

Modeling Louisiana Pine Snake (*Pituophis ruthveni*) Habitat Use in Relation to Soils

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Abstract - Ongoing surveys suggest that *Pituophis ruthveni* (Louisiana Pine Snake) has declined range-wide and that known extant populations have continued to decline. Seven known populations remain and occupy small, isolated blocks of habitat. Population sizes are unknown, but all of them are believed to be critically small. Management for the species' recovery requires an understanding of its habitat requirements and how resources used by these snakes are distributed in space. Research suggests that the species' primary prey, *Geomys breviceps* (Baird's Pocket Gopher), prefers sandy, well-drained soils. Thus soil attributes may be used to identify potential Louisiana Pine Snake habitat. Using Natural Resources Conservation Service Soil Survey Geographic Database (SSURGO) soil characteristics and available historical and recent telemetered snake locations, we developed resource selection functions describing Louisiana Pine Snake potential habitat at two spatial scales. SSURGO variable hydgrp, a soil characteristic developed for modeling precipitation runoff, incorporating soil permeability and depth to ground water, best predicted species occurrence and was used to map potential habitat selection and identify areas of high conservation value. Our model demonstrates that the distribution of Louisiana Pine Snakes on the landscape is strongly influenced by edaphic factors, which are unlikely to be changed at a landscape scale by human activities. Ample area of suitable soils remains available to support the species throughout its historical range; however, we suspect that a miniscule fraction of the potential habitat we identified has suitable vegetation communities on-site to support Louisiana Pine Snakes.

Introduction

Pituophis ruthveni Stull (Louisiana Pine Snake) historically occupied a limited range in eastern Texas and west-central Louisiana (Reichling 1995, Rudolph et al. 2006, Sweet and Parker 1991) coincident with the range of *Pinus palustris* Mill. (Longleaf Pine) on the west Gulf Coastal Plain (Conant 1956, Reichling 1995, Thomas et al. 1976). Presumed extirpated from much of its historical range (Rudolph et al. 2006), the species is now restricted to seven extant populations (one of which may be recently extirpated) which occupy a limited number of small and fragmented localities (Reichling 1995; Rudolph et al. 2006; J.B. Pierce, unpubl. data) on federally and privately owned lands. A limited number of studies have been published that focus on the ecology of Louisiana Pine Snakes. As a result, it is difficult to develop landscape-scale habitat models for this species, although these are essential to its management and conservation.

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Louisiana Pine Snake habitat suitability may be largely influenced by the presence of suitable soils. Sandy well drained soils, in particular, may dictate the presence and abundance of Louisiana Pine Snake's main prey *Geomys breviceps* Baird (Baird's Pocket Gopher) (Rudolph et al. 2012), the burrows of which also provide snakes with shelter from unfavorable environmental conditions (Rudolph and Burgdorf 1997; Rudolph et al. 1998, 2002). Attempts to model Louisiana Pine Snake habitat suitability that relied on expert opinion to select soil types based on perceived suitability yielded models of limited utility. Thus, robust models of Louisiana Pine Snake habitat selection were not available.

Resource selection occurs when a resource is used disproportionate to its availability and takes place in a hierarchical fashion at multiple spatial scales from the species' physical or geographic range (first-order), to selection of individual home ranges within the geographic range (second-order), to the animal's usage of features within its home range (third-order), to selection of particular elements such as food items (Johnson 1980). Resource selection functions (RSF) provide a tool to rank areas by their relative probability of selection (Johnson et al. 2006, Manly et al. 2002). Extrapolating those relative probabilities in a geographic information system (GIS) can provide spatially explicit models that can be used for prioritizing areas for conservation management (Aldridge and Boyce 2007).

