Modeling Louisiana Pinesnake Habitat to Guide the Search for Population Relicts

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Abstract - Pituophis ruthveni (Louisiana Pinesnake) is one of the rarest snakes in the United States. Efforts to refine existing habitat models that help locate relictual populations and identify potential reintroduction sites are needed. To validate these models, more efficient methods of detection for this rare species must also be developed. Here we expand recent habitat suitability models based on edaphic factors to include mature Pinus (pine) stands that have not been cut for at least 30 years and likely have vegetation structure with the potential to support the species. Our model identified a total of 1652 patches comprising 180,050 ha of potentially suitable habitat, but only 16 (1%) of these patches were more than 1000 ha and considered worthy of conservation attention as potential reintroduction sites. We also visited potentially suitable habitat, as determined by our model, and used camera traps to survey for relictual populations at 7 areas in Texas. We observed 518 snakes of 18 species in 8,388,078 images taken from April to October 2016, but no Louisiana Pinesnakes were detected. The patchiness of the habitat model and failure to detect Louisiana Pinesnakes corroborate independent conclusions that most populations of the species are small, isolated, probably in decline, and possibly extirpated. In the context of this extreme rarity, we believe this study will help manage limited conservation resources by narrowing the search areas for relictual populations, providing a more cost-effective method of surveying those areas, and identifying the best sites for future reintroduction efforts.

Introduction

Rarity and secretive behaviors of many conservation-reliant snake species have complicated research required to guide monitoring, conservation, and management of the species (Durso et al. 2011, Steen 2010, Steen et al. 2012). In particular, *Pituophis ruthveni* Stull (Louisiana Pinesnake) is an extremely rare, semi-fossorial species known historically from 8 parishes in Louisiana (Dundee and Rossman 1989, Stull 1929) and 12 counties in Texas (Dixon 2013, but see Adams et al. 2018). Despite increases in both trapping effort and opportunistic searching by observers participating in conservation, the Louisiana Pinesnake has been found in only 5 Louisiana parishes (Bienville, Natchitoches, Rapides, Sabine, and Vernon) and 4

Manuscript Editor: David Steen

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Texas counties (Angelina, Jasper, Nacogdoches, and Newton) between 2000 and 2020 (Rudolph et al. 2018; J.B. Pierce, unpubl. data). The US Fish and Wildlife Service (USFWS) listed the species as threatened in 2018, and recognized 7 extant populations, all occupying small, fragmented habitats on both federal and private lands (USFWS 2014, 2018). As 3 of those 7 populations are approaching the service's criteria for extirpation (i.e., no detections in the last 11 years with 5 years of trapping effort; USFWS 2016), efforts to refine existing habitat models are needed to guide attempts to locate additional relictual populations of the species as well as identify potential reintroduction sites.

Habitats suitable for Louisiana Pinesnakes contain sandy, well-drained soils that support *Geomys breviceps* (Baird) (Baird's Pocket Gophers), the snake's primary prey (Adams et al. 2017a; Rudolph and Burgdorf 1997; Rudolph et al. 1998, 2002). Based on published descriptions of soil preferences of Baird's Pocket Gopher (Davis et al. 1938), Wagner et al. (2014) used edaphic factors to model potentially suitable habitat for the Louisiana Pinesnake and then used independently derived telemetry data for the species to explore habitat use and validate their modeling results. Their model demonstrated that Louisiana Pinesnake distribution is strongly influenced by edaphic factors related to soil permeability and groundwater depth. Wagner et al. (2014) concluded that many areas across its historical range had suitable soils capable of supporting the Louisiana Pinesnake, but they also cautioned that the vegetation structure on those same sites may be insufficient to support the species.

In addition to certain soil conditions, the required vegetation structure for the Louisiana Pinesnake includes a pine overstory (primarily *Pinus palustris* Mill. [Longleaf Pine]) with a sparse midstory and a well-developed herbaceous understory to support healthy populations of Baird's Pocket Gopher prey (Himes et al. 2006, Rudolph and Burgdorf 1997). The 2003 candidate conservation agreement (CCA) with the US Forest Service (USFS), the Department of Defense (DOD), Texas Parks and Wildlife Department (TPWD), and Louisiana Department of Wildlife and Fisheries (LDWF) specified the need for maintenance of fire-climax, park-like, open-canopy pine forest structure to support Louisiana Pinesnake habitat (USFWS 2003). Combined with a lack of fire, harvest practices that include total removal of timber often do not allow for the development of vegetative structure required by Louisiana Pinesnakes (Frost 1993). As such, in this study we refined the existing soil-based habitat model by adding a range-wide analysis of total timber-removal harvests. Specifically, we attempted to identify existing mature pine stands with suitable soils that are greater than 1000 ha and have not been totally harvested for at least 30 years. We suggest these areas are large enough to support relictual populations or serve as future reintroduction sites for Louisiana Pinesnakes based on conservation actions proposed for similar snakes with expansive home ranges that also occupy open-canopy pine forests (e.g., Drymarchon couperi (Holbrook) [Eastern Indigo Snake], *Pituophis melanoleucus lodingi* (Blanchard) [Black Pinesnake]; USFWS 2019).

