**KATIE CANTRELLE**

*Harold and Pearl Dripps School of Agricultural Sciences*
*McNeese State University*
*Lake Charles, LA 70609*
*katiecantrelle@ymail.com*

**JUSTIN D. HOFFMAN**

*Department of Biology*
*McNeese State University*
*Lake Charles, LA 70609*
*jhoffman@mcneese.edu*

**EDDIE K LYONS**

*Harold and Pearl Dripps School of Agricultural Sciences*
*McNeese State University*
*Lake Charles, LA 70609*
*elyons@mcneese.edu*

## Appendix I

The number of individual records (not counting recaptures) of the Louisiana pine snake (*Pituophis ruthveni*) per county/parish and state.

| State | County/Parish | No. of snakes |
|---|---|---|
| Louisiana | Beauregard | 1 |
| Louisiana | Bienville | 109 |
| Louisiana | Jackson | 1 |
| Louisiana | Natchitoches | 16 |
| Louisiana | Rapides | 8 |
| Louisiana | Sabine | 8 |
| Louisiana | Vernon | 44 |
| Texas | Angelina | 8 |
| Texas | Hardin | 1 |
| Texas | Houston | 1 |
| Texas | Jasper | 8 |
| Texas | Nacogdoches | 2 |
| Texas | Newton | 15 |
| Texas | Polk | 1 |
| Texas | Sabine | 5 |
| Texas | San Augustine | 1 |
| Texas | Trinity | 1 |
| Texas | Tyler | 2 |

## APPENDIX II

Capture localities for Baird's pocket gopher (*Geomys breviceps*) from Texas and Louisiana used in this study to generate an occupancy model. Museum abbreviations and catalog numbers are provided in parentheses. Museum abbreviations follow Dunnum et al. (2018), as follows: Angelo State University (ASNHC), Chicago Academy of Sciences (CHAS), Fort Hays Sternberg Museum of Natural History (FHSM), Field Museum of Natural History (FMNH), University of Kansas Biodiversity Institute (KU), Natural History Museum of Natural History (LACM), Louisiana State Museum of Natural Science (LSUMZ), Museum of Southwestern Biology (MSB), Michigan State University (MSU), Texas A&M University Biodiversity Research and Teaching Collections (TCWC), Museum of Texas Tech University (TTU), University of Michigan Museum of Zoology (UMMZ), and National Museum of Natural History, Smithsonian Institution (USNM).