Past efforts to locate extant Louisiana Pine Snake populations were based on proximity to historical records, perceived suitable vegetative structure (i.e., pine overstory with a sparse midstory and a well-developed herbaceous understorey; Himes et al. 2006, Rudolph and Burgdorf 1997) and soils (Conant 1956, Thomas et al. 1976). Using those methods, extant populations might remain undiscovered. Based on the published descriptions of Baird's Pocket Gopher soil preferences (Davis et al. 1938), we hypothesized that selection would increase with increasing sand content and decreasing soil saturation. To examine this hypothesis, we used edaphic factors (i.e., soil characteristics) to model potential habitat for the Louisiana Pine Snake. To accomplish this, we analyzed existing location data for this species to create RSF models for soils across the Louisiana Pine Snake's historical range at two spatial scales: second- and third-order, described below. We examined habitat selection at multiple scales to test our RSF model with independently derived data (i.e., recent telemetered locations of this species). This approach allowed us to rigorously vet our model and insure that we made robust inferences about habitat selection. Our objectives were to 1) develop a robust landscape-scale RSF that described Louisiana Pine Snake potential habitat, 2) spatially depict potential habitat selection to identify areas of high probability of selection for focused LPS habitat management, restoration, potential conservation easement acquisition, and reintroduction, and 3) provide data to other researchers to identify areas of potential habitat not previously surveyed for Louisiana Pine Snakes.

Study Area

Our study area consisted of all counties in eastern Texas and parishes in west central Louisiana that contained three or more Louisiana Pine Snake historical locations. That area included Angelina, Jasper, Newton, and Sabine counties in

Texas, and Bienville, Natchitoches, Rapides, Sabine, and Vernon Parishes in Louisiana. The study area included all known recently extant populations of Louisiana Pine Snakes (Rudolph et al. 2006).

Methods

Location data development

Range-wide soils data from the Natural Resources Conservation Service (NRCS) Soil Survey Geographic database (SSURGO, 2007) were readily available. These data have been rigorously obtained through standardized methods by the NRCS. Therefore, they are of sufficient detail, spatial resolution, extent, and attribution to test hypotheses regarding Louisiana Pine Snake soil preferences.

To model habitat selection at multiple scales, we assembled two datasets of Louisiana Pine Snake locations: historical data and validation data. Historical data were the most complete set of range-wide location data available, with location dates ranging from 1 December 1927 to 23 June 2009. Historical data contained locations from literature records, museum collections, and our records of trap-capture sites (established and monitored by the US Forest Service (USFS), Southern Research Station, Wildlife Habitat and Silviculture Laboratory, Nacogdoches, TX, and Fort Polk Conservation Branch, Fort Polk, LA), road kills, and opportunistic sightings, along with similar records from other researchers (Rudolph et al. 2006; Sweet and Parker 1991; D.C. Rudolph, unpubl. data). Most locations collected after 1992 were estimated using GPS, which allowed for acceptable detail. We estimated the specific locations described in historical accounts from descriptive information contained in the sighting record. We excluded records that (1) lacked sufficient detail to accurately estimate snake locations, (2) were potentially misidentifications, and (3) were recapture locations for the same individual snake. The final dataset consisted of one location for each of 162 snakes and included records from all known extant populations.

Validation data consisted of 1094 unique telemetry relocations of 22 radio-tagged Louisiana Pine Snakes made between 1993 and 1997 used in previous studies (Ealy et al. 2004, Himes et al. 2006, Rudolph and Burgdorf 1997). Locations were distributed among four Texas counties (Angelina [$n = 75$], Jasper [$n = 50$], Newton [$n = 136$], and Sabine [$n = 223$]), and three Louisiana parishes (Bienville [$n = 470$], Sabine [$n = 14$], and Vernon [$n = 126$]). The number of locations per snake ranged from 8–130 (25th, 50th, and 75th percentile = 28, 42, and 73, respectively). Telemetry locations were obtained by tracking snakes at various times throughout the day on 1–7 day intervals, with relocation-site coordinates obtained using post-processed, differentially corrected GPS (Ealy et al. 2004; Himes et al. 2006; Rudolph and Burgdorf 1997; J.B. Pierce, unpubl. data).