As a secondary goal of this study, we used our refined habitat model to guide field surveys for relictual populations of Louisiana Pinesnakes. The goal of determining presence/absence of species in relictual populations comes with the burden of estimating their detection probabilities, and for an extremely rare species with a secretive biology (e.g., the Louisiana Pinesnake), this burden may require substantial survey effort and thus conservation resources (Kéry 2002). Unfortunately, for typical sampling designs (including the passive box traps and drift fences used to survey many rare snake species; e.g., Steen et al. 2012), producing sample sizes sufficient to estimate detection probabilities may be logistically impractical or cost-prohibitive (Steen 2010). In an attempt to generate robust sample sizes without the need for increasing logistic and financial costs, we modified the original sampling design for the species (described in Burgdorf et al. 2005) by exchanging a camera trap for the box trap, as they do not need to be checked every 1–3 days (Adams et al. 2017b). We report the results of this survey effort with a modified sampling design and discuss its potential to increase detection rates of rare and secretive snake species like the Louisiana Pinesnake.

Field-Site Description

The habitat modeling area we used encompassed 17 eastern Texas counties and 11 west-central Louisiana parishes representing the entire historic range of the species (Fig. 1), including the 14 counties and 7 parishes considered in the previous soil-based habitat model (Wagner et al. 2014). In addition, our habitat modeling area contained all verified Louisiana Pinesnake records (Rudolph et al. 2018), including a recently reintroduced population (USFWS 2016).

Methods

Habitat suitability model

To add a range-wide analysis of total timber-removal harvests to the existing soil-based habitat model, we first acquired pre-processed Landsat 5 TM, 7 ETM+, and 8 OLI 30-m imagery and normalized difference vegetation index (NDVI; i.e., an indicator of photosynthetic activity) products through the United States Geological Survey (USGS) Earth Resources Observation and Science (EROS) Center Science Processing Architecture (ESPA) On Demand Interface website (https://espa.cr.usgs.gov). Using an interactive supervised classification in ArcMap 10 (ESRI 2014), we identified existing pine from leaf-off Landsat imagery acquired during winter of 2014–2015 (Fig. 1, Fig. 2A). This data provided a baseline land-cover map of pine forest from which we eliminated areas where forest was not constantly present over time, using the change-detection analysis described below (Fig. 2B).

To identify where vegetation change occurred within the pine forest land-cover map described above, we performed an image-differencing change-detection analysis on Landsat-derived NDVI scenes collected in late summer or early fall from 1985 to 2015 (Fig. 1; Coppin et al. 2004, Lyon et al. 1998). We identified areas of vegetation change from 1985 to 2015 in 5-year intervals (e.g., change from 2010 to 2015, change from 2005 to 2010, etc.) by subtracting temporally consecutive

NDVI rasters for each time step (e.g., NDVI₂₀₁₀ - NDVI₂₀₀₅). Significant decreases in NDVI indicated a change of vegetation. Targeting scenes in this timeframe provided the best opportunity to correctly classify change of vegetation (Fig. 2B). NDVI, especially for evergreen forest-type land covers, remains generally stable during this time of year, meaning an observed decrease in NDVI during a particular time step is likely associated with change of vegetation, and not due to naturally occurring seasonal variation in photosynthetic activity.

To verify that identified changes in vegetation were consistent with the loss of pine forest, we confirmed appropriate difference thresholds chosen to represent forest-cover change by comparing vegetation-enhancing, false-color image composites (e.g., shortwave infrared, near infrared, and red-band combination) between each time step. We then estimated areas identified as vegetation change from any

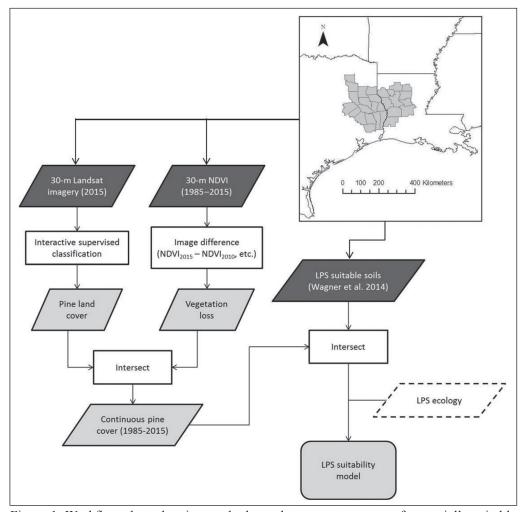


Figure 1. Workflow chart showing methods used to generate a map of potentially suitable Louisiana Pinesnake (LPS) habitat within a modeling area containing 17 eastern Texas counties and 11 west-central Louisiana parishes (upper right).