*Louisiana.*—Allen Parish: 3.4 mi NW of Mittie (LSUMZ 30584); Indian Village near Allen–Jefferson– Davis Parish line (LSUMZ 30880); Beauregard Parish: 1.5 mi E De Ridder (LSUMZ 13529); 6 mi W Longville, LA, on LA Hwy 110 (LSUMZ 33338); 8.9 mi W of Sugartown along La 112 (LSUMZ30889); Merryville (LSUMZ 8772; Bienville Parish: 5 mi SW of Ringgold (LSUMZ 7699); Bossier Parish: Bossier City (LSUMZ 15487); Caddo Parish: 10 mi S of Shreveport on Red River (LSUMZ 30878); 2 mi N Blanchard (LSUMZ 11217); 3 mi S, 2.5 mi W Blanchard (LSUMZ 16248); 7 mi WSW of Shreveport on Broadacres Road (LSUMZ 7697); Calcasieu Parish: 2 mi S Vinton (LSUMZ 6532); 3.5 mi NNW Iowa (LSUMZ 6545); Lake Charles (LSUMZ 405); Vinton (2 mi E) (LSUMZ 2216); Cameron Parish: 12 mi S Vinton, Cameron Farms (LSUMZ 10270); Claiborne Parish: 1 mi S Marsalis (LSUMZ 6509); 1.5 mi N Marsalis (LSUMZ 6510); 5 mi N Homer (LSUMZ 18698); 6 mi S Summerfield (LSUMZ 15210); Homer (LSUMZ 11393); De Soto Parish: 16 mi N Mansfield (LSUMZ 7706); Grant Parish: 0.3 mi NW of Grant–Rapides Parish line on US 71 (LSUMZ 30780); 1 mi NW Montgomery (LSUMZ 36212); Colfax (LSUMZ 1755); Fishville (LSUMZ 1067); Pollock (LSUMZ 2253); Jackson Parish: 0.7 mi NE of Watson on La 4 (LSUMZ 30752); Jefferson Davis Parish: 13.5 mi N of Iowa on La 383 (LSUMZ 30751); Lincoln Parish: 2 mi N Ruston (LSUMZ 13528); 2 mi N Tremont (LSUMZ 6345); 6 mi S Bernice on US 167 (LSUMZ 33331); 8 mi N Chouderant (LSUMZ6346); Ruston (LSUMZ 164); Morehouse Parish: 3.5 mi SW Mer Rouge (LSUMZ 6519); Collinston (LSUMZ 30832); W city limits Mer Rouge (LSUMZ 6528); Natchitoches Parish: 2 mi S of Bellwood (LSUMZ 30773); 2.5 mi E from Natchitoches on Hwy 6 (LSUMZ 33334); Kisatchie (LSUMZ 1381); Provencal (LSUMZ 1083); Rapides Parish: 2.5 mi SW Melder (TCWC 45936); 3 mi SW Boyce (LSUMZ 3404); Glenmora (2 mi W) (LSUMZ 2409); NE of Gardner at Jct. of La 28 and La 121 (LSUMZ 30888); Union Hill across from cemetery (LSUMZ 33332); Glenmora, 2.3 Mi N, 8.8 Mi W (USNM 512965); Red River Parish: ca. 8.1 mi W of Red River–Natchitoches Parish line along La 155 (LSUMZ 30778); Sabine Parish: 13 mi S Many (LSUMZ 9624); 2.5 mi N of Toledo Bend Dam (LSUMZ 30749); Union Parish: 4.5 mi NE Farmerville (LSUMZ 6516); 6.9 mi E of Farmerville on LA 2 (LSUMZ 30597); Marion (LSUMZ 9103); Vernon Parish: 0.5 km N Ranger Station (LSUMZ 29334); 0.5 mi S, 3.3 mi E Rosepine (LSUMZ 33997); 2 mi S, 3 mi W Rosepine (LSUMZ 30715); 3.5 mi E of Kurthwood (LSUMZ 30775); 5.5 mi NNW Leesville on Harris farm (LSUMZ 8771); 6 mi W Leesville (LSUMZ 6832); 8.5 mi N Merryville on Bayou Anacoco (LSUMZ 6530); Fort Polk National Forest, 0.5 km N Ranger Station (LSUMZ 29377); Fullerton (Junction Hwy. 458 and 399) (LSUMZ 31609); Hutton (LSUMZ 1409); Webster Parish: 5 mi E Minden (TCWC 1002); Haynesville–Shongaloo Hwy. at Claiborne Parish Line (LSUMZ 2552); On U.S. 80 (LSUMZ 30595); Winn Parish: 0.4 mi S of Jct. of La 126 and 1233, 5mi E of Readhimer (LSUMZ 30596); 2 mi SE St. Maurice (LSUMZ 36203).

*Texas.*—Anderson County: 1 mi W Palestine (TCWC 25544); 2 mi E Elkhart (LSUMZ 3755); 20 mi NW Palestine, Gus Engeling Wildlife Mgmt Area (TCWC 26122); Bowie County: 4 mi S, 6 mi W Texarkana (TTU 25846); Brazoria County: Peach Point Wildlife Management Area (TTU 78319); Angleton (CHAS 769); Danbury (CHAS 750); West Columbia (CHAS 758); Brazos County: 3 mi SW College Station, 367 ft (TCWC 23093); 4 mi SE of Kurten (FHSM 35581); 6 mi S College Station, 320 ft (TCWC 37307); 6.1 mi SE Kurten (TCWC 53589); 7 mi S College Station (TCWC 21265); Bryan (UMMZ 81683); Bryan, TAMU Riverside campus front pasture

