

THE RANGE, DISTRIBUTION AND HABITAT OF *SCELOPORUS ARENICOLUS* IN NEW MEXICO

FINAL REPORT

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SUMMARY

Sceloporus arenicolus, the sand dune lizard, is listed as threatened by the New Mexico Department of Game and Fish, and is a species of concern to wildlife and land use agencies in New Mexico and Texas. Many areas where *S. arenicolus* is known to occur are being developed or have already been developed for oil and gas production as well as ranching. Portions of the habitat of *S. arenicolus* have been altered by poisoning shinnery oak.

The extent of the range of *S. arenicolus* was heretofore undescribed. Empirical information describing the presence and absence of *S. arenicolus* in New Mexico is needed, as is the ability to predict with acceptable accuracy the likelihood the species will occur in areas where empirical data are lacking.

We conducted 169 standardized surveys at 157 sites during May and June 1994-1996 to define the geographic range of *S. arenicolus* in New Mexico, the pattern of distribution of the species throughout its range, and how sand dune lizards use the habitats available to them. The existence of *S. arenicolus* was confirmed in what previously were large gaps in the distribution of the species, and numerous localities extended the known range considerably to the northeast and northwest. The present range (i.e., the entire area encompassed by localities) of *S. arenicolus* is now well defined as evidenced by absence of the lizard at 33 sites surrounding the range. The range of *S. arenicolus* is crescent-shaped, extending from the vicinity of Milnesand, Roosevelt County and Northwest of Kenna, Chaves County, to the west of the Mescalero Ridge (Caprock), and arcing southeasterly to the border with Texas south of Hobbs, Lea County. The most apparent characteristic of the range of *S. arenicolus* is its small size. It possesses the second

smallest range of any lizard endemic to North America. The core of the range of *S. arenicolus* is the Mescalero Sands region of Eastern Chaves and Northeastern Eddy Counties. The range is more or less continuous from the localities near Crossroads, Lea County, through the Mescalero Sands to the border with Texas south of Hobbs. The northwestern portion of the range appears separated from the Mescalero Sands by a gap of about 23.8 km (15 miles). Three localities in Roosevelt County are isolated by 25.6 km (16 mi) from the closest localities to the west and by 27.5 km (17 mi) from the closest locality to the south. Extensive surveys in potential habitats extending from the WIPP site southeasterly to Jal lead us to conclude that *S. arenicolus* does not occur in this region.

Sceloporus arenicolus is not found at sites lacking shinnery dune habitat. Even at shinnery dune sites where the lizard does occur, it was not found in other habitats. Our results from habitat selection studies demonstrate that *S. arenicolus* is a remarkable habitat specialist, occurring exclusively within blowouts in shinnery dunes habitat. Sand dune lizards preferred large deep blowouts; small blowouts were underutilized while large ones were used significantly more than expected. Interestingly, there were significant differences in composition of sand between sites of presence and absence of *S. arenicolus*, implying that *Sceloporus arenicolus* may not occur in areas with high percentages of sand particles smaller than 250 μm . Though statistically significant, the differences in composition of sand are small. To more adequately address the importance of composition of sand to *S. arenicolus*, more thorough sampling of sand from within the range of *S. arenicolus* would be required along with experiments designed to identify mechanisms of how sand effects the lizards.

Within its range and within suitable habitat, *S. arenicolus* occurred at 60-76% of the sites surveyed. These results allow us to make several inferences: First, *S. arenicolus* will probably occur in areas of suitable habitat within its range, especially in areas with large active dunes possessing large dune blowouts. This relationship is far from absolute however, and *S. arenicolus* does not occur everywhere that we predict it could based on suitable habitat. These results imply the distribution of *S. arenicolus* is somewhat patchy for reasons that are not clearly associated with habitat type. Hence, it is probably impossible to predict with precision whether *S. arenicolus* should be absent from any areas of active shinnery dunes based on a suite of habitat variables measured remotely.

The pattern of distribution of localities within the range supports a dynamic view of the range and distribution of sand dune lizards. The shifting nature of dunes and associated vegetation, coupled with the vagaries of extinction and colonization, may explain patterns of presence and absence among patches of habitat that are similar today. An outstanding feature of the range is its narrow shape. At its widest points in the Mescalero Sands, the range spans only 16.7 to 25.7 km (10-16 mi). Because active shinnery dunes are not contiguous throughout the majority of the range, we are left with the impression that practically all the range of *S. arenicolus* has edge-like characteristics. For example, 21 survey sites where *S. arenicolus* was not found along the periphery of the range contained shinnery dune habitat suitable for *S. arenicolus*.

We recommend for the long-term conservation of *S. arenicolus*, the view must be embraced that the range, distribution, and even the populations of the lizards themselves are dynamic entities that move across the landscape. Considering together the dynamic nature of the shinnery dunes landscape, the habitat specificity of the lizards, and the finding that they were absent from more than 25% of suitable locations surveyed within their present range, it is imprudent to consider currently unoccupied patches of habitat within the range or along the edge of the range as useless to *S. arenicolus*. Ecosystem engineering by humans, either by default through indirect effects of activities that fragment the landscape (e.g., construction of roads), or directly by removing shinnery oak in areas where *S. arenicolus* do not occur presently can only be justified by a short term and static view of a landscape that is obviously dynamic. Our result that *S. arenicolus* was found at 60 - 76 % of sites within suitable habitat within the defined present day range shows there is a high probability the lizards will occur there, but also means that site surveys are required to answer the question whether or not *S. arenicolus* occurs at a site, regardless of probability of presence or absence.

INTRODUCTION

Sceloporus arenicolus, the sand dune lizard, is endemic to shinnery oak sand dune habitats in southeastern New Mexico and adjoining Texas (Conant and Collins 1991, Stebbins 1985, Degenhardt et al. 1996). Possessing the second smallest range of any lizard species endemic to North America and given its apparent habitat specificity, *S. arenicolus* is a species of concern to wildlife and land use agencies in New Mexico and Texas. Many areas where *S. arenicolus* is known to occur are being developed or have already been developed for ranching and oil and gas production. The short and long-term effects of development and pastoral activities in the Mescalero Sands on *S. arenicolus* are topics of current study (Snell et al. 1997, Sias et al. 1997).

The overall geographic range of *S. arenicolus* has not been systematically described. Prior to the initiation of this study in 1993, *S. arenicolus* was known in New Mexico primarily from a few historical localities concentrated in the Mescalero Sands east of Roswell, Chaves County, from north of Loco Hills, Eddy County, and from southeastern Lea County, south of Hobbs, New Mexico. (Fig 1). *Sceloporus arenicolus* is also known from Winkler, Andrews, Crane, and Ward counties, Texas (Dixon 1987). Large expanses of potential habitat for *S. arenicolus* had not been searched to determine if the species was present, or in some cases searches in the past were inconclusive (W.G. Degenhardt, pers. comm.).

