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Using LiDAR to Enhance Distribution Models for the Dunes Sagebrush Lizard (*Sceloporus arenicolus*) in Texas, USA

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Abstract.—**Mapping species distributions and habitat suitability guides policy decisions and conservation. Over the last few decades, multiple expert-derived, qualitative species occurrence and habitat availability maps have been developed in response to increasing conservation attention on the Dunes Sagebrush Lizard (*Sceloporus arenicolus*). Management and conservation decisions, however, necessitate development of a more structured, quantitative approach, based on the known occurrences of *S. arenicolus* and its habitat requirements. Thus, the goal of our work was to develop a continuous species distribution model for *S. arenicolus* in Texas. We used Generalized Linear (GLM) and Generalized Additive (GAM) models to predict areas where conditions were appropriate, using land cover covariates as well as rugosity covariates derived from Airborne Light Detection and Ranging (LiDAR), for *S. arenicolus* occurrence within its known Texas range. The best fitting GLM model indicated higher mean maximum rugosity and lower percentage cover of Shinnery Oak (*Quercus havardii*) increased the mean predicted probability of occurrence for *S. arenicolus*. Using the best-fitting model, we also predicted probability of occurrence via a GAM that included a spatial effect, which indicated that greater proximity to identified *S. arenicolus* presences increased the predicted probability of occurrence. Our species distribution maps can be used to inform the listing determination and support future conservation actions by identifying suitable areas for *S. arenicolus*, helping prioritize areas for future *S. arenicolus* surveys, and determining areas for high-value conservation or management actions.**

Key Words.—Benthic Terrain Modeler; Generalized Linear Model; Generalized Additive Model; habitat specialist; LiDAR digital elevation model; Mescalero Monahans Shinnery Oak Dunes; object-based image classification; terrain ruggedness

Introduction

Understanding the distribution of species within their geographic ranges is one of the earliest steps in guiding conservation for species at risk. Management of endangered species often relies on knowledge of the spatial pattern of occurrence and predictions of habitat suitability (Hirzel et al. 2001; Dayton and Fitzgerald 2006). Habitat suitability models attempt to map environmental conditions required by species, trying to capture and predict the niche of a species (Hirzel and Le Lay 2008). A common approach to identify niches is species distribution modeling, which links known occurrence information to environmental characteristics, typically via a statistical model, and uses the resultant model to predict a likelihood of occurrence for unsampled locations (Guisan et al. 2013). Predictions of occurrence, and variation in occurrence, are predominately driven by variation in quantifiable environmental characteristics, which, when combined with information on the natural history of a species, provide a robust approach for the development of accurate distribution predictions.

Accurate mapping and modeling of distributions of species guides policy decisions and conservation (Johnson and Gillingham 2005; Villero et al. 2017). Identification of suitable regions across the range of a species can increase the success of conservation actions, such as translocations (Griffith et al. 1989; Oldham et al. 2000; Fitzgerald et al. 2015; Baling et al. 2016), habitat restoration (Clauzel and Godet 2020), and mitigation of anthropogenic disturbances (Johnson and Gillingham 2005). Model predictions can also provide an objective assessment of critical habitat and priority conservation areas, although instances in the peer-reviewed literature of actual applications of distribution models in conservation policy decisions are sparse (McFarland et al. 2012; Guisan et al. 2013).

A challenge when developing species distribution models for species of conservation concern is that presence-absence data are often limited due to species rarity, lack of prior distribution knowledge, or population losses across the range (Thompson 2013; Crawford et al. 2020). Many species distribution models for species of conservation concern tend to use presence-only data due to lack of systematic surveys that document absence and the need to make conservation decisions (Burgman et al. 2005; Tulloch et al. 2016). Acknowledging the limitations of species distribution models may help conservation planners and policy makers better understand how to use these models while determining conservation goals and priorities (Sofaer et al. 2019). Additionally, species distribution models should not be viewed as static, and acknowledging their limitations can help guide future model iterations that build on each other by incorporating new knowledge of presence-absence, such as incorporating data from new surveys in data poor areas from previous modeling efforts or identifying additional or alternative predictors of habitat suitability (Guisan et al. 2013; Sofaer et al. 2019; Crawford et al. 2020).

The Dunes Sagebrush Lizard (*Sceloporus arenicolus*) is a small lizard endemic to the Mescalero-Monahans Shinnery-sands ecosystem of west Texas and southeastern New Mexico (Degenhardt et al. 1996; Degenhardt and Jones 1972; Fitzgerald and Painter 2009; Fig. 1). *Sceloporus arenicolus* is a habitat specialist using only dune blowouts within Shinnery Oak (*Quercus havardii*) dominated dune formations (Stebbins 1985; Degenhardt et al. 1996; Smolensky and Fitzgerald 2010, 2011). The species is of special interest to state and federal agencies, landowners, and the oil, gas, and sand mining industries in Texas and New Mexico because its entire range overlies the oil-producing Permian Basin. The history of legislative conservation actions surrounding *S. arenicolus* is extensive and detailed elsewhere (Sherwin 2014; Fitzgerald et al. 2022). To summarize, the species received protected status from the New Mexico Department of Game and Fish in 1975 but has never received special classification by the Texas Parks and Wildlife Department. State-level listings protect individual animals, but not their habitat. Federal listing under the U.S. Endangered Species Act was proposed in 2010 by the U.S. Fish and Wildlife Service (USFWS 2010) but withdrawn in 2012 by the agency (USFWS 2012), citing adequate protection from two candidate conservation agreements with assurances. In 2018, a petition for federal listing was filed (USFWS 2020) and a Species Status Assessment is expected in 2022.