(TCWC 61925); Burleson County: 0.1 mi E Ye Que Creek, 10.6 mi W Caldwell (FHSM 35108); 0.3 mi N, 0.7 mi W Clay (TCWC 35469); 1.3 mi NE Clay, Old River Ranch (TCWC 28402); 17 mi E Caldwell, W bank Brazos River (TCWC 580); 4 mi N Tunis (TCWC 30078); 8 mi SW Caldwell (TCWC 23362); Chambers County: 7 miles S of Anahuac (MSB 327305); Cherokee County: 18 mi S, 8 mi W Tyler (TTU 35058); Cooke County: 2.1 mi NW Lake Kiowa, CR 2112 (FHSM 35125); Denton County: 1.5 mi SW Mustang (FHSM 34206); 1.7 mi W Mustang (TCWC 53627); 1.8 mi NW Aubrey, Grubbs Rd (TCWC 53928); 1.9 mi NW Mustang (TCWC 53286); 2.3 mi SE Krugerville, Ike Byron Rd (FHSM 33723); 2.5 mi SE Pilot Point, Int Hwy 377 and Foutch Rd (FHSM 33384); Falls County: 0.3 mi S Cedar Springs (TCWC 30127); 1 mi SE Reagan (TCWC 585); 2.15 mi N Cedar Springs (TCWC 30125); Fort Bend County: 1 mi S Beasley, 200 ft (TCWC 4483); Richmond (CHAS 768); Freestone County: 3 mi N Buffalo (TCWC 45946); 3 mi N Fairfield (TCWC 30043); Fairfield (TCWC 30410); Galveston County: 1 mi N Texas City (TCWC 620); 1.4 mi S, 2.3 mi W Hitchcock (TTU 19248); Texas City (LACM 5494); Texas City, 1 mi N (FMNH 47609); Grayson County: 1.5 mi NE Tioga on Hwy 377 (TCWC 54193); 2 mi NW Sadler, FM 901 (FHSM 34215); Gregg County: 3 mi NW Longview (LSUMZ 19883); Ca. 2 mi S Longview (LSUMZ 20479); Grimes County: 2 mi E Carlos on Hwy 30 (TCWC 28014); 2 mi E Shiro (TCWC 21271); 5 mi E Kurten (TCWC 560); Ca. 2.5 mi SE Anderson (LSUMZ 13527); Navasota (TCWC 60889); Hardin County: 1.7 mi N, 3.5 mi E Village Mills (TCWC 33496); 1.7 mi N, 4.8 mi E Saratoga (TCWC 35486); 10.5 mi N, 4 mi E Silsbee (TCWC 39415); 5 mi N Silsbee (TCWC 2704); 2.5 mi N Hockley (TCWC 741); 3.0 mi N Mason's Bay La Porte (TCWC 733); 3.0 mi NE Webster (TCWC 738); 4.0 mi N Huffman (TCWC 740); 9 mi E Cypress, Weiser Air Park (TCWC 56968); Harrison County: 5 mi S Marshall (TCWC 45948); Henderson County: 4.2 mi SW Athens, FM 753 (FHSM 33411); Clements Scout Ranch (FHSM 34223); Houston County: Crockett (TCWC 26123); Jasper County: 15 mi N Jasper (TCWC 2715); 4.8 mi N, 2.2 mi E Evadale, Neches River Unit (TCWC 35485); 5 mi S, 1.1 mi E JASPER (TTU 19239); 7 mi SW Buna (TCWC 2721); Kirbyville (LSUMZ 924); Jefferson County: 7 mi SW Fannett (TCWC 1132); Lamar County: 2 mi NE Paris (TCWC 53637); Pat Mayse WMA (PMWMA-13) (TTU 80655); Slate Shoals (TCWC 45950); Leon County: 13 mi E Centerville (TCWC 587); 2 mi E Flynn, 300 ft (TCWC 23357); 3 mi E Centerville (TCWC 586); 3 mi S Centerville (TCWC 45958); 5 mi NW Normangee (TCWC 53638); 5 mi W Jewett (TCWC 23356); 5.6 mi NW Normangee (TCWC 53657); 7 mi N Normangee (TCWC 21270); Jewett (TCWC 23341); Liberty County: 12 mi N Liberty (TCWC 21277); 2 mi E Liberty (TCWC 1121); Madison County: 4.5 mi NNE Madisonville on FM 3091 (TCWC 30321); 5 mi W Madisonville (TCWC 53658); 5.5 mi SW Madisonville (TCWC 53672); 8.8 mi S Midway (TCWC 53660); Madisonville, Jct Hwys 21 & I-45 (TCWC 30322); Madisonville (CHAS 760); Marion County: 1 mi W Jefferson (MSB 181167); Kellyville (USNM 18751); Milam County: 0.9 mi NW Gause (by road) (TCWC 56955); 2.6 mi S Wilderville (TCWC 30095); 9.1 mi SE Cameron on Hwy 36 (TCWC 27998); Milano (TCWC 60413); Montague County: 7.7 mi NE Alvord (TCWC 54012); Montgomery County: 2 mi E Decker Prairie (TCWC 27988); 5 mi W Conroe on Hwy 105 (TCWC 27989); 7 mi E Tomball (TCWC 23358); Morris County: White Oak Creek WMA (WOCWMA-2) (TTU 80711); Daingerfield (CHAS 745); Nacogdoches County: 11 mi N Nacogdoches (TCWC 2690); Alazan Bayou Wildlife Management Area (ASNHC 12227); SFA campus, Nacogdoches (TTU 430); Newton County: 13 mi NE Kirbyville (TCWC 2719); 3 mi NE Kirbyville (TCWC 2718); 7.4 mi N Burkeville (TCWC 31518); Panola County: 4 mi NE Carthage (TCWC 1016); Polk County: 3.0 mi W Livingston (TCWC 428); 4.7 mi N Dallardsville on FM 1276 (TCWC 33503); Rains County: Emory (MSU 5504); Emory, 5.5 mi E of courthouse (KU 114325); Robertson County: 1.7 mi jct 1373 and 413 on 413 (TTU 39672); 10.7 mi NE on FM 2549 from jct. Hwy 2549 and Hwy 6 (TCWC 60724); 2.3 mi N Calvert, Hwy 6 (TCWC 27396); 4 mi NE Hearne, Hwy 79 (TCWC 27399); 5 mi W Hearne on Hwy 190 (TCWC 28005); Mumford (TCWC 56900); Rusk County: 3 mi N Cushing (TCWC 45968); 3 mi W Henderson (TCWC 2699); 6 mi W Timpson (TCWC 2697); Sabine County: 8 mi W Hemphill (TCWC 2705); San Augustine County: 8 mi S San Augustine (TCWC 2712); 8 mi SE San Augustine (TCWC 2714); San Jacinto County: 3 mi WSW Evergreen (TCWC 21272); 6 mi SE Coldspring (TCWC 21274); Shelby County: 9 mi S Center (TCWC 2692); Center (CHAS 771); Smith County: 10 mi S Tyler, Flint Community (TCWC 23078); 2.6 mi N Lindale (LSUMZ 29608); 20 mi NW Tyler (TCWC 45975); 6 mi N Tyler (FHSM 9949); 6 mi W Tyler (FHSM 9950); Trinity County: 1.5 mi N Trinity (TCWC 1140);