Second-order selection

Second-order selection contrasts available resources sampled throughout the study area with a sample of used resources from all animals within the study area, equivalent to the Manly et al. (2002) sampling protocol A (SP-A), design I. To account for variable location precision and imprecision in the mapping of edaphic

factors, we defined used resources as all resources within a 0.25-km radius of historical snake locations. We considered all resources within a 3-km radius of historical data snake locations as available. We chose the 3-km radius based on the distribution of maximum distances among relocations for each snake in the validation dataset. We accepted the 95th percentile of the maximum distance distribution among snakes as a reasonable definition of available resources (median, 95th percentile, and maximum = 1.4, 2.9, and 3.6 km, respectively). We used ArcView (ESRI, Redlands, CA) to create used and available buffer polygons.

We used SSURGO databases and GIS layers to create our initial list of candidate predictor variables. We accomplished this by extracting from those data the edaphic factor values that existed within used and available buffer polygons. The edaphic factors extracted included values from the SSURGO component and chorizon tables restricting the results to the dominant map unit components (e.g., soil series) and H1, or upper soil horizon, respectively. Each map unit (individual polygons shown on the soil map) represents an area dominated by one to three kinds of soils or components with individual properties, and each component has data for each soil horizon in the chorizon table. We included edaphic factors that appeared to influence Louisiana Pine Snake use, mostly complete within the SSURGO dataset across the study area, variable among mapped soil units, and relatively uncorrelated with other candidate factors considered. We evaluated collinearity among candidate predictor variables using variable clustering (Harrell 2001)—a technique to choose among highly correlated variables and avoid multicollinearity during model development.

Because few published studies of Louisiana Pine Snake habitat selection exist, we used expert opinion to develop a competing set of a priori RSF models ($n = 26$) from the set of candidate predictor variables (Appendix 1). When developing models, we chose variables so that all competing models were biologically supportable while avoiding inclusion of collinear variables and over-fitting (maintaining ≥ 15 used locations per predictor degree of freedom; Harrell 2001). To accommodate both continuous and categorical predictors, competing RSFs were structured as weighted logistic regression models with weights proportional to soil types within each location's used and available buffer. We used Akaike's information criterion adjusted for small sample size (AIC_c ; Burnham and Anderson 1998) to rank the set of a priori models and when ΔAIC_c among models was < 2 , we selected the most parsimonious model (Arnold 2010, Burnham and Anderson 1998). We used the coefficients of the selected ΔAIC_c model to estimate the relative probability of selection by Louisiana Pine Snakes (Johnson et al. 2006, Manly et al. 2002) and used 95% confidence intervals to evaluate differences among categories. Using the relative selection probabilities, we estimated more readily interpreted selection indices (w_i ; Manly et al. 2002). Selection indices > 1 indicate that a resource was used in greater proportion than available, w_i not different than 1 suggests use was in proportion to availability, and $w_i < 1$ indicates use was less than available (Manly et al. 2002). We classified $w_i > 1$ as preferred, not different from 1 as suitable, and < 1 as avoided.

We conducted post-hoc analyses to test for additive and interaction effects between the selected second-order RSF model variables and area. This was completed to determine if the large number of locations from the Bienville population, the largest extant population known, biased the results. We created a new categorical variable, area, to distinguish used and available resources in Bienville Parish, LA, from those within the balance of the study area. Two new models were created from the selected second-order model by adding area as an additive and interaction term. We then compared model parsimony using AIC_c.

Third-order selection and validation

Third-order selection contrasts used and available resources sampled for each animal (SP-A, Design III; Manly et al. 2002). We used the validation data to investigate third-order selection. Unlike the historical data, the validation data were precise locations; thus, we accepted the point estimates as our definition of used resources. We defined available resources for each snake as all resources within composite 564-m radius buffers around the locations for each snake. A 564-m radius encompasses the estimated 100-ha minimum multi-year home range for Louisiana Pine Snakes (J.B. Pierce, unpubl. data). As in the second-order analysis, we extracted the edaphic factor values for the used locations and available resource buffers using GIS. However, because our goals were to contrast hierarchical selection, examine selection variability among animals, and validate the second-order model, we only extracted the variable included in the selected second-order model.