In addition to *S. arenicolus* having a very restricted and naturally patchy distribution, current land-use practices have caused fragmentation and loss of habitat, disrupted population connectivity, and caused some local population extinctions (Smolensky and Fitzgerald 2011; Leavitt and Fitzgerald 2013; Walkup et al. 2017). Thus, understanding the distribution of *S. arenicolus* and suitability of habitat across its range is important for management and conservation actions. Several

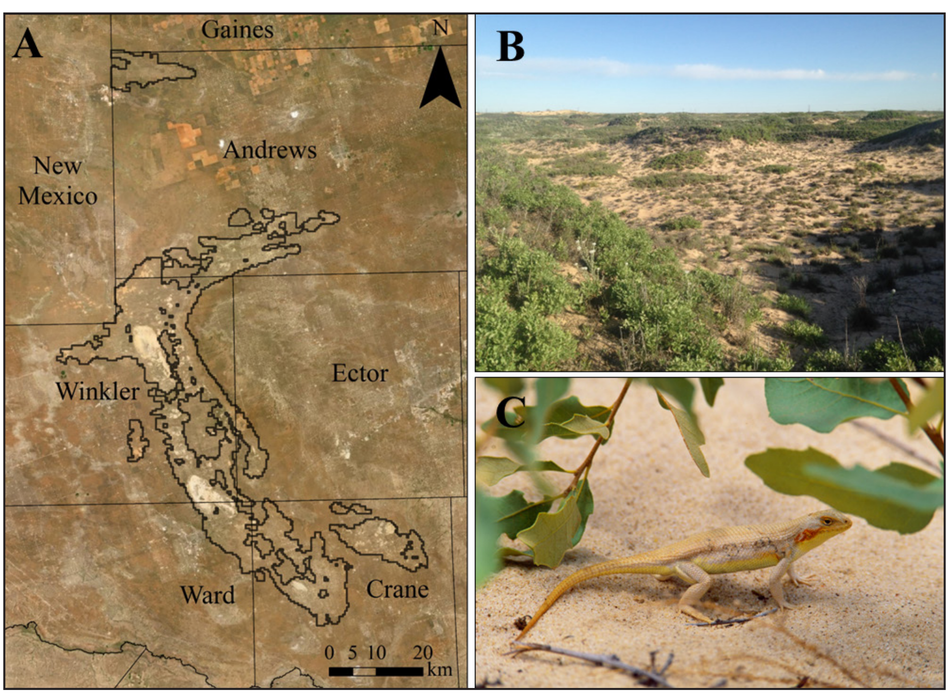

Figure 1. (A) Satellite view of the target area in west Texas, USA, selected for modeling. (B) An example of Shinnery Oak (*Quercus havardii*) sand dune habitat stabilized by Shinnery Oak with dune blowouts (Photographed by Danielle K. Walkup). (C) An adult female Dunes Sagebrush Lizard (*Sceloporus arenicolus*). (Photographed by Don Sias).

species occurrence and habitat distribution maps were developed for *S. arenicolus* (e.g., Laurencio, L.R., and L.A. Fitzgerald. 2010. Atlas of Distribution and Habitat of the Dunes Sagebrush Lizard (*Sceloporus arenicolus*) in New Mexico. Texas Cooperative Wildlife Collection, Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas. Available from https://agrilifecdn.tamu.edu/fitzgerald/files/2012/07/TX-lizard-surveys_2011-report.pdf; Ralph Axtell, unpubl. data), with some key maps produced to guide conservation agreements. In 2011, a map of the range of *S. arenicolus* in Texas was produced using expert knowledge of the habitat requirements of the species (Texas Comptroller of Public Accounts [TCPA]. 2011. Texas Conservation Plan for the Dunes Sagebrush Lizard (*Sceloporus arenicolus*). TCPA. Available from https://www.fws.gov/southwest/es/documents/r2es/tx_cons_plan_dsl_20110927.pdf [Accessed: 14 October 2021]; Lee Fitzgerald et al., unpubl. report). Areas were classified as very high, high, low, or very low likelihood of occurrence based on all known localities, extensive surveys by experts on the species, and the extent of Shinnery Oak Dune formations, delineated from aerial imagery (TCPA 2011, *op. cit*.). In 2015, the Natural Heritage New Mexico used image classification of LandSat and National Agriculture Imagery Program (NAIP) imagery to produce a map of *S. arenicolus* habitat in New Mexico designating suitable, treated or fragmented, potentially restorable, or occupied habitat (Johnson et al. 2015). A similar mapping effort in Texas in 2018, incorporated into the most recent Candidate Conservation Agreement with Assurances of the USFWS for *S. arenicolus* in Texas, used aerial photography and remote-sensing techniques for image classification to designate four classes of *S. arenicolus* habitat that have different management values: high, intermediate I, intermediate II, and low habitat suitability (Canyon Environmental, LLC. 2020. Candidate conservation agreement with assurances for the Dunes Sagebrush Lizard (*Sceloporus arenicolus*). Canyon Environmental, LLC. Available from https://www.fws.gov/southwest/es/Documents/R2ES/AUES_Final_TX_DSL_CCAA_Signed.pdf [Accessed 14 October 2021]; Thomas Hardy et al., unpubl. report).

With another listing determination approaching, conservation planning would likely benefit from the availability of a distribution map based on a predictive model that incorporates as much information as possible on the known occurrences of *S. arenicolus* and the extensive body of knowledge on its habitat requirements (Fitzgerald et al. 2022). Of particular interest is the recently released digital elevation models derived from Airborne Light Detection and Ranging (LiDAR) for the Texas West Central Region, which encompasses the distribution of *S. arenicolus* in Texas. These newer digital elevation models for the Texas West Central Region provide the opportunity to calculate rugosity of the Shinnery Oak sand dune habitat used by *S. arenicolus*, which has been shown to be an important landscape feature determining presence, movements, habitat selection, and population dynamics (Fitzgerald and Painter 2009; Hibbitts et al. 2013; Ryberg et al. 2013; Walkup et al. 2019; Fitzgerald et al. 2022). By including rugosity measures, along with other remotely sensed data that capture aspects of habitat quality, the species distribution model results presented here provide the most fine-scale evaluation of occurrence for *S. arenicolus* in Texas to date, which will help inform the listing determination and future conservation actions.