To manage public lands and balance the needs of industry, agriculture, and recreation with the preservation of biological diversity, the Bureau of Land Management, and the New Mexico Department of Game and Fish need precise information on the range of *S. arenicolus* in New Mexico. Empirical information describing the presence and absence of *S. arenicolus* in New Mexico, coupled with the ability to predict with acceptable accuracy the likelihood the

species will occur in areas where empirical data are lacking would help land use agencies and others to evaluate the effects of different types of land use on populations of *S. arenicolus*.

Coupled with the problem that the geographic range of *S. arenicolus* was undescribed was the related problem that within its range, the distribution of the species has not been documented. It was unknown for example, whether *S. arenicolus* is widespread throughout its range or patchily distributed across the landscape.

Herein, we define the geographic range of *S. arenicolus* in New Mexico based on extensive field surveys, and describe patterns of distribution of the species within its range. The relationships between range, distribution, and habitat affinity are intertwined. To understand the distribution of *S. arenicolus* within its range, we describe the degree of habitat affinity exhibited by *S. arenicolus*, and analyze habitat selection by the lizard. The habitat specificity of *S. arenicolus* for blowouts in active shinnery dunes has been suggested repeatedly since the lizard was discovered (Degenhardt and Sena 1976, Degenhardt et al. 1996, Degenhardt and Jones 1972, Snell et al. 1997). In this report, we test the hypothesis that *S. arenicolus* actively selects its microhabitat sites by comparing points where the lizard was found to a randomly chosen set of points in the same habitat. These data, plus an analysis of sand at sites where the species was present and absent point to key factors that help explain patterns of occurrence of *S. arenicolus*.

HYPOTHESES

Patterns of presence and absence

Several hypotheses can be put forth to explain patterns of occurrence of *S. arenicolus* within its range. If its distribution is patchy, populations might occur at random locations across the landscape or populations might only occur where environmental conditions favor

their colonization and persistence. If *S. arenicolus* populations occur at random across the landscape, then the occurrence of the species should not be associated with microhabitat variables we consider important to the lizard's ecology, for example, type and availability of substrate, topographic relief, microclimate, or proximity to other occupied sites.

Alternatively, if the distribution of *S. arenicolus* is determined by ecological factors (not random), then we would expect the presence of the species to be associated with microhabitat characteristics that differ from characteristics at unoccupied localities. Finally, historical patterns of dispersal and colonization may have influenced the present distribution of *S. arenicolus* within its range, and areas of apparently suitable habitat may actually lie outside the present range. For example if *S. arenicolus* were found to occur more or less evenly throughout large areas of its range, but absent from other ecologically similar areas, then historical factors such as colonization events and natural local extinctions may have been important in shaping the present day distribution of the species. Hence, the role of history in shaping the distribution of *S. arenicolus* should be taken into account when analyzing distributional patterns.

Sceloporus arenicolus distribution and composition of sand

The distribution of lizards which bury or burrow in sand, such as *S. arenicolus*, may be constrained by characteristics of the sandy soils available to them. Sand that is too fine or too coarse may pose physiological or behavioral problems for *S. arenicolus*. Fine sand may facilitate burying, for example, but very fine sand might present problems for respiration while buried. Sand grain size (coarse or fine) could influence lizards' abilities to run, to forage, or nest. Alternatively, sand grain size-composition may not interfere directly with *S. arenicolus* physiology and behavior, but could influence vegetation associations of sand

dunes, or the sizes and shapes of sand dune blowouts, which in turn could influence suitability of the habitat for *S. arenicolus*. During the 1996 field season, we quantified the proportions of sand grain sizes from sites of presence and absence of *S. arenicolus* and tested whether the proportions of sand grain sizes differed between sites where *S. arenicolus* was present or absent.

METHODS

TERMINOLOGY

Terms referring to the habitat, distribution, and occurrence of *S. arenicolus* should be clarified.

As used in this report, a **point** is the exact spot where an individual *S. arenicolus* was observed. Microhabitat measurements were taken at points and at **random points** to study microhabitat selection in *S. arenicolus* (see methods below).

A **site** is a place where surveys were conducted to determine the presence or absence of *S. arenicolus*. Our surveys generally covered one-sixteenth of a section (400 x 400 m) or greater. Geographical coordinates are given for sites for the practical purposes of mapping, while it is acknowledged that sites are the area surrounding the coordinates.

A **locality** is a place where *S. arenicolus* was verified to occur, as documented by museum voucher specimens. Historical localities are places where *S. arenicolus* were known to occur, as documented by voucher specimens not produced as part of this study. Individual *S. arenicolus* move around in their environment and belong to populations of the species spread throughout their habitat. Thus the geographical coordinates given for a site or locality refer to an area much larger than a single point.

Surveys, such as those conducted in this study, prove beyond doubt the presence of *S. arenicolus* at a site, and common sense allows inference about the occurrence of *S. arenicolus* beyond the scale of a survey site. Continuous shinnery dune complexes where *S. arenicolus* occur are usually larger than a site. It is reasonable to assume that *S. arenicolus* occurs throughout an area of continuous habitat that contains a locality. Conversely, it is unreasonable to assume occurrence of *S. arenicolus* in dune complexes that have not been surveyed, or that are several kilometers from localities, regardless of habitat similarity. Absence of *S. arenicolus* is claimed when the lizards weren't found during rigorous surveys. Based on evaluation of our methods (below) it is very improbable that *S. arenicolus* is present and not detected.

The **geographical range** of *S. arenicolus* is the entire area encompassed by localities. **Distribution** refers to the spatial arrangement of localities within the range of *S. arenicolus*.

Potential habitat is any mosaic of habitat types within or near the range of *S. arenicolus* where it might be feasible to find *S. arenicolus*. For purposes of this study, potential habitats are found in eastern Chaves and Eddy Counties, southern Roosevelt County and Lea County, NM. Though the exact range of *S. arenicolus* was undefined prior to this study, we do know that *S. arenicolus* does not occur in other regions of New Mexico (Degenhardt et al. 1996). Potential habitat types are shinnery oak flats, shinnery dunes, open sand dunes, dune grasslands, and mesquite scrublands and grasslands. Descriptions of habitats are given below. **Suitable habitat** refers to habitat of sufficient similarity to habitat at known localities that biologists consider it plausible that *S. arenicolus* could occur there. *Sceloporus arenicolus* may not occur in all areas of suitable habitat due to chance, and the dynamic nature of extinction and colonization of suitable habitat through time.

In discussions of range and distribution, and potential and suitable habitat for *S. arenicolus*, it is important to acknowledge that our perceptions reflect current knowledge. It is unavoidable that as more data and different types of data become available, our perceptions of suitable and potential habitat may change.