time period from the existing pine classification. This procedure provided a raster layer of areas expected to have continuous pine cover from 1985 to 2015. We further refined our pine model by extracting coincident areas identified in the Wagner et al. (2014) suitability model (Fig. 2C). The resulting map identified existing mature pine stands with suitable soils that have not been totally harvested for at least 30 years, highlighting areas with potential to support Louisiana Pinesnakes. Given the extremely low detection rate of the this species, traditional approaches to model

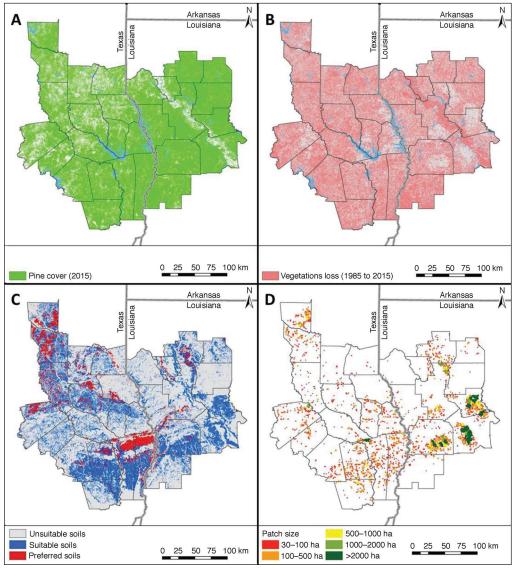


Figure 2. Maps depicting (A) pine tree cover in 2015 and (B) perceived change of vegetation through change-detection analysis between 1985 and 2015 within the study area. (C) The suitable soils model followed methods from Wagner et al. (2014). (D) Model of potentially suitable Louisiana Pinesnake habitat classifying remnant mature pine stands with suitable soils by total patch size in hectares. Patch characteristics summarized in Table 1.

validation using data across localities are not practical. Instead, we qualitatively evaluated the model results by comparing the location of known extant or recently extant populations to patches identified as potentially suitable by the model.

To help identify potential reintroduction sites within the model results, we used a home-range-fitting approach to color code and visualize patches of potentially suitable habitat by size class (Table 1). Similar approaches have been used to help evaluate habitat patch sizes for other snakes with expansive home ranges that also occupy open-canopy pine forests, the threatened Eastern Indigo Snake (listed as Drymarchon corais couperi) and Black Pinesnake (USFWS 2019). Specifically, we used the number of non-overlapping home ranges able to fit in a given patch to estimate the minimum number of individuals that could occupy a potentially suitable habitat patch. For example, we assumed that a 1000-ha patch of potentially suitable habitat would encompass ~30 Louisiana Pinesnake home ranges based on the mean home-range size of 33 ha (min-max = 6.5-107.6ha) estimated from telemetry data by Himes et al. (2006). Because Louisiana Pinesnakes are known to exhibit home-range overlap to varying degrees in wild populations (Himes et al. 2006), the expected number of individuals in a 1000-ha patch could be larger. Following this approach, our conservative estimates for the number of pinesnakes per patch are shown in Figure 2D as follows: red patches represent suitable habitats large enough to encompass at least 1-3 home ranges (30-99 ha), orange patches are large enough to encompass at least 4-15 home ranges (100-499 ha), yellow patches are large enough to encompass at least 16-30 home ranges (500–999 ha), and light and dark green patches are large enough to encompass ≥ 30 home ranges (≥ 1000 ha).

Empirical data necessary to estimate a viable population size for Louisiana Pinesnakes are not available. As such, we draw inference on the importance of potentially suitable habitat patch sizes from comparisons with Eastern Indigo Snakes and Black Pinesnakes. To maintain population viability, reserve areas of at least 4000 ha are recommended for Eastern Indigo Snakes and 2000 ha for Black Pinesnakes, although much larger reserve areas are recommended for certain populations of both species (Speake et al. 1982, USFWS 2019). However, a 1000-ha patch is still considered worthy of conservation attention for these species as habitat is dynamic and species may move among many habitat patches over time (Moler

Table 1. Patch characteristics for model of potentially suitable Louisiana Pinesnake habitat. Suitability classes are defined in Methods. All area measures are in hectares.

| Suitability class (size) | Number of patches | Actual patch size (min-max) | Mean patch area | Total area | % of total area |
|--------------------------|-------------------|-----------------------------|-----------------|------------|-----------------|
| Red (30–99) | 1321 | 30–99 | 51 | 67,630 | 37.6 |
| Orange (100–499) | 296 | 100-492 | 180 | 53,292 | 29.6 |
| Yellow (500–999) | 19 | 527-948 | 712 | 13,523 | 7.5 |
| Light green (1000–2000 |) 6 | 1159-1697 | 1377 | 8262 | 4.6 |
| Dark green (>2000) | 10 | 2006-9807 | 3734 | 37,343 | 20.7 |
| Total | 1652 | | | 180,050 | |

1992, USFWS 2019). For this reason, we focus our discussion of possible reintroduction sites on potentially suitable habitat patches greater than 1000 ha in size.