Materials and Methods

Study area.—Our study area encompassed the Mescalero-Monahans Sandhills ecosystem in west Texas, covering parts of Andrews, Crane, Ector, Gaines, Ward, and Winkler counties (Figs. 1, 2). This area is characterized by a range of vegetation associations and landforms ranging from areas of relatively flat terrain

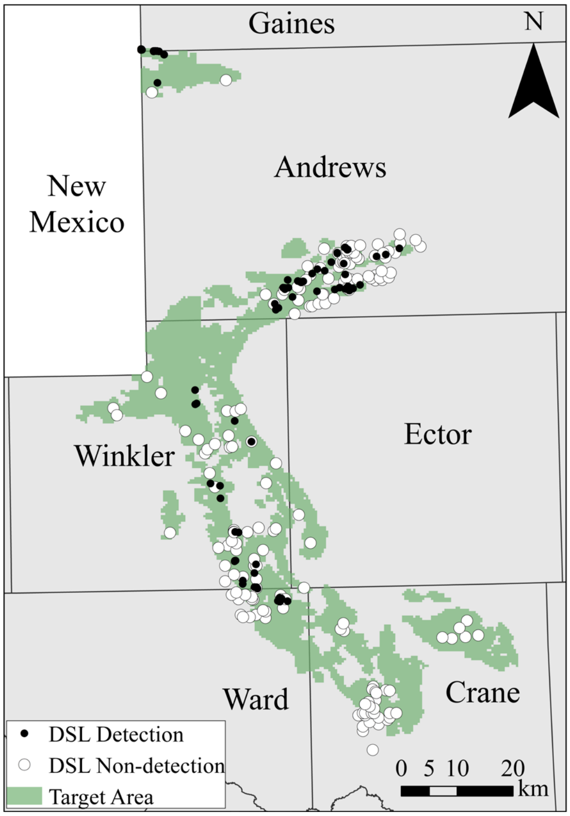

Figure 2. The target area selected for modeling the Texas, USA, distribution of the Dunes Sagebrush Lizard (*Sceloporus arenicolus*; DSL), with survey detections and non-detections from 1998–2019. The target area encompasses the entirety of two previous habitat models used for management (Lee Fitzgerald et al. unpubl. report; Thomas Hardy et al. unpubl. report).

like Honey Mesquite (*Prosopis glandulosa*) shrublands and grasslands, mesquite hummocks, and Shinnery Oak flats, to areas with more varied elevations like dune grasslands, open sand dunes, and Shinnery Oak Dunes (Fitzgerald et al. 2022). While the range of *S. arenicolus* includes parts of Eddy, Lea, Chaves, and Roosevelt counties in New Mexico, the LiDAR data that we used for our rugosity values was only recently made available in Texas and there is not comparable data for New Mexico. Because this new LiDAR data has the potential to improve upon previous models, we chose to model the Texas portion of the range of *S. arenicolus*, with the potential to expand our model if similar data becomes available for New Mexico.

We limited our study area to the maximum estimated range in Texas by combining the two most recent conservation agreement maps (hereafter, target area; Figs. 1, 2) as these two maps are generally acknowledged to encompass more than the entire Texas range of *S. arenicolus* (TCPA 2011, *op. cit*.; Canyon Environmental 2020, *op. cit*.). The target area is comprised primarily of Shinnery Oak Dunes and sandy soils but includes area around these formations to ensure we encompassed the entire potential range of *S. arenicolus* in Texas. For the modeling and mapping efforts detailed below, we overlaid the target area with 16-ha (400 × 400 m) grid cells (n = 9,459) to correspond to the area covered during previous *S. arenicolus* surveys (Walkup et al. 2018; pers. obs.). We plotted occurrence records of *S. arenicolus* into their corresponding grid cells for analysis, collapsing multiple occurrences in a grid cell into a single occurrence record.

Presence data.—We included *S. arenicolus* localities collected from multiple survey efforts in our study (Hibbitts et al. 2013; Walkup et al. 2018; Young et al. 2018; Laura Laurencio et al., unpubl. report; Lee Fitzgerald et al., unpubl. report), as well as localities collected during opportunistic studies, including specimens collected between 1998 and 2019 (Biodiversity Research and Teaching Collections, Texas A&M University; Supplemental Information Table S1). There were 454 surveys performed across these studies (Supplemental Information Table S1); however, five of those surveys were performed in Cochran County, which was not included in our target area as no *S. arenicolus* have ever been documented there. The remaining 449 surveys fell within 152 unique 16-ha cells in the target area and well represented the variation in the environmental covariates throughout the target area (Supplemental Information Fig. S1).

Survey protocols for the surveys conducted between 2005 and 2013 in Texas are as follows: in brief, two or more trained observers slowly walked through potential habitat searching for lizards at each site (i.e., covering 1/16 of a section [16-ha] or greater). When *S. arenicolus* were found, we recorded the locations using a handheld GPS (error ± 3 m). We terminated surveys if *S. arenicolus* was found, after six person-hours of searching, or when an available potential habitat was completely surveyed.

In 2015–2017, we modified the earlier survey protocols for distribution surveys designed to validate the accuracy of the TCPA (2011, *op. cit*.) likelihood of occurrence map (Walkup et al. 2018). Under the modified protocol, we overlaid areas in Andrews, Crane, Ward, and Winkler counties where we had access to private lands with 16-ha grid cells (400 × 400 m; note these are different cells than used in the current analysis), then we randomly chose 100 cells for surveying. During the surveys, four researchers systematically surveyed each cell, with one researcher in each quadrant. Each researcher surveyed their quadrant for 30 min regardless of how many *S. arenicolus* were found. During surveys in Hibbitts et al. (2013), researchers surveyed six 25-ha (500 × 500 m) plots exhaustively, three separate times in 2012, for 180 person-hours each survey. During a telemetry study by Young et al. (2018), search effort was intensive, and we used only the initial capture locality of *S. arenicolus* individuals in our current modeling effort.