Potential habitats surveyed

Surveys were carried out in a variety of habitat types (including habitats where *S. arenicolus* had not been found previously), and the presence/absence of *S. arenicolus* was noted according to habitat type.

Potential habitat types where surveys were conducted were classified into 7 microhabitat types. **Shinnery dunes** are active sand dune complexes dominated by shinnery oak (*Quercus havardi*). Shinnery dunes were characterized by the presence of open blowouts of varying size and with varying densities of grasses and other plants growing in them. (Blowouts are more or less bowl-shaped depressions among sand dunes). Shinnery oak covered the dune ridges and areas between blowouts. **Shinnery flats** are sandy soils dominated by shinnery oak with relatively little topographic relief. In shinnery flats, both low and high areas were covered with shinnery oak and other plants. **Open sand dunes** are large active dunes with steep slopes and open expanses of bare sand and sparse vegetation. **Dune grasslands** are sand dune formations with grasses predominating more than shinnery oak, including areas treated for shinnery oak removal. **Mesquite grasslands and mesquite scrub** are areas with varied topographic relief characterized by mesquite (*Prosopis* sp.), shinnery, and grasses. Several mesquite scrubland sites were characterized by mesquite hummocks, where clumps of mesquite formed hummocks separated by open sandy areas with sparse

vegetation including shinnery oak. Some sites were characterized by short grasslands and Tabosa flats, lacking shinnery oak and dominated by grasses and scattered mesquite.

SURVEY TECHNIQUE

Surveys were designed to increase the probability of finding *S. arenicolus* if any were present. Surveys were carried out during May and June, the months of peak activity of the lizards, in 1994, 1995, and 1996. Most surveys were carried out between 0800 and 1300 h during the morning activity period of the lizards, when conditions were most favorable.

To determine the presence or absence of *S. arenicolus*, two or more observers walked slowly through potential habitat searching for lizards. At each site, the occurrence of each habitat was noted and observers searched for lizards in all habitat types present at every site (Appendices 1 and 2). The time and duration of surveys was noted, and in 1995 and 1996 the number of person-minutes elapsed before finding the first *S. arenicolus* were tabulated.

When spotted, lizards were collected by hand or by shooting with revolvers loaded with .22 cal. shot shells (protocol approved by University of New Mexico Animal Use and Care Committee; permits issued by New Mexico Department of Game and Fish). Collecting was necessary to document the presence of the species at all sites with properly documented voucher specimens. Voucher specimens, with associated locality and ecological data, are the only permanent verifiable data base of the presence of *S. arenicolus* at a specific place and time. Additionally, *S. arenicolus* can be difficult to identify from afar even for skilled herpetologists not working regularly with *S. arenicolus* in the field.

Specimens were identified in the field, and when *S. arenicolus* was verified at a site, the team moved to a new site. The survey was discontinued if no *S. arenicolus* were found after a maximum of 6 person-hours of searching or if it became evident further searching was

not productive because an entire area had been searched, or due to unfavorable conditions (i.e. extreme temperatures, inappropriate time of day, rain, overcast conditions). Finally, specimens of other lizard species were collected to document the assemblages of lizards present at each site. All specimens were deposited in the Museum of Southwestern Biology, University of New Mexico.

Thirteen sites were “priority sites” (Appendix 1) of special interest to the Roswell District of the BLM. The priority sites were parcels of land with leases pending for oil and gas development.

Survey site locations were determined as precisely as possible in the field with a Trimble Scout hand held GPS unit. Site locality data were recorded as latitude and longitude as well as in UTM coordinates (Appendix 1). The Township, Range and Sections where each survey was conducted were also noted. In most cases, the search area at survey sites was a minimum of one quarter of one section (approximately 400 x 400 m). In a few cases the search area crossed section boundaries.

MAPPING

All survey sites and historical localities of *S. arenicolus* were mapped on 1:250,000 BLM maps. A USGS 1:500,000 map of southeastern New Mexico was prepared to show the current known distribution of the species in New Mexico on a single map. Figure 1 was prepared from the 1:500,000 map to show more clearly the distribution of *S. arenicolus* and survey sites in relation to major roads. All known historical localities of *S. arenicolus* were also plotted (Appendix 3).

HABITAT SELECTION

At two localities where *S. arenicolus* were abundant (sites 23 and 104) we tested the hypothesis that *S. arenicolus* actively selects the microhabitats it uses. At points where individual lizards were first observed, we compared a suite of variables measured from the exact points where we found lizards to an identical set of measurements from random points. Random points were located 10 paces along a random compass bearing from the point where an individual *S. arenicolus* was observed. Variables at both points were measured immediately. Thus each random point represents a paired observation for each lizard sighting. Microhabitat variables taken at points and random points were: air temperature (T_a) measured 2 cm above the substrate, substrate temperature (T_s), distance to cover, aspect, and whether the point was in sun or shade. Aspect was measured as the compass bearing of the slope to the nearest degree. The cosine and sine of the aspect measure the north-south and east-west orientations of points, respectively, and were used as variables in the analyses. Cover was measured from the points where undisturbed lizards were seen to the nearest clump of vegetation providing refuge.

The microhabitat and behavior of the lizard were noted, and if the specimen was observed in a sand dune blowout, the largest dimension of the blowout was measured to the nearest meter by pacing. Dune blowouts were classified according to 4 depth categories: Class I blowouts were 0-2 feet (0-60 cm) deep at their deepest point; Class II blowouts were 2-5 feet (60-140 cm) deep, Class III blowouts were 5-10 feet (140-300 cm) deep, and Class IV blowouts were > 10 feet (> 300 cm) deep. In addition to the paired random points, we measured a sample of 102 blowouts available to *S. arenicolus* at these sites along 5 haphazardly placed transects.

SAND GRAIN SIZE

To test the hypothesis that graininess of the sand may be associated with presence of *S. arenicolus*, we measured the proportions of sand grain sizes at eight sites where *S. arenicolus* occurred and at six sites where it did not occur (Table 1, Fig. 1). At each site, we sampled three blowouts. Within each blowout, we took five samples of sand: one at the center of the blow-out, and four ten paces (approximately 14.3 m) from the center in each of the four cardinal directions.