Surveys

We also used the refined habitat model to guide surveys for relictual populations of Louisiana Pinesnakes on private lands in Texas (Louisiana was not surveyed due to funding restrictions). In 2016, access to private land was provided for Louisiana Pinesnake surveys at 7 sites in Texas where the refined habitat model highlighted areas with potential to support the species (Fig. 3). At each survey site,

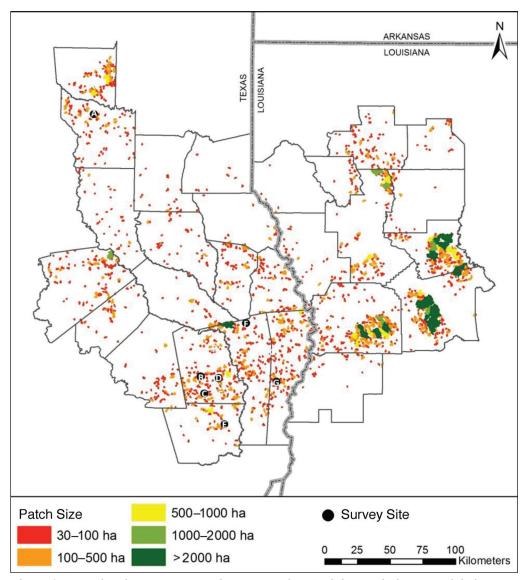


Figure 3. Map showing camera trapping survey sites A–G in proximity to modeled potentially suitable Louisiana Pinesnake habitat patches. Trapping effort per site is summarized in Table 2.

we constructed drift fences matching those used to monitor Louisiana Pinesnake populations since the mid-1990s with 1 modification: instead of using a box trap in the middle of the drift fences, we used a Reconyx PC800TM game camera mounted facing the ground as described by Adams et al. (2017b). All other aspects of the original sampling design were retained. We constructed the drift fences of 6.4-mm mesh hardware cloth, ~15 m in length and 61 cm in height (Burgdorf et al. 2005, Rudolph et al. 2006). For each camera trap, we buried 4 drift fences 10 cm deep in a "+" configuration with a 1-m² opening at the center (Burgdorf et al. 2005, Rudolph et al. 2006). We mounted the camera on a conduit pole ~2 m above the ground with a flexible GorillapodTM camera tripod, so that the camera's field of view included the end of each drift fence at the target area in the center of the fences (~1 m²).

Within each survey site, we placed 4 camera traps with drift fences separated by at least 450 m, except for 1 site that had only 2 camera traps with fences due to space limitations (n = 26 camera traps total). We programmed the cameras to take an image every 30 sec, with the assumption that large snakes, such as pinesnakes, exhibiting common behavior would likely move slowly across the target area and thus be "captured" in at least 1 image. Each image was date and time stamped. Ealy et al. (2004) documented that the Louisiana Pinesnake is primarily diurnal; thus, we programmed the cameras to be operational from 0545 to 2200 hrs, and we deployed them from March to October 2016, the standard trapping period for this species (Burgdorf et al. 2005). We stored all images on Verbatim Premium 32 GB SD cards, which we replaced, along with 12 Energizer® AA lithium ion batteries, approximately every 24 days. During each replacement visit, we raked the camera's target area to remove debris. We processed images using the Reconyx MapView Professional program and recorded species, time of detection, and number of consecutive images in which an observation occurred for each observation. Approximately 1.0–1.5 person hours were needed to analyze 10,000 images.

Results

Habitat suitability model

A total of 1652 patches comprising 180,050 ha of potentially suitable habitat were identified throughout the modeling area (Table 1; Figs. 2D, 3). Patch size

Table 2. Trapping effort and observations for 26 camera traps deployed across 7 survey sites in Texas from March to October 2016. Survey sites A–G are mapped in Figure 3. No Louisiana Pinesnakes were observed on any site.

| Survey site | County | Number of traps | Trap-days | Snake observations | Trap-days per snake |
|-------------|--------|-----------------|-----------|--------------------|---------------------|
| A | Smith | 4 | 703 | 65 | 10.8 |
| В | Tyler | 4 | 572 | 57 | 10.0 |
| C | Tyler | 4 | 655 | 89 | 7.4 |
| D | Tyler | 2 | 376 | 19 | 19.8 |
| E | Hardin | 4 | 689 | 117 | 5.9 |
| F | Jasper | 4 | 653 | 69 | 9.5 |
| G | Newton | 4 | 704 | 102 | 6.9 |
| Total | | 26 | 4352 | 518 | 8.4 |

varied from 30 to 9807 ha, but 99% of patches were less than 1000 ha (n = 1636). Only 16 patches were greater than 1000 ha and considered potentially large enough to support at least 30 home ranges. Together, these 16 patches contained 25% of the total modeled potentially suitable habitat for the species (Table 1).