Environmental covariates.—For each of the 16-ha grid cells, we calculated a suite of ecological metrics identified to correlate with *S. arenicolus* occurrence. In New Mexico, researchers found *S. arenicolus* in Shinnery Oak Dune blowouts and on ridges between blowouts in Shinnery Oak and showed the lizards prefer relatively large blowouts (i.e., blowouts > 3 m in depth; Fitzgerald et al. 2022). Additionally, Hibbitts et al. (2013) showed that *S. arenicolus* were more likely to be found in areas with steeper slopes with open sand, compared to random points within the same sites. Therefore, we included percentage cover of Shinnery Oak, percentage cover of sand, and two rugosity metrics (calculated to capture the variation in the elevation/slopes throughout the 16-ha cells) in the models (Table 1).

We calculated percentage cover metrics using object-based image classification methods on high resolution (1 m^2) aerial imagery to create land cover maps. We used color-infrared imagery collected by the U.S. National Agriculture Imagery Program (NAIP) in October 2016. The NAIP imagery dataset includes a near-infrared (NIR) band along with red, green, and blue visible wavelength bands, which improves our ability to discriminate vegetation from other features on the ground. We made a mosaic of two tiles of imagery that provided geographic coverage of our study area. We calculated the Normalized Difference Vegetation Index by taking the difference of the NIR and red bands and dividing it by the sum of the same (Rouse et al. 1973).

Table 1. Covariates included in the candidate models. The mean, median, and range values from the full target area (n = 9,459 16-ha cells) used to predict the probability of the Dunes Sagebrush Lizard (*Sceloporus arenicolus*) occurrence in Texas, USA, as well as for the 16-ha grid cells in which *S. arenicolus* surveys occurred (n = 152 cells).

		Full Target Area			Surveys		
Name	Description	Mean	Median	Range	Mean	Median	Range
Shinnery Oak percentage cover	Percentage of the 16-ha cell classified as Shinnery Oak (from 1 m object-based classification)	0.7575	0.8145	0.0001–0.9964	0.6831	0.7297	0.0617–0.9789
Sand percentage cover	Percentage of the 16-ha cell classified as sand (from 1 m object-based classification)	0.1705	0.1065	0.0000–0.9690	0.2412	0.1957	0.0120–0.9178
Mean maximum rugosity	Average for the 16-ha cell of the maximum rugosity (from 10 m^2 cells)	0.0072	0.0058	0.0001–0.0408	0.0095	0.0080	0.0008–0.0255
Binary rugosity	Average for the 16-ha cells of the reclassified 1 (meets or exceeds 0.005 rugosity threshold) or 0 (does not meet threshold) (from 5 m^2 cells)	0.1008	0.0674	0.0000–0.5563	0.1478	0.1194	0.0002–0.4505

We applied a K-means clustering approach to segment the image into objects by clustering spectrally similar pixels into spatially contiguous groups that we then used to calculate the average spectral properties for the pixels within each cluster. We manually digitized points that corresponded to one of six classes (mesquite, Shinnery Oak clusters, individual Shinnery Oak, sand dunes, large sand dunes, and well pads) to develop training and testing data. We placed 132 points for model training and testing and assigned each point to a class. We divided points into two groups: one for training the classifier and one for accuracy assessment (60% training, 40% validation). Using a random forest classifier, we assigned each pixel cluster to a land cover class. When tested for accuracy using the validation data, the resulting land cover map had an overall accuracy of 82% (Table 2). Finally, we reclassified the land cover map into two separate binary rasters that represented Shinnery Oak and sand dune (Supplemental Information Figs. S2, S3).

We calculated rugosity (a measure of changing amplitude in surface height) in two different ways: binary rugosity (BR) and mean maximum rugosity (MMR). First, we downloaded LiDAR digital elevation models (U.S. Geological Survey, Texas West Central Lidar) and created a seamless mosaic for the entire study area. We calculated rugosity (i.e., terrain ruggedness) using the Benthic Terrain Modeler toolbox v. 3.0 (Walbridge et al. 2018) in ArcGIS v. 10.7.1, using a neighborhood size of five cells. Our rugosity metric captured the variability in slope and aspect into a single value (where 0 = no terrain variation and 1 = complete terrain variation; Supplemental Information Fig. S4).

We calculated BR by extracting rugosity values within 30 × 30 m cells centered on *S. arenicolus* presence points (mean rugosity ± standard deviation = 0.0076 ± 0.0027, median = 0.0073, range = 0.0011–0.0160, n = 79) and randomly sampled unknown points (mean rugosity = 0.0029 ± 0.0023, median = 0.0023, range = 0.0003–0.0129, n = 116). After reviewing the

Table 2. Confusion matrix comparing reference and classified land cover values for the Dunes Sagebrush Lizard (*Sceloporus arenicolus*) in Texas, USA. The values in bold indicate the number of pixels that were classified correctly. Producer accuracy is the probability that a value in a given class was classified correctly. User accuracy is the probability that a value predicted to be in a given class really is in that class.

Classified	Mesquite	Shinnery Oak (cluster)	Shinnery Oak	Well pad	Sand dune	Sand dune (small)	Total	User Accuracy
Mesquite	**17**	6	0	0	0	0	23	0.73
Shinnery (cluster)	5	**13**	5	0	0	0	23	0.57
Shinnery	0	4	**12**	0	0	0	16	0.75
Well pad	0	0	0	**21**	0	0	21	1
Sand dune	0	0	0	2	**25**	1	28	0.89
Sand dune (small)	0	0	0	1	0	**20**	21	0.95
Total	22	23	17	24	25	21	**132**	
Producer Accuracy	0.77	0.57	0.71	0.88	1	0.95		
Overall Accuracy	**0.82**							

distribution of rugosity values from the *S. arenicolus* and unknown points (Supplemental Information Fig. S5), we used a rugosity value 0.005 as the threshold for suitability. We then reclassified the 5 × 5 m cells above the 0.005 threshold as 1s (indicated likely appropriate for *S. arenicolus*) and cells below it as 0s (indicated likely not appropriate for *S. arenicolus*). We averaged the reclassified 5 × 5 m cells within the larger 16-ha grid cells, which returned the proportion of the 16-ha grid cell that met or exceeded rugosity where *S. arenicolus* has been previously found. For MMR, we retained the maximum terrain ruggedness value for 10 × 10 m cells then averaged those values for each 16-ha cell.