Site	<i>S. arenicolus</i> Present?	County	T	R	Sec
90	NO	Lea	26S	37E	21
92	NO	Lea	23S	35E	5
142	NO	Lea	23S	35E	6
144	NO	Lea	24S	38E	4
153	NO	Lea	20S	35E	1
163	NO	Lea	10S	32E	2
23	YES	Lea	18S	32E	6
28	YES	Lea	20S	38E	36
149	YES	Lea	19S	33E	9
152	YES	Lea	20S	35E	12
154	YES	Lea	20S	37E	19
159	YES	Lea	10S	34E	3
161	YES	Lea	9S	32E	24
5 mi. N Crossroads (historical locality)	YES	Lea	10S	35E	

We used a Keck Model SS-94 Sand Shaker to separate the grains from each of the sand samples into four sand grain size classes: Coarse (larger than or equal to 355 μm), Medium (smaller than 355 μm but larger than or equal to 250 μm), Fine (smaller than 250 μm but larger than or equal to 147 μm), and Very fine (smaller than 147 μm). An aliquot of approximately 65 g of sand was sifted from each sample, and the portions corresponding to each grain size class were weighed to the nearest 0.01 g on a Sartorius laboratory balance. The mass of each portion was divided by the mass of the total sample to obtain the proportions of each grain size class in a sample.

A multivariate analysis of variance (MANOVA) (Proc GLM, SAS Institute Inc. 1988) was used to compare differences in the proportions of sand grain sizes between sites of presence and absence of *S. arenicolus*. Coupled with our sampling design, this statistical test allowed us to determine whether differences in sand grain size composition were attributed to differences within a single blow-out, differences among blowouts at a single site, or

differences between sites of presence or absence. The proportional data were arcsine transformed prior to analysis.

RESULTS

EFFECTIVENESS OF SURVEYS

From 1994 to 1996, we carried out 169 standardized surveys at 157 sites to determine the presence or absence of *S. arenicolus* (Appendix 1). *Sceloporus arenicolus* was found at 72 (45.9 %) of 157 sites surveyed. All of these sites were new localities for the species, though some were very close to historical localities south of Oasis, Chaves County, NM. The number of surveys is more than the number of sites, because surveys were repeated at several sites to further confirm the presence or absence of *S. arenicolus*. Sites 50, 62, 63, and 86 were visited three times, and sites 30, 92, 104 and 105 were visited twice (Appendix 1). *Sceloporus arenicolus* was collected at 69 of the sites where it was found, and visually confirmed at 3 sites (3 sightings at site 50; multiple witnesses at site 55; shot at and missed at site 66; Table 1). We have sufficient confidence in these sightings to include these localities in subsequent analyses.

We have great confidence that if *S. arenicolus* were present at a site, it was detected during our surveys. *Sceloporus arenicolus* was found within 31 person-minutes of searching (e.g. 3 observers searching for 10 minutes) at 74% (34 of 46) of sites surveyed in 1995-96 and within 68 person-minutes at 96% (42 of 46) of the sites. It took 106 person minutes to find *S. arenicolus* at site 149, and 115 person-minutes to find *S. arenicolus* at site 60 (Fig. 2). It should be noted, however, that site 60 was the first survey conducted by the team in 1995. The average duration of surveys where *S. arenicolus* was found was 91.3 person-minutes (N =

46; sd = 27.6; range = 1 - 115 person-minutes). The average survey where *S. arenicolus* was not found lasted 153.7 person-minutes (N = 67; sd = 81.1; range = 46 - 390 person-minutes).

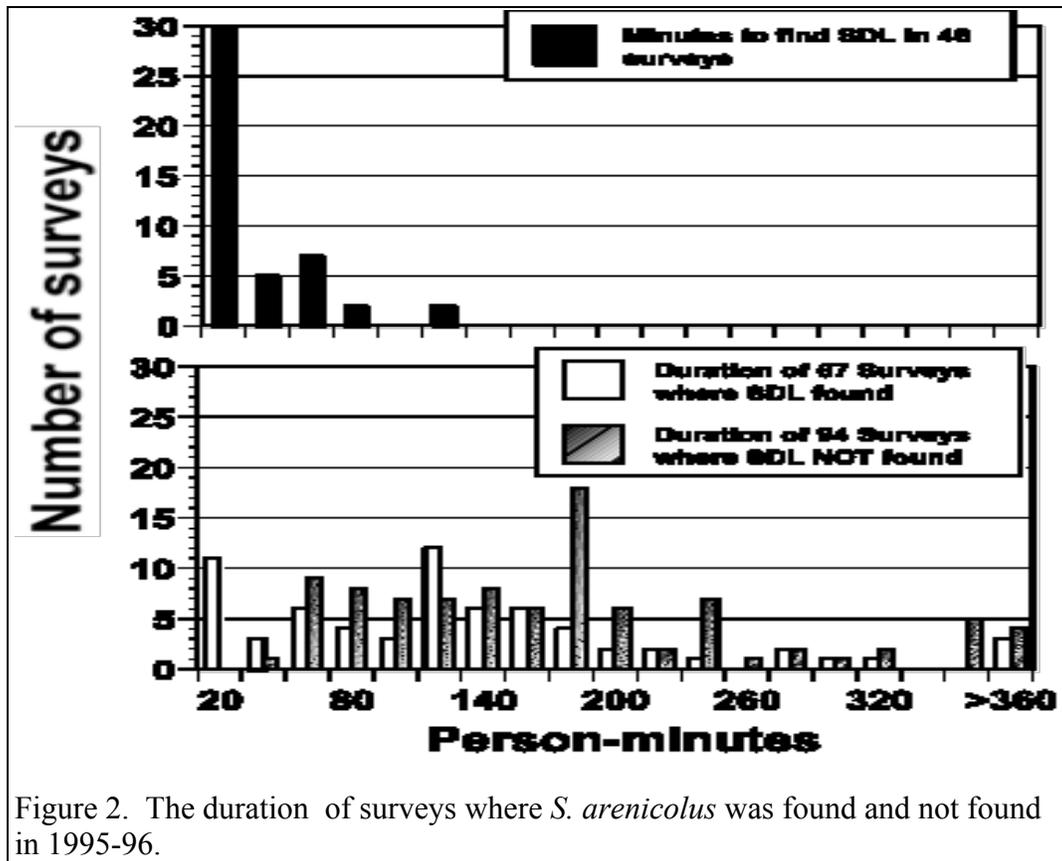


Figure 2. The duration of surveys where *S. arenicolus* was found and not found in 1995-96.

The Range of *Sceloporus arenicolus* in New Mexico

COVERAGE OF SURVEYS

To conform with the objective of documenting the geographical range of *S. arenicolus*, survey sites covered the entire geographical limits of the species' distribution in New Mexico. Sites with potential habitat were surveyed beyond the northwestern, northeastern, southern, and southeastern limits of the species' known distribution without finding *S. arenicolus* (Fig. 1).

Thirty-three sites were surveyed that we may now consider to lie outside the range of *S. arenicolus* (i.e., the entire area encompassed by all localities) (Appendix 2). Twenty-one of

these contained shinnery dunes habitat, 7 contained only shinnery dunes, while 14 contained at least one other habitat type. These sites serve to define the present limits of the range of *S. arenicolus* in New Mexico (Fig. 1).