The selected second-order model included only a single categorical variable simplifying third-order RSF modeling and second-order validation. We examined log-likelihoods of used versus available proportions to estimate third-order RSFs using methods described by Manly et al. (2002) for studies with resources defined by several categories. We tested the null hypothesis that no selection across resource unit categories occurred using likelihood-ratio tests, both within and across animals. If selection occurred (at $\alpha < 0.05$), then we used likelihood-ratio tests to determine if selection indices (w_i) were different from 1 (at Bonferoni adjusted $\alpha < 0.05$). We classified third-order selection indices as preferred, suitable, or avoided, as we did with the second-order model results.

To validate the second-order model, we relied on used and available resource estimates from the averaged third-order selection evaluation. We averaged used and available resource estimates across all radio-tagged animals in the validation dataset to approximate second-order selection, and compared these validation model results to the selected second-order model results. Following model validation, we mapped potential habitat throughout the species' historical range by linking RSF results with the SSURGO database and GIS layer for each county and parish.

Results

Second-order selection

Based on evaluations of completeness, variability, and collinearity, we identified seven candidate edaphic factors from the SSURGO data that were suitable

predictor variables for development of a priori RSF models (Table 1). Of 26 models considered, the best-approximating model describing second-order Louisiana Pine Snake potential habitat selection included only hydgrp (Appendix 1), a categorical soil characteristic variable developed for modeling precipitation runoff, incorporating soil permeability and depth to ground water. Because the best model included only a single categorical variable and was developed from the proportions of used and available resources at each location, w_i was the proportion of used resources (P_{Used}) divided by the proportion of available resources ($P_{Available}$) within resource unit i (Table 2).

Based on our w_i estimates (Table 2), hydgrp category A was preferred and differed statistically from all other categories (depth to ground water and soil permeability decrease from hydgrp category A, to A/D, to C, to D). Categories B and C were not statistically different than 1 and were thus classified as suitable, although the confidence interval for Category C was large. Category D was avoided. These results strongly support our hypothesis that selection increases with increasing sand content and decreasing soil saturation. Data were insufficient to classify the

Table 1. Candidate variables used to develop competing resource selection functions describing second-order Louisiana Pine Snake potential habitat selection. Descriptions adapted from attribute descriptions in SSURGO Metadata—Table Column Descriptions; SSURGO Metadata Version: 2.2.3 (obtained from <http://soildatamart.nrcs.usda.gov/SSURGOMetadata.aspx> on 5 December 2007).

SSURGO ID (table.field name)	df	Description
muaggatt.floodfreqdcd	4	Annual flooding probability class
component.drainagecl	7	Classes based on drainage, flood frequency and duration
chorizon.sandtotal_r	1	% sand
chorizon.claytotal_r	1	% clay
chorizon.om_r	1	% organic matter
component.taxorder	6	Highest soil taxonomy level; e.g., Entisols, Ultisols
component hydgrp	5	Hydrologic group consisting of classes of soils having similar runoff potential based on depth to a seasonally high water table, and soil permeability

Table 2. Model results for second-order Louisiana Pine Snake potential habitat selection and percent of available ($P_{Available}$) and used (P_{Used}) habitat based on the historical data. β_i is the model estimated coefficients for the i^{th} hydgrp, and $SE(\beta_i)$ its standard error. The selection index is w_i , estimated as $\exp(\beta_i)$, and w_i CI₉₅ its 95% confidence interval.

	Hydgrp				
	A	A/D	B	C	D
$P_{Available}$	28.1%	0.2%	31.3%	12.7%	27.7%
P_{Used}	47.2%	0.2%	33.5%	7.9%	11.1%
β_i	0.517	-0.011	0.069	-0.470	-0.911
$SE(\beta_i)$	0.187	2.303	0.195	0.356	0.279
w_i	1.68	0.99	1.07	0.62	0.40
w_i CI ₉₅	1.16–2.42	0.01–90.46	0.73–1.57	0.31–1.26	0.23–0.69

suitability of hydgrp category A/D. The A/D w_i confidence interval was so wide that the estimate was considered unreliable. The imprecision in the A/D selection likelihood was a function of its rarity within the study area (<0.2% of the study area).