Two of these large (>1000 ha) patches were located in Texas, ~95 km from one another. The western-most patch of potential Louisiana Pinesnake habitat was located in the Davy Crockett National Forest (Houston County), and the other patch was located in the Angelina National Forest (Angelina and Jasper counties). These 2 large patches were surrounded by smaller patches (<500 ha) and were more than 30 km from moderately sized patches (500–999 ha).

The remaining 14 patches, located in Louisiana, were naturally aggregated into 4 clusters (Figs. 2D, 3). In Vernon Parish, the cluster was composed of 4 large patches (>1000 ha) spread across the Calcasieu District of Kisatchie National Forest and Fort Polk, the Army's Joint Readiness Training Center. In Rapides Parish, 3 large patches were clustered in the Calcasieu District of Kisatchie National Forest. Five large patches were clustered in the Catahoula District of Kisatchie National Forest, Grant Parish, and a pair of large patches was located in the Winn District of Kisatchie National Forest, Natchitoches Parish. Each of these clusters also included 1–5 moderately sized patches (500–999 ha).

Surveys

The 26 camera traps collected 8,388,078 images resulting in 518 snake observations of 18 snake species (Table 2). This equals 1 snake for every 16,193 images or about 1 snake every 8.4 camera days. Although no Louisiana Pinesnakes were detected, we did observe the following species: Agkistrodon contortrix (L.) (Eastern Copperhead), Agkistrodon piscivorus (Lacépède) (Northern Cottonmouth), Coluber constrictor L. (North American Racer), Diadophis punctatus (L.) (Ring-necked Snake), Heterodon platirhinos Latreille (Eastern Hog-nosed Snake), Lampropeltis calligaster (Harlan) (Prairie Kingsnake), Lampropeltis holbrooki (Stejneger) (Speckled Kingsnake), Coluber flagellum Shaw (= Masticophis flagellum (Shaw)) (Coachwhip), Micrurus tener (Baird and Girard) (Texas Coralsnake), Nerodia erythrogaster (Forster) (Plain-bellied Watersnake), Nerodia fasciata (L.) (Southern Watersnake), Opheodrys aestivus (L.) (Rough Greensnake), Pantherophis obsoletus (Say) (Western Ratsnake), Pantherophis slowinskii (Burbrink) (Slowinski's Cornsnake), Storeria dekayi (Holbrook) (Dekay's Brownsnake), Storeria occipitomaculata (Storer) (Red-Bellied Snake), Thamnophis proximus (Say) (Western Ribbonsnake), and Virginia striatula (L.) (Rough Earthsnake). Detections of these snake species occurred over the entire daily sampling period, 0545–2200 hrs. Most individual snake detections (n = 303, 58%) were from single images, or 2 consecutive images (n = 92, 18%). Only 24% (n = 123) of individual snake detections were from 3 or more consecutive images (see also Adams et al. 2017b). These individual snake detection rates provide context for evaluating whether we could have detected a Louisiana Pinesnake if present at a camera trap.

Discussion

Our model demonstrated that only 9.0% (180,050 ha) of the slightly more than 2 million ha of potentially suitable soils for the Louisiana Pinesnake (Fig. 2C; Wagner et al. 2014) also contained mature pine stands that had not been totally harvested between 1985 and 2015 (Fig. 2D) and thus have the potential to support the species. When considering only remnant patches greater than 1000 ha (n = 16), the amount of potentially suitable habitat shrinks to 2.3% (45,605 ha), and all of it is contained on federal lands. We suggest it is not surprising that this suitable habitat is restricted to federal lands; as early as the 1980s the federal government implemented forest restoration and management plans in these areas to restore and maintain open-canopy pine forest for *Picoides borealis* (Vieillot) (Red-cockaded Woodpecker), a species with similar habitat and management requirements as Louisiana Pinesnakes.