Species distribution modeling.—There are a wide variety of species distribution modeling approaches (Elith et al. 2006; Guisan et al. 2006) useful for identifying and predicting potential species distributions based on various model and data combinations. Two commonly used approaches for presence-only and presence-absence data include Generalized Linear Modeling (GLM) and Generalized Additive Modeling (GAM). Both GLM and GAM are based on the class of models wherein the response variable is allowed (but not required) to be a non-linear function of the environmental covariates. As ecological data are regularly non-linear, especially when considering species distributions within landscapes (Yackulic and Ginsberg 2016), we used both non-spatial and spatially dependent approaches to develop predictions of the likely occurrence of *S. arenicolus* within the west Texas landscape.

Our response variable was the presence of *S. arenicolus* within 16-ha grid cells in the target area. Because we used data collected from a variety of sources, we used known presence locations (e.g., locations where presence within a 16-ha grid cell was visually confirmed) as the occurrence data for our analysis. As absence was not consistently confirmable across all these studies (e.g., non-detection during surveys does not equate to absence), we used pseudo-absences in the target area to use as locations where *S. arenicolus* were potentially not located (VanDerWal et al. 2009; Barbet-Massin et al. 2012). We used ArcGIS to randomly draw 335 16-ha grid cells from the 9,459 16-ha cells that comprise the target area (5× the number of 16-ha cells with *S. arenicolus* presence points).

Next, we developed a candidate GLM model set (Table 3) wherein each model represented a biological hypothesis regarding which environmental characteristics impacted *S. arenicolus* occurrence within our study landscape. Because the potential rank of the model set (e.g., using Akaike Information Criterion [AIC] or similar) would inherently depend upon the sample of pseudo-absences used, we replicated our entire model selection analysis (n = 1,000) by iteratively randomly drawing a new set of pseudo-absences (n = 335) for each of the nth model selection analyses. Then, we estimated the frequency that each model was ranked first (based on AIC) in each model run, and we selected the most frequent best-ranked model for prediction analysis using both GLM and GAM. To project our results across all 16-ha grid cells within our target area, we replicated our analysis (n =1,000) using a randomly selected set of pseudo-absences (n = 335 per replicate) for the best fitting candidate models and predicted the probability of occurrence, based on covariate values for each grid cell. As each replicated analysis, based on a different set of pseudo-absences, would potentially provide a different mean prediction for each 16-ha grid cell, we estimated the mean, median, and range for each grid cell from the 1,000 replicated model runs, and we used the average prediction as our estimate of occurrence for each grid cell.

Results

Presence data.—We identified 122 *S. arenicolus* presence points from survey data and other observations documented between 1998 and 2019 (Fig. 2). Once we aggregated those surveys to the 16-ha cells, there were 67 non-overlapping occurrences for use in modeling. Many of our points clustered in Andrews and Winkler counties due in part to limited access to private lands in other areas and also the natural patchiness of the

Table 3. A priori candidate model list for habitat predictors of the Dunes Sagebrush Lizard (*Sceloporus arenicolus*) presence in Texas, USA. Proportion of model runs shows the proportion of times the candidate model was ranked best among all models evaluated. Abbreviations are Sand = sand percentage cover, Shin = Shinnery Oak percentage cover, BR = binary rugosity, and MMR = mean maximum rugosity.

Model	Model Structure	Proportion Model Runs
M11	Shin + MMR + Shin*MMR	51.7
M3	MMR	19.4
M10	Sand + MMR + Sand*MMR	13.3
M9	Shin + BR + Shin*BR	9.8
M8	Sand + BR + Sand*BR	4.6
M2	BR	0.8
M7	Shin + MMR	0.2
M5	Sand + MMR	0.1
M13	Sand*Shin + BR	0.1
M1	Sand	0
M4	Sand + BR	0
M6	Shin + BR	0
M12	Sand + Shin + Sand*Shin	0

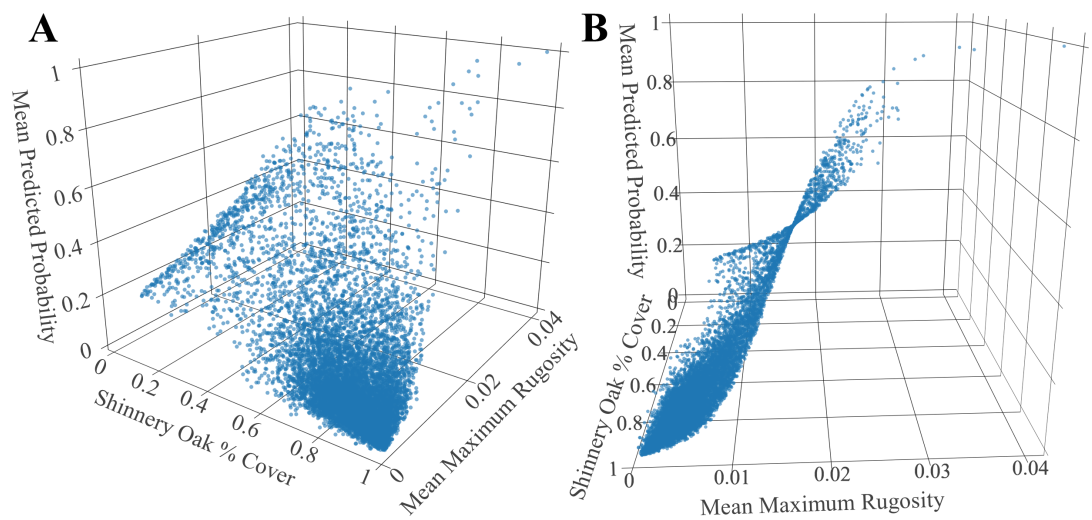

Figure 3. Relationships between percentage cover of Shinnery Oak (*Quercus havardii*), mean maximum rugosity, and the mean predicted probability of occurrence for the Dunes Sagebrush Lizard (*Sceloporus arenicolus*) in Texas, USA, from the top Generalized Linear Model with the mean maximum rugosity and percentage cover of Shinnery Oak interaction. The points are partially transparent so the higher the density of points the darker blue they appear. (A) The graph at an angle showing the interaction of mean maximum rugosity and percentage cover of Shinnery Oak. The densest area of points corresponds to high values of percentage cover of Shinnery Oak, low values of mean maximum rugosity, and low mean predicted probability. (B) The same graph at a different angle showing the strong positive relationship between mean maximum rugosity and mean predicted probability.