We found no evidence that the habitat selection results were influenced by the large number of locations from the Bienville population or differed between Bienville and the balance of the study area. Additive or interaction effects between hydgrp and area were not supported by the data (ΔAIC_c hydgrp x area = 7.5; ΔAIC_c hydgrp + area < 2). The additive model ΔAIC_c was <2, but differed from the selected second-order model with hydgrp alone by 1 parameter and had essentially the same deviance. Therefore, there was no support for the more complex additive model and the more parsimonious selected second-order model was the best model (Arnold 2009, Burnham and Anderson 1998).

Third-order selection and validation

Used and available resources varied among snakes resulting in differences in resource selection among animals (Table 3). Most snakes (19 of 22; 86%) demonstrated selection across hydgrp categories, but only hydgrp A was preferred. Of those snakes demonstrating selection, hydgrp category A was available to 18 and was preferred by 13 (72%); no snakes avoided hydgrp A. The remaining hydgrp categories were avoided by the following percentages of snakes for which the category was available: category B 15% (2 of 13), category C 38% (5 of 13), and category D 53% (10 of 19).

Based on the across-snake validation model estimates of w_i , we obtained results similar to those from the second-order model with hydgrp A preferred, B suitable, and D avoided. However, unlike the second-order model, the validation model estimate of w_i for hydgrp C had sufficient power to determine that snakes avoided C. Based on validation results, we classified hydgrp A as preferred, B as suitable, and C and D as avoided (Fig. 1). Category A/D did not occur within the validation data available area and thus, we could not evaluate the selected second-order suitable classification. Because A/D represented an insignificant portion of three parishes within the species' historical range (Bienville, Vernon, and Winn), we used the second-order suitable classification for mapping purposes, but the resulting map should be interpreted with caution.

Discussion

The SSURGO database variable hydgrp, developed for modeling precipitation runoff, incorporated the factors that we believed most influenced Louisiana Pine Snake potential habitat selection: percent sand and depth to ground water. Percent sand was highest in hydgrp category A and decreased in each subsequent class A/D through D with corresponding increases in variability (Fig. 2). As we hypothesized, the likelihood of Louisiana Pine Snake use increased with increasing percent sand and depth to water table. Hydgrp, which incorporated both components, explained a greater fraction of the variance among snake locations than percent sand alone.

Table 3. Number of telemetry locations per snake (n), and percent of used (P_{Used}) and available ($P_{Available}$) area, selection index (w_i), and selection classification by snake and hydgrp for radio-tagged Louisiana Pine Snakes. Blank cells indicate hydgrp i was not available.