With respect to future Louisiana Pinesnake reintroductions, our model identified several patches greater than 1000 ha that could be potential candidate sites. Of the 4 clusters of patches observed in Louisiana (Fig. 3), 2 coincide with extant populations of Louisiana Pinesnake, one of which is a recently reintroduced population and the other is a wild population on Fort Polk. The other 2 clusters contained historical Louisiana Pinesnake populations that are now considered extirpated by USFWS. For this reason, additional habitat surveys should be conducted at these candidate sites to confirm that other elements of Louisiana Pinesnake habitat (e.g., herbaceous understory for populations of Pocket Gopher prey) are present before initiating reintroduction efforts. In Texas, 1 of the 2 patches identified coincides with an extant Louisiana Pinesnake population (southern Angelina National Forest), although snakes have not been detected there since 2012. This site is managed for Louisiana Pinesnakes and is the largest patch of habitat remaining in Texas, but it is bisected by a heavily traveled state highway. The patch in the Davy Crockett National Forest would require considerable sustained habitat management to reduce the dense midstory and increase the herbaceous understory for populations of Pocket Gopher prey before it could be considered a viable candidate site for future Louisiana Pinesnake reintroduction efforts. Consequently, the patch in the Davy Crockett National Forest provides another example of why additional habitat surveys are required to evaluate the candidacy of reintroduction sites identified by our model.

Of the 7 extant populations of Louisiana Pinesnakes recognized by the USFWS (USFWS 2014, 2018), 3 persist in areas that were not completely identified as potentially suitable habitat by our model. Specifically, portions of the areas containing those extant populations were identified, but the entire area estimated to be occupied by Louisiana Pinesnake populations was not included (USFWS 2018). Unidentified areas occupied by Louisiana Pinesnake populations were small (<100 ha), suggesting it is unlikely the model missed entire viable populations (i.e., populations residing on suitable habitat greater than 1000 ha in size) elsewhere. The Bienville population in Bienville Parish, LA, and portions of the Kisatchie National Forest (Kisatchie District) population in Natchitoches Parish, LA, contain open

pine savannahs that were not included in the pine forest Landsat imagery used in our model due to the low density of individual pine trees. In addition, the Peason Ridge population in Vernon and Sabine parishes, LA, and portions of the Kisatchie National Forest population occupy habitats with soils that were not identified as preferred in the previous habitat model (Wagner et al. 2014) and thus were not included in our model.

These observations highlight shortcomings in our approach to modeling potentially suitable Louisiana Pinesnake habitat. Future habitat-modeling efforts should try to incorporate additional spatial data capable of identifying open pine savannah habitats with low tree density or possibly include an estimate of time since harvest so areas with sufficient regeneration time since harvest and proper habitat management might be identified as potentially suitable habitat in the future. However, even with these potential improvements to our modeling approach, approaches based on remote sensing would still be incapable of identifying whether the appropriate herbaceous ground cover is present within the forest patches identified as potentially suitable. We know from past research that this is another key habitat factor that allows for the presence of Pocket Gophers and in turn for potential populations of Louisiana Pinesnakes (Himes et al. 2006, Rudolph and Burgdorf 1997). These habitat attributes may never be characterized accurately with remote-sensing approaches like the ones used in our model, so additional habitat surveys will likely always be required to completely evaluate the potential suitability of modeled habitat. For these reasons, we stress that this model alone is inadequate for determining critical habitat for the species under the Endangered Species Act. Rather, like its predecessor based on soil features (Wagner et al. 2014), it helps narrow the area of interest by targeting sites for future habitat surveys as described above and identifying potentially suitable candidate sites for reintroduction.

Our model also helped identify locations of potentially suitable habitat for future surveys on private, state, and federal lands that may not have been surveyed for Louisiana Pinesnakes in the past. At the survey sites selected in this study, we recorded 518 observations of 18 snake species, but no Louisiana Pinesnakes. While these data illustrate that our modified sampling design is capable of detecting large snakes, they do not allow us to conclude absence of Louisiana Pinesnakes without knowing detection probabilities. However, ongoing research in habitats occupied by Louisiana Pinesnakes should eventually provide these values (J.B. Pierce, unpubl. data). The current study provided relevant information by characterizing a detectability window for large snakes like the Louisiana Pinesnake using timeinterval camera-trapping methods. Specifically, 75% of individual snakes detected moved through the field of view of the camera in less than 1.5 min. Some species (e.g., Coachwhips) moved through in less than 30 sec, suggesting that longer time intervals between images should be used with caution. For example, if we had used a 1-min photograph interval we would have missed ~150 snake detections. Alternatively, reducing the time interval for photographs could increase snake detections, but it will also increase the number of images to process, which increases the cost and time of survey efforts (Adams et al. 2017b, Neuharth et al. 2020).