The range of *S. arenicolus* can be divided into three regions to facilitate analysis and discussion: The northeastern and northwestern region, the Mescalero Sands region, and the southern and southeastern region.

NORTHEASTERN AND NORTHWESTERN BOUNDARIES

Sceloporus arenicolus were found at 4 localities in Roosevelt County, north of Milnesand (sites 20, 112, 113, 115). These localities extended the known range of *S. arenicolus* considerably toward the east and defined the northeastern boundary of the species' range in New Mexico. *Sceloporus arenicolus* was not found at other localities further east in Roosevelt County (sites 21, 22, 107, 116). The historical locality 5 miles south of Crossroads, Lea County along with four new localities southwest of Crossroads (sites 157, 158, 159, 160) further delimit the northeastern range of *S. arenicolus* (Fig. 1, Appendix 2).

Several new localities in the northwestern part of the species' range northwest of Kenna, Chaves County delimit the range of *S. arenicolus* towards the north and west (sites 16, 17, and 18; Fig. 1, Appendix 2). Extensive reconnaissance in vehicles failed to locate additional shinnery dune habitat to the northwest of sites 16 and 17. *Sceloporus arenicolus* was not found at sites 119, 120, or 46 along US Hwy 70 near Elkins, Chaves County, in areas of isolated shinnery dunes, nor at site 140 consisting of mesquite scrub east-southeast of Elkins.

BOUNDARIES OF THE MESCALERO SANDS PORTION OF THE RANGE

The central part of the range of *S. arenicolus* lies in the narrow band of shinnery dunes making up the Mescalero Sands of Chaves and Eddy Counties, extending from northwest of

Caprock south to US Hwy 62/180. Sites 70, 73, 75, 76, 77, 78, 81, and 84 where *S. arenicolus* is present, and sites 7, 8, 51, 121, 122 where it is absent, demonstrate the species' range is bounded by the Mescalero Ridge (the Caprock) running north-south and bending southeasterly towards Hobbs, Lea County. *Sceloporus arenicolus* was not found at 6 sites to the west of the Mescalero Sands east of NM 360 (sites 13, 14, 37, 44, 52, and 123). Three localities where the lizard was present (1 historical, plus sites 12 and 53) define the western boundary of the range of *S. arenicolus* at the southern end of the Mescalero Sands.

SOUTHERN AND SOUTHEASTERN BOUNDARIES

The southern boundary of *S. arenicolus* in New Mexico was clearly defined by 15 localities (1 historical plus 14 survey sites) where the species was present north of US Hwy 62/180 and north of NM 176, and 12 sites (sites 79, 82, 83, 85, 124, 125, 126, 127, 128, 146, 147, 148) where *S. arenicolus* was absent. The localities south of Hobbs, Lea County, (sites 28, 131, 137, 138, 154, 155, 156) are the most southeasterly localities for *S. arenicolus* in New Mexico.

An interesting result was the apparent absence of *S. arenicolus* from broad expanses of suitable habitat (i.e., shinnery dunes) south of US Hwy 62/180 in Eddy County and south of NM 176 in Lea County, extending from the area near the WIPP site southeasterly to Jal (Fig. 1). The area was well studied. Thirty-four surveys at 30 sites in this region alone comprised 20% of all the surveys and 35% (30 of 85) of the survey sites where *S. arenicolus* was not found. Sites 30 and 92 were surveyed twice; site 86 was surveyed 3 times.

HABITAT AFFINITY AND MICROHABITAT SELECTION

The researchers on our team observed hundreds of *S. arenicolus* during the surveys. *Sceloporus arenicolus* was found exclusively (100% of observations) in active shinnery oak

sand dunes with blowouts. Of 72 sites where *S. arenicolus* was found, 31 sites contained two or more habitat types (Appendix 2). In two instances, *S. arenicolus* were found in association with human artifacts. Two *S. arenicolus* were found under a board on sand at a corral in shinnery dune habitat, and one was found on sand under a water tank at a windmill completely surrounded by shinnery dunes adjacent to site 104. All remaining *S. arenicolus* seen during three seasons of field work were observed in blowouts and on the ridges between blowouts in shinnery oak. Sand dune lizards were never observed in shinnery flats.

Sceloporus arenicolus appeared to avoid shallow blowouts and used deep dune blowouts significantly more often than expected based on their availability in shinnery dune habitat (Chi-square = 50.75; df = 3; $P < 0.001$; Table 2). Similarly, blowouts used by lizards were significantly longer than the sample of blowouts measured along 5 transects at the same sites where the lizards were observed (Student's $T = 4.86$; $P < 0.0001$; Table 2).

Comparison of microhabitat variables from points and random points revealed statistically significant selection by *S. arenicolus* for points with cooler substrate (T_s) and again, deeper blowouts (Table 3). Differences were not statistically significant, but the mean for air temperature was lower where *S. arenicolus* was observed than at random points, and blowout length was greater on average where *S. arenicolus* were found. It should be noted that because random points were 10 paces from points where sand dune lizards were observed, many random points were in the same blowouts as points used by the lizards. On average, *S. arenicolus* was found at points that were more northerly and easterly facing than the paired random points. Distance to cover is related to the openness of habitat, as well as to the lizards' use of cover. On average, *S. arenicolus* was found at points with greater distance to

cover (i.e., more in the open) than were the random points. This difference was not statistically distinct at the 0.05 alpha level, however (Table 3).

Table 2. Sizes of dune blowouts used by *S. arenicolus* compared to a sample of dune blowouts measured along 5 transects at the same sites where the lizards were observed. *Sceloporus arenicolus* was found much less frequently than expected in shallow blowouts and much more often than expected in deep blowouts. Similarly, *S. arenicolus* was found in blowouts that were longer on average than blowouts measured along random transects.

BLOWOUT DEPTH CLASS	Used by SDL	Available	expected freq.	Chi-square value
I (0-2 ft (0 - 60 cm))	4	29	17.06	9.997
II (2-5 ft (60 - 140 cm))	14	30	17.65	0.754
III (5-10 ft (140 - 300 cm))	10	24	14.12	1.201
IV (> 10 ft (> 300 cm))	32	19	11.18	38.798
TOTALS	60	102	60.00	50.75 P < 0.001

BLOWOUT SIZE	Used by SDL (n =60)	Available (n =102)	Student's T	P-value
Mean blowout length (m) (standard deviation)	32.90 (29.46)	13.54 (12.05)	4.86	< 0.0001

Table 3. Means, standard deviations, and P-values from paired t-tests for microhabitat variables measured at points and random points for 60 *S. arenicolus*.