Snake	n	P_{Used} hydgrp				$P_{Available}$ hydgrp				w_i hydgrp				Selection ^B hydgrp			
		A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D
1	45	1.00	0.00	0.00	0.00	0.61	0.26	0.05	0.08	1.63	0.00	0.00	0.00	+	-	-	-
2	82	0.72	0.16	0.12	0.52	0.23	0.25	1.39	0.69	0.48	+	-	-	-	-	-	-
3	72	0.47	0.00	0.51	0.01	0.26	0.04	0.59	0.11	1.79	0.00	0.88	0.12	+	-	-	-
4	83	0.72	0.28	0.00	0.00	0.54	0.19	0.14	0.13	1.34	1.43	0.00	0.00	+	-	-	-
5	130	0.98	0.02	0.00	0.00	0.57	0.31	0.05	0.08	1.73	0.08	0.00	0.00	+	-	-	-
6	14	0.50	0.07	0.43	0.15	0.20	0.65	3.26	0.36	0.66	+	-	-	-	-	-	-
7	27	0.89	0.11	0.00	0.00	0.51	0.25	0.13	0.11	1.75	0.45	0.00	0.00	+	-	-	-
8	73	0.92	0.04	0.04	0.52	0.25	0.23	1.77	0.16	0.18	+	-	-	-	-	-	-
9	52	0.23	0.77	0.00	0.13	0.75	0.12	1.81	1.02	0.00	-	-	-	-	-	-	-
10 ^A	25	0.48	0.28	0.24	0.00	0.44	0.26	0.22	0.08	1.10	1.09	1.08	0.00	-	-	-	-
11	8	1.00	0.00	0.00	0.63	0.26	0.11	1.59	0.00	0.00	-	-	-	-	-	-	-
12	37	0.73	0.00	0.27	0.41	0.13	0.46	1.79	0.00	0.58	+	-	-	-	-	-	-
13 ^A	9	0.78	0.00	0.22	0.62	0.13	0.25	1.26	0.00	0.88	-	-	-	-	-	-	-
14	88	0.40	0.22	0.35	0.03	0.46	0.15	0.29	0.10	0.86	1.49	1.21	0.34	-	-	-	-
15	41	0.90	0.00	0.05	0.05	0.52	0.01	0.28	0.19	1.73	0.00	0.18	0.25	+	-	-	-
16	43	0.81	0.19	0.00	0.76	0.10	0.14	1.07	1.87	0.00	-	-	-	-	-	-	-
17	51	0.02	0.98	0.00	0.03	0.87	0.10	0.57	1.13	0.00	-	-	-	-	-	-	-
18	93	0.86	0.03	0.11	0.47	0.22	0.31	1.83	0.15	0.35	+	-	-	-	-	-	-
19	31	0.97	0.00	0.03	0.78	0.00	0.22	1.24	0.00	0.15	+	-	-	-	-	-	-
20 ^A	34	0.76	0.00	0.24	0.78	0.01	0.22	0.99	0.00	1.08	-	-	-	-	-	-	-
21	33	1.00	0.00	0.00	0.72	0.10	0.18	1.39	0.00	0.00	+	-	-	-	-	-	-
22	23	1.00	0.00	0.00	0.00	0.92	0.08	1.09	0.00	0.00	-	-	-	-	-	-	-
Overall	1094	0.69	0.19	0.06	0.07	0.47	0.21	0.13	0.19	1.48	0.84	0.52	0.30	+	-	-	-

^ALikelihood ratio test for resource selection was not significant (at $\alpha = 0.05$).

^BIf selection occurred and w_i values were different than 1 (Bonferroni adjusted $\alpha < 0.05$), a + indicates $w_i > 1$ (which supports selection) and - indicates $w_i < 1$ (which supports avoidance).

Despite known differences in vegetation structure across snake locations used in model development, our successful modeling of Louisiana Pine Snake second- and third-order potential habitat selection suggested that edaphic factors may also influence first-order selection. Although we did not have the data necessary to critically examine first-order selection, as an exploratory analysis we estimated hydgrp proportions within the counties and parishes throughout the snake's historical range ($A = 7.9\%$, $B = 31.7\%$, $C = 24.6\%$, and $D = 35.8\%$). We replaced the estimated available habitat in the selected second-order selection RSF with the range-wide available estimates to estimate hypothetical first-order selection indexes by hydgrp. Compared to the selected second-order selection results, preference for hydgrp A increased ($w_i = 5.97$), B and D remained approximately the same, and avoidance of C increased ($w_i = 0.32$). Although only an approximation of first-order potential habitat selection, these results together with the second- and third-order results suggest that soils strongly influenced the species' historical range.

Encouraged by our modeling and validation results, we distributed the maps of potential habitat (Fig. 1) to researchers and managers responsible for Louisiana Pine Snake conservation. Those maps were used to delineate the boundary of a proposed conservation area for the Bienville population, which provided a