We believe this camera-trapping method would be useful for future Louisiana Pinesnake surveys, especially in potentially suitable habitats identified on private lands or federal holdings such as military installations. In these areas with restricted access, this camera-trapping method can provide a less-intrusive alternative to traditional trapping methods (Burgdorf et al. 2005, Rudolph et al. 2006), because it reduces scheduled interactions required of private landowners or military personnel from daily trap checking down to just monthly visits for data download and camera maintenance (Adams et al. 2017b). This reduction in trap visitation using the camera-trapping method also saves time and money for field technicians, and its passive sampling design could relieve problems associated with physical species capture (e.g., trap mortality, trap shyness; Adams et al. 2017b). Although this camera-trapping method is limited to research applications requiring species detection only, we believe it could also complement research applications that require data collected from animals in hand (e.g., morphology, mark/recapture, genetics) by first establishing presence and characterizing the target species' detectability profile to allow for more efficient species capture using traditional box-trapping methods.

In conclusion, the patchiness of our habitat model results as well as our failure to detect Louisiana Pinesnakes at the small number of suitable sites identified by the model are consistent with previous conclusions that populations in Texas are small, isolated, and probably in decline, if not already extirpated (Rudolph et al. 2018). Model results for Louisiana identified much larger potentially suitable habitat patches, although populations still appear to be in decline (Rudolph et al. 2018). With limited conservation resources, decisions to invest in searches for relictual populations of the species compete with efforts to create new populations through captive breeding and reintroduction programs. The results of this study should help inform the decision-making process by narrowing the search areas for relictual populations, providing a more cost-effective method of surveying those areas, and identifying the best sites for future reintroduction efforts.

Acknowledgments

We thank the following landowners for access to properties for surveys: Campbell Global, Hancock Forest Management, The Nature Conservancy, and Tyler State Park. We especially thank Texas A&M Forest Service for helpful comments on this manuscript and access to John Henry Kirby Memorial State Forest and E.O. Siecke State Forest for surveys. We also thank Lauren Dyess, Aaron George, and Jerrott Abernathy for help viewing images. This research was funded by the Texas Comptroller of Public Accounts. This research was conducted under Texas A&M University animal care permit number 2016-0178 and Texas Parks and Wildlife Department Scientific Research Permit No. SPR-0506-662. This is publication number 1628 of the Biodiversity Research and Teaching Collections, Texas A&M University.

Literature Cited

Adams, C.S., J.B. Pierce, D.C. Rudolph, W.A. Ryberg, and T.J. Hibbitts. 2017a. *Pituophis ruthveni*. Catalogue of American Amphibians and Reptiles 910. Society for the Study of Amphibians and Reptiles.16 pp.

- Adams, C.S., W.A. Ryberg, T.J. Hibbitts, B.L. Pierce, J.B. Pierce, and D.C. Rudolph. 2017b. Evaluating effectiveness and cost of time-lapse triggered camera-trapping techniques to detect terrestrial squamate diversity. Herpetological Review 48:44–48.
- Adams, C.S., J.B. Pierce, D.C. Rudolph, W.A. Ryberg, and T.J. Hibbitts. 2018. Resolving questionable records of *Pituophis ruthveni* (Louisiana Pinesnake). Southeastern Naturalist 172:286–292.
- Burgdorf, S.J., D.C. Rudolph, R.N. Conner, D. Saenz, and R.R. Schaefer. 2005. A successful trap design for capturing large terrestrial snakes. Herpetological Review 36:421–424.
- Coppin, P., I. Jonckheere, K. Nackaerts, B. Muys, and E. Lambin. 2004. Digital change-detection methods in ecosystem monitoring: A review. International Journal of Remote Sensing 25:1565–1596.
- Davis, W.B., R.R. Ramsey, and J.M. Arendale Jr. 1938. Distribution of Pocket Gophers (*Geomys breviceps*) in relation to soils. Journal of Mammalogy 19:412–418.
- Dixon, J.R. 2013. Amphibians and Reptiles of Texas. Third Edition. Texas A&M University Press, College Station, TX. 447 pp.
- Dundee, H.A., and D.A. Rossman. 1989. The Amphibians and Reptiles of Louisiana. Louisiana State University Press, Baton Rouge, LA. 300 pp.
- Durso, A.M., J.D. Willson, and C.T. Winne. 2011. Needles in haystacks: Estimating detection probability and occupancy of rare and cryptic snakes. Biological Conservation 144:1508–1515.
- Ealy, M.J., R.R. Fleet, and D.C. Rudolph. 2004. Diel activity patterns of the Louisiana Pine Snake, *Pituophis ruthveni*, in eastern Texas. Texas Journal of Science 56:383–394.
- Environmental Systems Research Institute (ESRI). 2014. ArcMap, Version 10.3. Redlands, CA.
- Frost, C.C. 1993. Four centuries of changing landscape patterns in the Longleaf Pine ecosystem. Proceedings Tall Timbers Fire Ecology Conference 18:17–43.
- Himes, J.G., L.M. Hardy, D.C. Rudolph, and S.J. Burgdorf. 2006. Movement patterns and habitat selection by native and repatriated Louisiana Pine Snakes (*Pituophis ruthveni*): Implications for conservation. Herpetological Natural History 9:103–116.
- Kéry, M. 2002. Inferring the absence of a species: A case study of snakes. Journal of Wildlife Management 1:330–338.
- Lyon, J.G., D. Yuan, R.S. Lunetta, and C.D. Elvidge. 1998. A change-detection experiment using vegetation indices. Photogrammetric Engineering and Remote Sensing 64:143–150.
- Moler, P.E. 1992. Eastern Indigo Snake. Pp. 181–186, *In P.E.* Moler (Ed.). Rare and Endangered Biota of Florida, Volume III: Amphibians and Reptiles. University Press of Florida, Gainesville, FL. 272 pp.
- Neuharth, D.B., W.A. Ryberg, C.S. Adams, T.J. Hibbitts, D.K. Walkup, S.L. Frizzell, T.E. Johnson, B.L. Pierce, J.B. Pierce, and D.C. Rudolph. 2020. Searching for rare and secretive snakes: Are camera-trap and box-trap methods interchangeable? Wildlife Research WR1930. https://doi.org/10.1071/WR19230.
- Rudolph, D.C., and S.J. Burgdorf. 1997. Timber Rattlesnakes and Louisiana Pine Snakes of the West Gulf Coastal Plain: Hypotheses of decline. Texas Journal of Science 49(supplement):111–122.
- Rudolph, D.C., S.J. Burgdorf, R.R. Schaefer, R.N. Conner, and R.T. Zappalorti. 1998. Snake mortality associated with late season radio-transmitter implantation. Herpetological Review 29:155–156.