		Variable						
		Ta	Ts	Dist. to cover (cm)	Blowout depth class	Blowout length (m)	Cos(Aspect)¹ N-S orientation	sin(Aspect)² E-W orientation
Point	mean	31.31	37.68	124.27	3.15	32.90	0.05	-0.05
	st. dev.	3.19	5.69	142.07	1.05	29.46	0.66	0.75
Random point	mean	32.16	38.50	104.86	2.15	29.62	0.13	0.13
	st. dev.	3.77	6.38	165.80	1.81	40.35	0.64	0.75
P-value (paired T-test)		0.1462	0.0021	0.3898	0.0001	0.5031	0.4467	0.1796

1 Cosine of aspect shows N-S orientation of points (N =1.00, E & W = 0.00, S = -1.00).
2 Sine of aspect shows E-W orientation of points (E =1.00, N & S = 0.00, W = -1.00).

Microhabitat variables are expected to covary; for example, air and substrate temperature are related, as are dune blowout depth and length. To evaluate the overall pattern of habitat selection and reveal further patterns of habitat selection by *S. arenicolus*, we

performed a principal components analysis (PCA) on the microhabitat variables from points where lizards were observed and the random points. Five PC axes explained 90% of the variance in the habitat measurements at points and random points (Table 4). Principal component I described a temperature gradient, as evidenced by the high positive loadings for air and substrate temperature on that axis. Axis II described a gradient in blowout size, based on blowout depth class and blowout length together, while axis III was a gradient of sites facing the northeast and with relatively large distances to cover on the high end and southwest facing slopes that were more vegetated on the low end (Table 4).

Principal Component Axis	Eigenvalue	Proportion of variance explained	Cumulative variance explained		
PCI	2.06398	0.29	0.30		
PCII	1.56935	0.22	0.52		
PCIII	0.99218	0.14	0.66		
PCIV	0.91180	0.13	0.79		
PCV	0.76766	0.11	0.90		
Variable	Loadings				
	PCI	PCII	PCIII	PCIV	PCV
Air temp.	0.59	-0.27	0.11	-0.26	0.14
Substrate temp.	0.62	-0.21	0.01	-0.21	0.10
Distance to cover	0.19	0.38	-0.53	0.29	0.67
Blowout depth class	0.25	0.55	0.33	-0.057	-0.16
Blowout length	0.15	0.60	0.36	0.02	-0.03
Cosine(aspect)	-0.35	-0.08	0.51	-0.34	0.69
Sin(aspect)	0.15	-0.27	0.45	0.83	0.11

Using the PC axis scores as new variables describing environmental gradients of temperature, blowout size, aspect, etc., we plotted the differences between axis scores for points and random points (Fig. 3). The differences in PC scores from points and random points therefore represent measures of habitat selection along independent environmental gradients. These plots demonstrate how *S. arenicolus* was selecting its microhabitat relative to the random points. No habitat selection along an axis would result in a zero value for each pair of points. Figure 3 shows a strong pattern of selection for relatively large blowouts and

cool points. Essentially no lizards were using relatively hot sites in small blowouts (Fig. 3, upper graph). Selection for aspect plotted against blowout size selection showed a pattern where large blowouts were favored and southwest facing slopes were avoided.

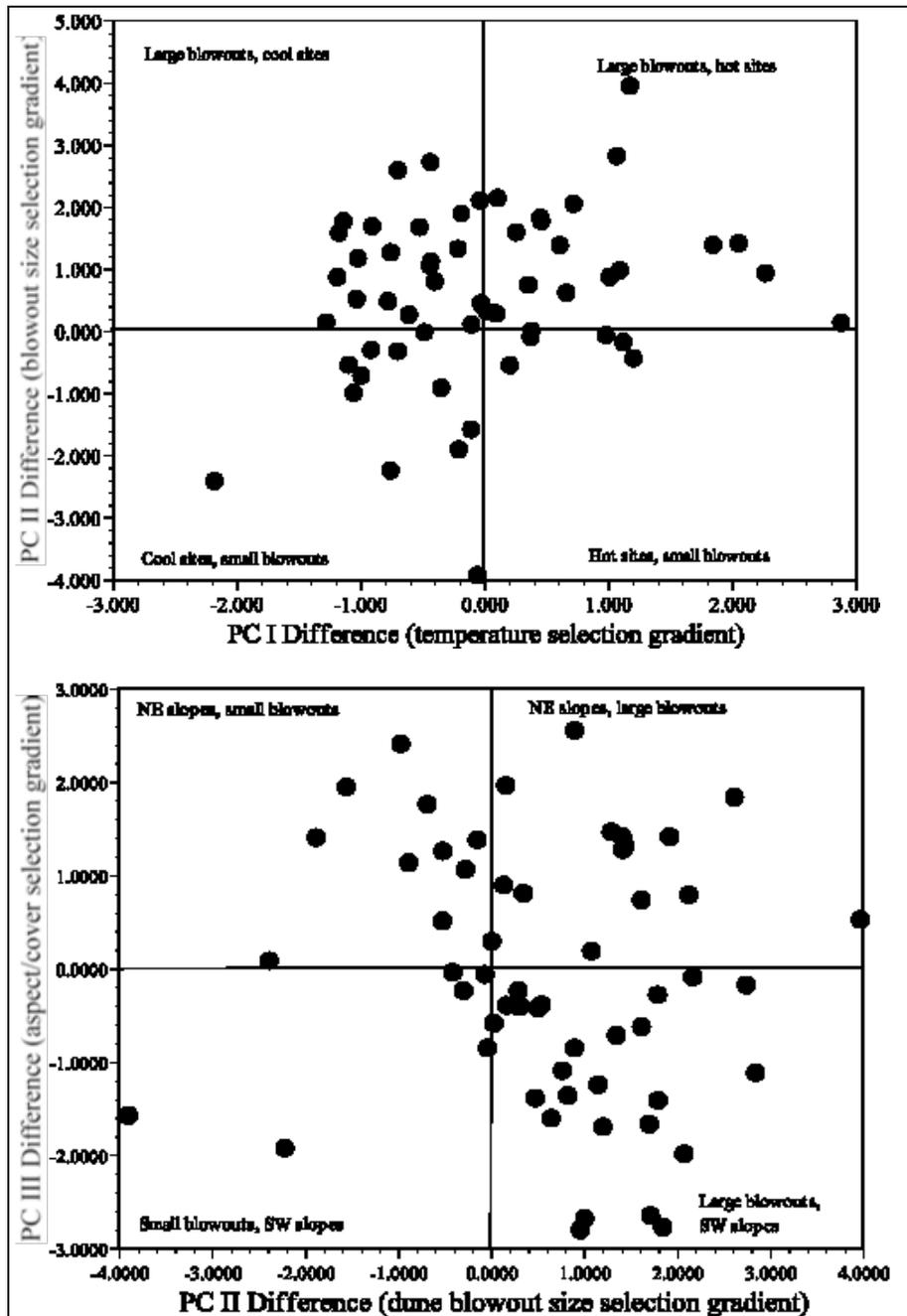


Fig. 3. The difference between principal component axis scores for points where lizards were observed and paired random points show independent gradients of microhabitat selection in *S. arenicolus*. Values of zero would indicate no selection. The upper graph shows selection for large blowouts and relatively cool sites. The

lower graph shows southwest facing slopes with relatively dense cover were disfavored for northeasterly facing slopes and large blowouts.