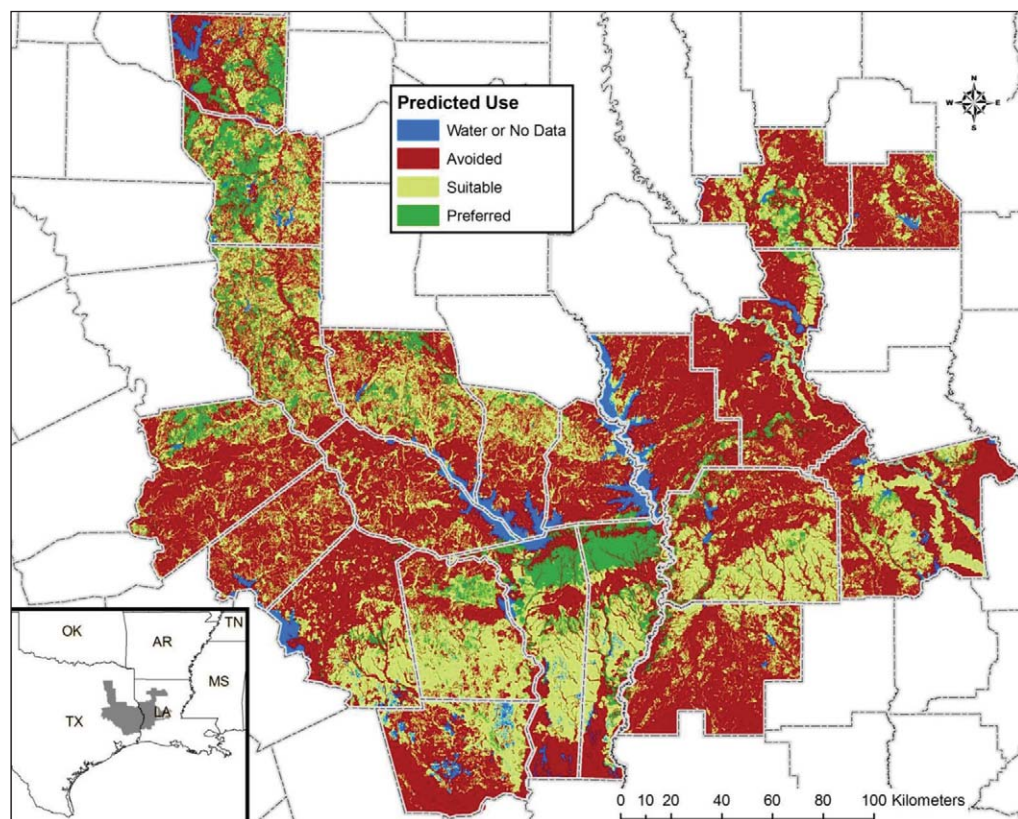


Figure 1. Potential Louisiana Pine Snake habitat predicted, based on validation model estimates for hydgrp categories.

target area for the acquisition of protective easements by conservation organizations. The maps were also used to focus habitat management of federal lands, identify reintroduction sites outside of extant populations, and assess threats to extant populations. We plan to use the results of this study to quantify the spatial extent and location of potential habitat on federal lands and determine if there are areas of suitable habitat that have not been adequately surveyed for Louisiana Pine Snake occurrence. When available, these results will be provided to the US Fish and Wildlife Service for consideration.

Our models focused on edaphic factors unlikely to be changed at a landscape scale by human activities and thus were useful for identifying potential Louisiana Pine Snake habitat. Suitable habitat consists of potential habitat with an appropriate vegetative cover. Louisiana Pine Snake declines have been attributed to a loss of suitable habitat associated with loss of the Longleaf Pine ecosystem, due largely to conversion to short-rotation *Pinus taeda* L. (Loblolly Pine) plantations and exclusion of frequent fire. We suspect that a miniscule fraction of the potential habitat we identified has vegetation communities on-site suitable to support Louisiana Pine Snakes. In addition to the presence of suitable soils, increasing the acreage