- Rudolph, D.C., S.J. Burgdorf, R.N. Conner, C.S. Collins, D. Saenz, R.R. Schaefer, and T. Trees. 2002. Prey handling and diet of the Louisiana Pine Snakes (*Pituophis ruthveni*) and Black Pine Snakes (*P. melanoleucus lodingi*), with comparisons to other selected colubrid taxa. Herpetological Natural History 9:57–62.
- Rudolph, D.C., S.J. Burgdorf, R.R. Schaefer, R.N. Conner, and R.W. Maxey. 2006. Status of *Pituophis ruthveni* (Louisiana Pine Snake). Southeastern Naturalist 5:463–472.
- Rudolph, D.C., J.B. Pierce, and N.E. Koerth. 2018. The Louisiana Pinesnake: At risk of extinction? Herpetological Review 49:609–619.
- Speake, D.W., J. McGlincy, and J. Diemer, 1982. Eastern Indigo Snake recovery plan. US Fish and Wildlife Service, Atlanta, GA. 23 pp.
- Steen, D.A. 2010. Snakes in the grass: Secretive natural histories defy both conventional and progressive statistics. Herpetological Conservation and Biology 5:183–188.
- Steen, D.A., C.J. McClure, J.C. Brock, D.C. Rudolph, J.B. Pierce, J.R. Lee, W.J. Humphries, B.B. Gregory, W.B. Sutton, L.L. Smith, and D.L. Baxley. 2012. Landscape-level influences of terrestrial snake occupancy within the southeastern United States. Ecological Applications 22:1084–1097.
- Stull, O.G. 1929. The description of a new subspecies of *Pituophis melanoleucus* from Louisiana. Occasional Papers of the Museum of Zoology, University of Michigan. No. 205. 4 pp.
- United States Fish and Wildlife Service (USFWS). 2003. Candidate conservation agreement for the Louisiana Pine Snake (*Pituophis ruthveni*) between the USFWS, USFS, DOD, TPWD, and LDWF. 30 pp. Available online at https://www.fws.gov/southwest/es/ArlingtonTexas/pdf/LPS CCA Final.pdf. Accessed August 2020.
- USFWS. 2014. Species assessment and listing priority assignment form for the Louisiana Pine Snake (*Pituophis ruthveni*). 34 pp. Available online at https://esadocs.defenders-cci.org/ESAdocs/candidate/C02C_V01.pdf. Accessed August 2020.
- USFWS. 2016. Endangered and Threatened Wildlife and Plants: Threatened species status for Louisiana Pine Snake. Department of Interior, Washington DC. Federal Register 81:69454–69475.
- USFWS. 2018. Threatened species status for Louisiana Pinesnake. Federal Register 83:14958–14982.
- USFWS. 2019. Draft Eastern Indigo Snake recovery implementation strategy. Atlanta, GA. 37 pp.
- Wagner, R.O., J.B. Pierce, D.C. Rudolph, R.R. Schaefer, and D.A. Hightower. 2014. Modeling Louisiana Pine Snake (*Pituophis ruthveni*) habitat use in relation to soils. Southeastern Naturalist 13(Special Issue 5):146–158.