distribution of the species (Chan et al. 2020). We detected no *S. arenicolus* in Crane County, despite several surveys in the northern and southwestern areas of the county conducted over many years (Fig. 2). We were unable to survey some parts of our target area, such as southwestern Andrews County, northern Winkler County, and much of the southern part of the target area in Ward County due to lack of access to private lands. We also had limited survey data from southwestern Andrews County, northern Winkler County, eastern Ward County, Ector County, and northern and central Crane County (Fig. 2).

Species distribution modeling.—While the top GLM models (i.e., the models with the highest frequency of being ranked first for the replicate candidate model set runs) all included mean maximum rugosity (MMR), the model that ranked highest in over half of our replicates was the MMR and percentage cover Shinnery Oak interaction model (M11; Table 3). Combined, the next two highest ranked models, the MMR model (M3) and the MMR and percentage cover sand interaction model (M10), ranked highest in a third of our replicates (Table 3). Quantitative comparisons among the top three models showed little difference in the mean predicted probability of occurrence between M11 and M10 (Supplemental Information Fig. S6). There were larger, but consistent, differences between M11-M3 and M10-M3, where areas primarily in the large, open sand dunes in Winkler County had a higher mean predicted probability of occurrence under M3 than either M10 or M11 (Supplemental Information Fig. S6). Because there were only slight differences between the top three GLM models, we chose to use the most-supported M11 model to predict the mean probability of occurrence for *S. arenicolus*. Model M11 indicated that as the mean maximum rugosity increased and the percentage cover of Shinnery Oak decreased, the mean predicted probability of occurrence increased, although some areas with very high mean maximum rugosity and very high percentage cover of Shinnery Oak also had a high mean predicted probability of occurrence (Fig. 3).

For the GLM output, the model primarily identified large areas of dune habitat in Winkler and Crane counties as having a relatively high probability of *S. arenicolus* occurrence (i.e., > 0.4; Fig. 4). High probability areas were also identified in Andrews, Ector, and Ward counties. The areas with a higher probability of occurrence in Winkler County overlapped *S. arenicolus* presence points closely; however, the probability of occurrence was low in much of Andrews County relative to the high number of *S. arenicolus* observations there. Conversely, the GLM predicted a relatively high probability of occurrence in Crane County despite the absence of *S. arenicolus* observations from that county (Figs. 2, 4).

We used model M11 to predict the probability of occurrence while incorporating the effect of space via a GAM (Fig. 5). The GAM approach resulted in a much higher probability of occurrence in Andrews

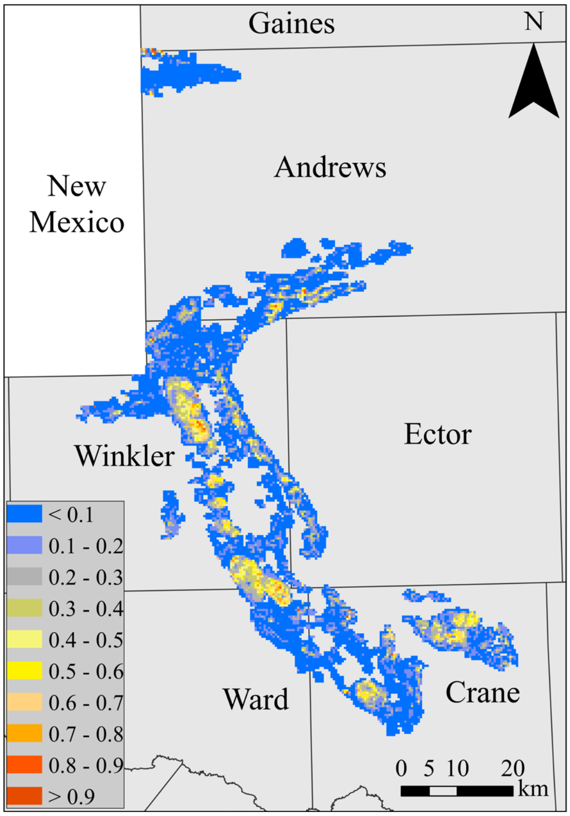

Figure 4. Mean predicted probability of the Dunes Sagebrush Lizard (*Sceloporus arenicolus*) occurrence in the target area of Texas, USA, from the top Generalized Linear Model including the interaction of mean maximum rugosity and Shinnery Oak (*Quercus havardii*).