The selection gradient for blowout size (PC axis II) was statistically significant (paired t-test: $T = 3.26$; $P < 0.0019$). Average differences for the other habitat selection gradients were not statistically significant.

COMPOSITION OF SAND

We found significant differences in composition of sand between sites of presence and absence of *S. arenicolus*. Sites where the lizard was present had a greater percentage of medium sand grains and slightly smaller percentages of coarse, fine, and extra fine grains (Table 5). Though the proportional differences were small (Table 5) the MANOVA revealed significant differences in the proportions of all grain size classes between sites of presence and absence (univariate tests: coarse: $DF = 1,209$; $F = 7.76$; $P < 0.006$; medium: $DF = 1,209$; $F = 25.04$; $P < 0.0001$; fine: $DF = 1,209$; $F = 16.76$; $P < 0.0001$; very fine: $DF = 1,209$; $F = 29.21$; $P < 0.0001$) The multivariate test takes into account that the proportions of sand grain sizes in a sample are not independent from each other. This test showed the composition of sand differed significantly between sites of presence and absence (Pillai's Trace statistic = 0.174; $F = 9.3168$; $DF = 4/177$; $P < 0.0001$). There were no significant differences between sand grain size composition within a single blowout (i.e., the five samples from each blowout). Nor did sand sampled from different blowouts at a single site vary significantly. These results suggest the observed differences in sand grain sizes can only be attributed to differences among sites.

DISTRIBUTION OF *S. ARENICOLUS* WITHIN ITS RANGE

The general result from the site surveys was that within the range of *S. arenicolus*, the probability was high that *S. arenicolus* would be found in suitable habitat consisting of active dunes associated with shinnery oak (Table 6, Appendix 2). Of the total sites surveyed, 102 fell

within the range of *S. arenicolus* as defined above. Two sites not containing shinnery dunes (sites 11 and 136) were deleted from further analyses.

Sceloporus arenicolus was present in 72 (73%) of the sites surveyed containing suitable habitat. Within the Mescalero Sands portion of the range, where habitat is most contiguous, *S. arenicolus* was present at 76% of the sites, and absent from 11 of 45 sites surveyed (25 %). Sand dune lizards were found at 8 of 10 “priority” sites containing suitable habitat within the range where surveys were requested by BLM.

Table 5. Proportions of sand grain sizes from 6 sites where *S. arenicolus* was absent and 8 sites where it was present. There was a significant difference in sand grain size composition between sites of presence and absence and no detectable differences within sites or blowouts.

Grain size	N (samples)	Mean	Std Dev	Min	Max
Present (8 sites)					
Coarse (>354 μm)	120	12.16	6.84	4.00	48.00
Medium (250-354 μm)	120	64.46	10.94	16.00	86.00
Fine (147-249 μm)	120	15.64	4.57	7.00	30.00
Very fine (< 147 μm)	120	7.36	2.4	2.00	14.00
Absent (6 sites)					
Coarse (>354 μm)	90	14.96	8.19	4.00	39.00
Medium (250-354 μm)	90	57.38	8.53	28.00	74.00
Fine (147-249 μm)	90	18.42	4.98	9.00	30.00
Very fine (< 147 μm)	90	9.22	2.62	5.00	19.00

Table 6. Numbers and percent of sites surveyed where *S. arenicolus* was present or absent according to region within the range. This analysis includes only sites within the species' range that contained shinnery dunes. Sites outside the defined range were not included.

REGION	Absent	Present	Totals	% absent	% present
Mescalero. Sands ¹	11	34	45	24.5%	75.6%
NE	7	12	19	36.8%	63.2%
NW	6	9	15	40.0%	60.0%
S & SE	4	17	21	19.0%	81.0%
Overall	28	72	100	27.3%	72.7%
BLM priority sites ²	2	8	10	20.0%	80.0%

¹ In Mescalero Sands, sites 11 and 136, not containing shinnery dunes were not included.

² Priority sites 7 and 8 were outside the range of *S. arenicolus*, and site 11 did not contain shinnery dunes.

DISCUSSION

THE RANGE OF SCELOPORUS ARENICOLUS

The existence of *S. arenicolus* was confirmed in what previously were large gaps in the known distribution of the species, and numerous localities extended the known range considerably to the northeast and northwest (compare maps in the 1994 and 1995 Progress Reports; Fitzgerald et al. 1994, Fitzgerald et al. 1995). The present range of *S. arenicolus* is now well defined as evidenced by the lack of localities at numerous sites surrounding the range (Fig. 1, Appendix 2). The range of *S. arenicolus* in New Mexico is narrow and crescent-shaped, extending from the vicinity of Milnesand, Roosevelt County and Northwest of Kenna, Chaves County, to the west of the Mescalero Ridge (Caprock), and arcing southeasterly to the border with Texas south of Hobbs, Lea County. The most apparent characteristic of the range of *S. arenicolus* is its small size. It possesses the second smallest range of any lizard endemic to North America (Conant and Collins 1991, Stebbins 1985). The core of the range of *S. arenicolus* is the Mescalero Sands region of Eastern Chaves and Northeastern Eddy Counties. The range is more or less continuous from the localities near Crossroads, Lea County, through the Mescalero Sands to the border with Texas south of Hobbs. The northwestern region appears separated from the Mescalero Sands, however, by a gap of about 23.8 km (15 miles; distance from site 96 to site 106; Appendix 4) in eastern Chaves County. The three localities in Roosevelt County are isolated by 25.6 km (16 mi) from the closest localities to the west and by 27.5 km (17 mi) from the closest locality to the south (Appendix 4). Reconnaissance by vehicle throughout this area, including on private land with permission, failed to identify additional areas of suitable habitat. It is possible, however, that some patches of habitat exist that we did not find.

The results from extensive surveys in the region of potential habitat extending from the WIPP site southeasterly to Jal lead us to conclude that *S. arenicolus* does not occur at those sites, and probably does not occur in this region of potential habitat. Additionally, biologists at the WIPP site sampled lizard fauna with pitfall traps in the most promising areas and did not find *S. arenicolus* (D.C. Lynn, pers. comm.). This pattern is intriguing, because *S. arenicolus* occurs in Texas southeast of Jal (Axtell 1988, Dixon 1987), and the shinnery dunes at WIPP and near Jal appear suitable for *S. arenicolus*. It is possible the range of *S. arenicolus* never encompassed this area, or that unknown characteristics about the habitat, effects of weather, or biotic factors prohibit *S. arenicolus* from occupying areas of potential habitat in this region. Finally, it is plausible that *S. arenicolus* once occurred in the area but went extinct due to natural causes. Regardless of why *S. arenicolus* does not occur in this region, its conspicuous absence serves to emphasize that *S. arenicolus* may not readily disperse into areas of suitable habitat even if barriers of unsuitable habitat seem narrow to us.