Tyler County: 0.5 mi N, 3.2 mi E Warren (TCWC 35483); 1.2 mi N, 1.9 mi W Spurger (TCWC 34194); 13 mi NE Colmesneil (TCWC 56972); 17 mi S Woodville (TCWC 2728); 2.8 mi S, 1.8 mi W Town Bluff (TCWC 33513); 4.7 mi S, 0.8 mi W Warren, Hickory Creek (TCWC 33514); Upshur County: 1 mi NW Gilmer (TCWC 27402); 7 mi W Gilmer (TCWC 27403); Van Zandt County: 0.5 mi N Grand Saline (TTU 6423); 7 mi N Hedgewood, Gammon's Ranch (TCWC 26121); Walker County: 6 mi S Huntsville (TCWC 190); Huntsville (TCWC 45983); Waller County: Pattison (LSUMZ 11185); Washington County: 13 mi W Brenham, 100 ft (TCWC 23364); 2 mi S, 2.5 mi W Washington (TCWC 44027); 4 mi S, 1 mi E Somerville (TCWC 59239); Wise County: 7 mi NE Decatur on FM 730 (TCWC 54020); Wood County: 2 mi E Quitman (TTU 69288); 3.5 mi SE Quitman, Timberlake Farms (TCWC 56561); 4 mi S Winnsboro (TCWC 25553).

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