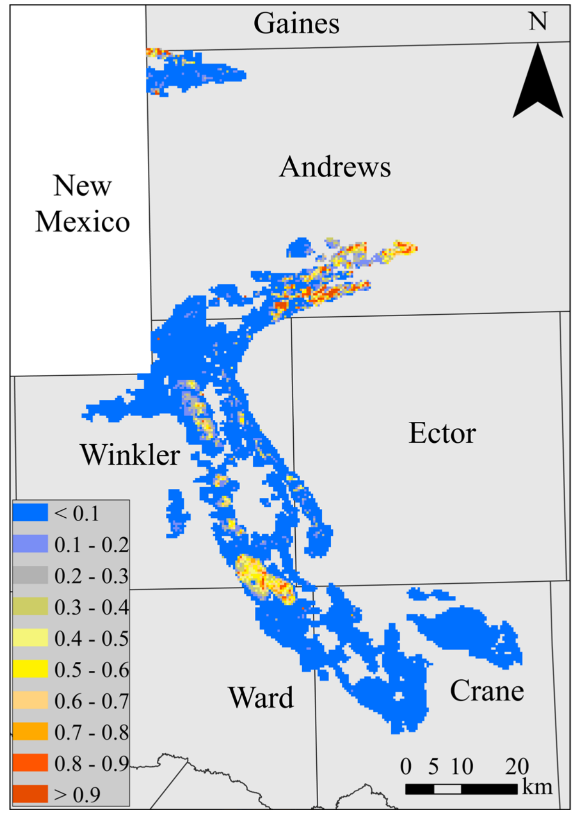

Figure 5. Mean predicted probability of the Dunes Sagebrush Lizard (*Sceloporus arenicolus*) occurrence in the target area of Texas, USA, from the Generalized Additive Model including the interaction of mean maximum rugosity and Shinnery Oak (*Quercus havardii*) with an added spatial term.

County, and a much lower probability of occurrence in Crane County compared to the GLM (i.e., differences > |0.3|; Supplemental Information Fig. S7). In the GAM predictions, the distribution of high probability of occurrence and the raw presence points for *S. arenicolus* align closely, especially in Andrews and Crane counties (Figs. 2, 5).

Discussion

Our results provide predictions of the distribution of *S. arenicolus* in Texas, which should facilitate habitat protection and conservation actions in areas that will likely provide the greatest benefit. By including LiDAR-derived rugosity measurements, the fine-scale predictability of our models demonstrated that the naturally patchy and disjunct distribution of habitat for the species depicted in earlier mapping attempts is likely further subdivided into areas of higher and lower suitability. Though similar in appearance, the two modeling approaches employed here captured distinct aspects of the habitat affinity of the species. The GLM predicts the areas that best matched the habitat in which *S. arenicolus* had been previously found, keying in on structural characteristics (mean maximum rugosity and Shinnery Oak percentage cover). Indeed, rugosity (calculated as MMR) was present in all the top habitat suitability models predicting *S. arenicolus* presence. Our model results are consistent with previous research showing that *S. arenicolus* prefers larger dune blowouts and uses the interface of the Shinnery Oak and sand (Fitzgerald and Painter 2009; Hibbitts et al. 2013). Thus, the GLM model is important for identifying areas of potential *S. arenicolus* habitat and helps prioritize areas for *S. arenicolus* surveys in the future.

In comparison, the GAM approach predicts where *S. arenicolus* is likely to be found given where it has been found in the past, based on the habitat structure but incorporating the additional effect of space. Predictions from the GAM provide evidence that *S. arenicolus* occur in interconnected, locally structured populations within contiguous areas of Shinnery Oak Dunes (Ryberg et al. 2013). Indeed, at the local scale, areas that are closer to known *S. arenicolus* locations are more likely to be occupied by *S. arenicolus* (Walkup et al. 2019). As such, the GAM predictions could be used to determine areas for high-value conservation or management actions, as it predicts where suitable habitat is likely to be occupied. Importantly, the spatial weighting of habitat suitability based on species presence indicates that the GAM model output will change if *S. arenicolus* is detected in areas where it has not been detected previously.

We found a lower predicted probability of occurrence in Andrews County than expected, given the large number of locations in that portion of the target area where the species is present. Because the mean maximum rugosity was driving model output, the inconsistency most likely reflects variation in the size of dune systems across the landscape. The areas of large contiguous and more active dune systems had higher values for mean maximum rugosity and correspondingly high probabilities of occurrence, while smaller chains of dunes like those found in Andrews County (which are also good habitat for *S. arenicolus*) had moderate values for mean maximum rugosity and probabilities of occurrence because the dunes comprised less of the grid cell area. We also noted some areas had high predicted probability of occurrence based on the GLM model, like Crane County, despite the lack of presence points there and knowledge the species is unlikely to occur anywhere in Crane County. Because the GAM approach incorporates the spatial effect of occurrence locations into predictions for *S. arenicolus*, cells closer to locations where the species is present had an inherently higher probability of occurrence. Conversely, any cells far from presence points, like those in Crane County, had a lower probability of occurrence.

Interpreting the differences between the two modeling approaches requires careful consideration. Areas where the GAM predicted a higher probability of occurrence is relatively straight-forward, in that we predict a higher occurrence of *S. arenicolus*, given that it has been found there (or nearby) in the past, as we see in Andrews County. Interpreting predictions for areas with lower probabilities of occurrence, however, is more nuanced (e.g., northern Winkler and Crane counties). Some of the areas with lower probability of occurrence likely reflect the true state of occurrence. Crane County, for example, had a high probability of occurrence in the GLM, but low probability of occurrence in the GAM. Although this area has the structure identified as habitat for *S. arenicolus*, no *S. arenicolus* have been found in Crane County since 1970 (pers. obs.), despite survey efforts over the last decade (e.g., Walkup et al. 2018; Crump and Forstner 2019; Lee Fitzgerald et al., unpubl. report). The cause of the presumed local extinction is unknown. Other areas with lower probabilities of occurrence could be representative of gaps in geographic sampling. For example, areas in northern Winkler County and northeast Ward County have not been as extensively surveyed. Thus, we recommend caution when interpreting low predicted probabilities of occurrence produced by our models.