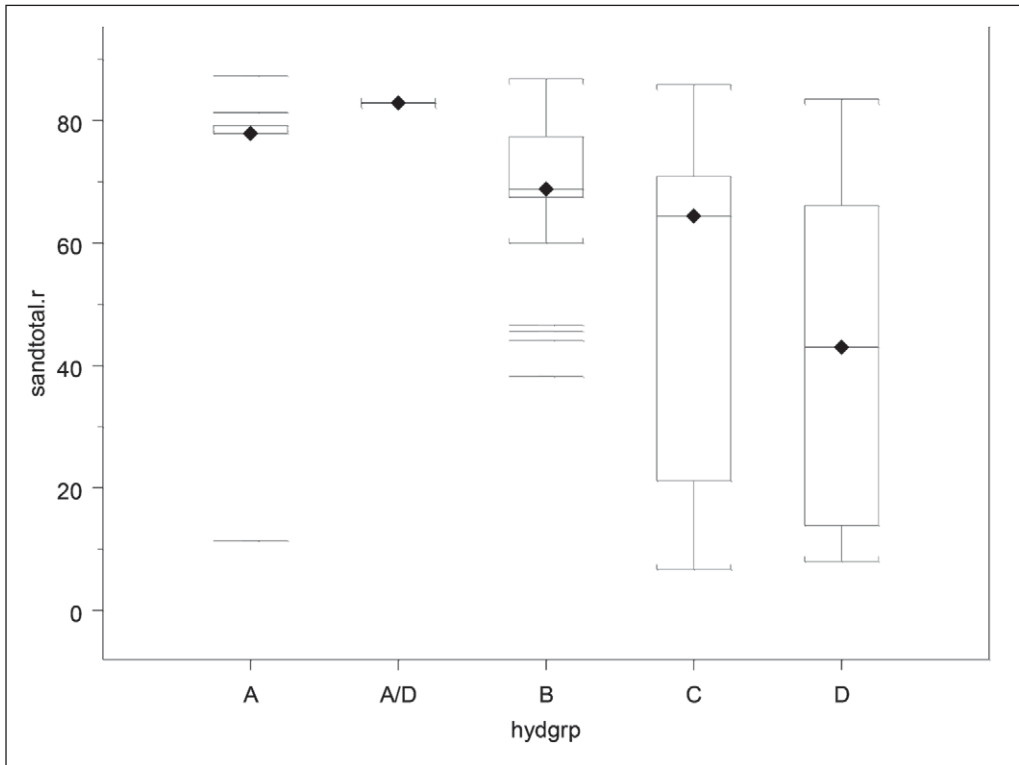


Figure 2. The percent sand (sandtotal.r) within hydrgrp categories. The box represents the inner quartile range (25th to 75th percentiles), and upper and lower whiskers extending from the box represent the smallest and largest observations within one step (1.5 times inner quartile range). The median (◆) is marked by a line through the box, and horizontal bars (—) represent extreme values.

of Longleaf Pine communities on areas with these soils is likely needed for species recovery. We believe that this can be achieved through the reestablishment of appropriate timber stocking and fire regimes within and adjacent to extant populations. A more detailed understanding of the vegetation communities required to support this species is a topic worthy of future research.

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Appendix 1. A priori RSF candidate models for historical Louisiana Pine Snake locations. fl = flodfreqded, dr = drainagecl, sa = sandtrotal.r, cl = claytotal.r, and om = om.r.

Model	Variable								K	$\Delta AICc$	w_i
	fl	dr	sa	cl	om	taxorder	hydgrp				
1	x		x	x	x				7	12.29	0.001
2	x		x		x				6	12.79	0.001
3	x		x			x			9	17.06	0.000
4	x		x				x		9	6.66	0.017
5		x	x	x	x				10	14.53	0.000
6		x	x						8	11.03	0.002
7		x				x			11	15.41	0.000
8		x					x		11	11.40	0.002
9			x	x	x	x			8	10.89	0.002
10			x	x	x		x		8	5.62	0.029
11			x	x		x			7	10.47	0.003
12			x		x	x			7	11.20	0.002
13			x	x			x		7	3.56	0.081
14			x		x		x		7	3.53	0.082
15			x			x	x		10	8.14	0.008
16						x	x		9	6.51	0.018
17			x			x			6	10.93	0.002
18			x				x		6	1.50	0.227
19	x		x						5	11.72	0.001
20			x	x	x				4	7.08	0.014
21	x								4	12.66	0.001
22		x							7	9.12	0.005
23			x						2	6.58	0.018
24						x			5	10.03	0.003
25							x		5	0.00	0.479
Null									1	11.42	0.002