The continuous predictive models for Texas we present here made use of all known occurrences of *S. arenicolus* in Texas. Validation is an important step in model development, especially for models used in conservation (Sofaer et al. 2019). Collection of new survey data should be prioritized and used to verify the accuracy of our predictions; however, the known range of *S. arenicolus* is unlikely to change even with new data (Fitzgerald et al. 2022). Although we were unable to include the New Mexico portion of the range of *S. arenicolus* in our models, the occurrence patterns observed in Texas are similar in New Mexico, despite some differences in the dune formations between the two states. Muhs and Holliday (2001) found the Monahans Sandhills of Texas have more variable dune formations than the Mescalero Sands of New Mexico, ranging from large, fully active dunes with barchanoid ridges to parabolic dunes with blowouts (usually described as *S. arenicolus* habitat) to small coppice dunes (1–3 m depth) to thin, discontinuous sand sheets. Comparatively, the Mescalero Sands in New Mexico have more areas of large, semi-stabilized parabolic dunes with some areas of low coppice dunes (Muhs and Holliday 2001). Additional data from New Mexico may serve to refine our models but would not be expected to identify additional patches of suitable habitat in Texas than are already apparent. Because of the extent of variation in the Monahans Sandhills in Texas, we have likely captured the range of conditions available for *S. arenicolus* throughout its entire geographic distribution. Further refinement of the predictors (for example, narrowing the range of rugosity for which *S. arenicolus* is predicted to occur), however, may be possible by incorporating data from New Mexico.

At the regional scale, the observed spatial pattern of suitability within larger disjunct habitat patches helps explain observed phylogeographic patterns in *S. arenicolus* (Chan et al. 2020). Within the Monahans Sandhills of Texas, three divergent and stable populations correspond to the large, naturally disjunct patches of suitable habitat occurring in Andrews County, northern Winkler County, and the Winkler-Ward County boundary (Chan et al. 2020). Earlier, coarse-scale conservation maps without measures of rugosity (TCPA 2011, *op. cit.*; Canyon Environmental 2020, *op. cit.*) captured only narrow, naturally occurring breaks in the Shinnery Oak Dune landform. We were able to improve delineations of Shinnery Oak Dunes and blowouts through use of fine-scale rugosity data. As a result, the models better distinguish less suitable flat terrain (Shinnery Oak Flats) from areas of Shinnery Oak Dune and illustrate how local populations may be more isolated than previously thought. Thus, our model results reinforce conclusions from phylogenetic analyses that dune dynamics over geologic time, not contemporary dispersal, caused the genetic signature of low historical connectivity among populations of *S. arenicolus* (Chan et al. 2020). With respect to conservation actions, results from our study, in the context of Chan et al. (2020), suggest that strategies involving habitat corridors to link genetically distinct and geographically isolated populations should be left to geologic dune-forming processes and translocations should be mindful of source populations as well as geologic trends.

The probability of occurrence at the finer-scale resolution (16-ha) generated by our models provides a better understanding of variation in patterns of *S. arenicolus* occupancy across the landscape, and settlement and vacancy dynamics locally within populations (Walkup et al. 2018, 2019). At landscape scales, our models predict large expanses of highly suitable habitat that are perforated, in various ways, with areas of less suitable habitat. Heterogeneity in habitat suitability affords insight into fine-scale source-sink dynamics that occur within contiguous areas of habitat (Ryberg et al. 2013). Studies of *S. arenicolus* demography and movement suggest that areas of highly suitable habitat with robust reproduction sustain areas of less suitable or disturbed habitat with low or no reproduction through the movement of individuals (Leavitt and Fitzgerald 2013; Ryberg et al. 2013; Walkup et al. 2017). Fine-scale environmental conditions result in local variation in habitat quality, and previous work demonstrated that lower quality habitat in an occupied area was used intermittently through time (Walkup et al. 2019). The over-arching implication for conservation from previous studies is that areas of high habitat suitability are needed to support thriving populations of *S. arenicolus*, and these areas are key to sustaining occupancy in areas of lower habitat suitability. Because of the tight linkages between population dynamics and the dune blowout formations, highly suitable areas are critical for sustaining broader patterns of occurrence across the distribution of the species.

In previous expert-derived mapping attempts, rugosity of *S. arenicolus* habitat was captured implicitly by classifying Shinnery Oak Dunes based on aerial photography and remote sensing techniques (TCPA 2011, *op. cit*.; Johnson et al. 2015; Canyon Environmental 2020, *op. cit*.). By treating rugosity implicitly, expert-derived maps were coarse polygons, which tended to over-predict suitable habitat. While a certain degree of over-prediction may be important for insuring protection of all possible highly suitable habitat, over-predicting suitability can carry unintended consequences for habitat conservation. Over-prediction may cause conservation policies to focus on areas that are not able to be used by the target species, and possibly lead to devaluation of actual highly suitable habitat. For example, Shinnery Oak Flats exhibited the lowest predicted habitat suitability for *S. arenicolus* across all candidate models in our study; however, Shinnery Oak Flats were frequently included within coarse habitat polygons derived from previous expert-derived mapping attempts (Johnson et al. 2015; Canyon Environmental 2020, *op. cit*.). With the addition of the explicit LiDAR-derived rugosity covariate we used in our model, our approach produced fine-scale habitat suitability maps that distinguished less suitable land-cover features from those known to support populations of *S. arenicolus*, namely interconnected Shinnery Oak Dunes with blowouts.

Future work should focus on testing new management and conservation strategies to protect the habitat of *S. arenicolus*. For example, throughout the range of *S. arenicolus*, Shinnery Oak Dune habitat has been fragmented or disturbed by roads, well-pads, sand mining, and herbicide treatments that have negatively impacted habitat quality and connectivity (Ryberg et al. 2015). Anthropogenic impacts to the Shinnery Oak Dunes have resulted in population declines, demographic instability, and local extirpations (Smolensky and Fitzgerald 2011; Leavitt and Fitzgerald 2013; Hibbitts et al. 2017; Walkup et al. 2017). The most imperative conservation action to benefit *S. arenicolus* is to avoid fragmentation of suitable habitat at all scales through strategic placement of infrastructure. Conservation actions at the smallest scale, such as reconnecting fragmented highly suitable habitats by strategic placement of road, well-pad, and mine reclamation projects, is good land stewardship and has the potential to improve habitat quality at the local scale. Our predictive models and maps serve to guide the placement of conservation actions and inform pending decisions that will determine the future of this imperiled endemic species.

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