THE OCCURRENCE OF SCELOPORUS ARENICOLUS WITHIN ITS RANGE

Based on our habitat selection studies, we conclude that *S. arenicolus* is not found at sites lacking shinnery dune habitat. Even at shinnery dune sites where the lizard does occur, it was not found in other habitats. Our surveys throughout the range of *S. arenicolus* in 5 habitat types corroborate the observations of others (Degenhardt and Sena 1976, Degenhardt et al. 1996, Degenhardt and Jones 1972, Snell et al. 1997), and clearly demonstrate that *S. arenicolus* is a remarkable habitat specialist, occurring exclusively within blowouts in shinnery dunes habitat. Our results clearly showed *S. arenicolus* prefers large deep blowouts relative to those available to them. Class I blowouts were under-utilized while Class IV blowouts were used significantly more than expected. Sand dune lizards also preferred points that were relatively open compared to random, paired points. Finally, relatively cool air and

substrate temperatures and northeasterly facing slopes within blowouts were variables related to thermoregulation of the lizards, and were very important determinants of microhabitat preference.

In pristine shinnery dune habitat, large deep blowouts possess more edge for cover, more open sand, and steeper slopes. The deeper blowouts present a much larger three-dimensional surface area from which the lizards may choose microsites that combine their thermoregulatory needs with those of foraging, protection from predators and mate seeking. These results may help explain why some areas of suitable habitat comprised of relatively inactive dunes were unoccupied or why numbers of *S. arenicolus* were low there. Snell et al. (1997) found positive, but insignificant correlations between numbers of *S. arenicolus* and blowout size, while Sias et al. (oil and gas study, 1996-97 progress reports and in progress) are finding significant correlations between numbers of *S. arenicolus* and blowout size.

Interestingly, there were significant differences in composition of sand between sites of presence and absence of *S. arenicolus* of a few per cent. The results imply that *Sceloporus arenicolus* may not occur in areas with high percentages of sand particles smaller than 250 μm (Table 6). It is unknown whether areas with fine sand are avoided by *S. arenicolus*, or what it is about fine sand that is incompatible with the life history of *S. arenicolus*. Fine sand grains might impede respiration by the lizards by blocking air passages in the nares when they are buried, or respiration under fine sand may be more difficult if there is not enough air. There are no data to support this hypothesis, however, and we did not experimentally test this explanation. The correlation between sand grain composition and *S. arenicolus* distribution may be due to factors other than the lizards' physiology, such as adequate substrate for nesting and incubation of eggs. It also could be more difficult for the lizards to escape by

diving into fine sand.

It is possible the composition of sand is merely associated with the geographical differences in the region south of US Hwy 62/180 instead of being a determining factor in the absence of *S. arenicolus* from otherwise apparently suitable habitat. Four of six sand samples from sites of absence were from this region where sand dune lizards do not occur. Sand composition may be a factor that precludes persistence of *S. arenicolus* in the region from WIPP to Jal, but the equally valid hypotheses that *S. arenicolus* never colonized this area, or that other environmental factors preclude the existence of *S. arenicolus* in the region were not falsified by the analyses of sand. To more adequately address the importance of composition of sand to *S. arenicolus*, more thorough sampling of sand from within the range of *S. arenicolus* would be required along with experiments designed to identify mechanisms of how sand effects behavior and physiology of the lizards.

Within its range and within suitable habitat, *S. arenicolus* occurred at 60-76% of localities surveyed. These results allow us to make several inferences: First, in areas of suitable habitat within its range as defined here, *S. arenicolus* will probably occur in shinnery dune habitat, especially in areas with large active dunes possessing large (classes III and IV) dune blowouts. This relationship is far from absolute however, and *S. arenicolus* does not occur everywhere we predict it should based on suitable habitat. These results imply the distribution of *S. arenicolus* is somewhat patchy for reasons that are not clearly associated with habitat type.

THE INTERPLAY BETWEEN RANGE, DISTRIBUTION AND HABITAT: STATIC AND DYNAMIC VIEWS

Range maps portray a static view of species' distributions. Localities are fixed, and their geographical coordinates exist in perpetuity. In reality, species' distributions are dynamic, moving on the face of the earth as climate and landscapes change. Ranges also shift in response to population growth of the species itself and in response to changes in the occurrence of competitors and predators. Our maps, based on three seasons of intensive work plus historical localities, portray the static view of the present range of *S. arenicolus* in New Mexico.

The pattern of distribution of localities within the range also supports a dynamic view. Anyone who visits the Mescalero Sands immediately grasps the dynamic nature of the shinnery dunes landscape. The habitat moves. In a thought experiment, imagine a time lapse film of the Mescalero Sands taken from the sky. What would the landscape do if we compressed 100, 500, or 1,000 years into one hour? The landscape would appear to boil with movement as the dunes and shinnery shift around the landscape.

As the dunes move, so do the organisms that depend on them. This must be especially true for the sand dune lizard, a species obligated to live in the ephemeral microhabitat of sand dune blowouts. Our thought experiment predicts that through time, populations of *S. arenicolus* would essentially be transported from place to place along with their habitat. This scenario is completely reasonable for *S. arenicolus*, especially if shinnery dunes experience periods of relative stability with few blowouts followed by periods of high dune activity that create many. Changes in the density of vegetation in the Mescalero Sands over the last 30 years have been observed, probably associated with wet and drought periods (W.G. Degenhardt pers. comm.). Results from mark-recapture studies show *S. arenicolus* have small

home ranges, a short lifespan, and other life history traits consistent with low rates of dispersal (Snell et al. 1997). We suggest that “riding” on shifting dunes may be one mechanism whereby populations of *S. arenicolus* might colonize new areas. Additionally the shifting nature of dunes and associated vegetation, coupled with the vagaries of extinction and colonization, may explain patterns of absence in patches of habitat that appear highly suitable today.

Another prediction from our thought experiment is the interactions between the shifting landscape and the distribution of sand dune lizards should be more stochastic at the edges of the species’ range, especially if shinnery dunes are more patchy and isolated there. Thus the edges of the range of *S. arenicolus* would appear fuzzy in our time lapse film due to the vagaries of extinction and colonization in habitat fragments.

Our data support this prediction. An outstanding feature of the range is its narrow shape. At its widest points in the Mescalero Sands, the range is between 16.7 and 25.7 km (10-16 mi) wide (distances from sites: 1 to 43; 73 to 53; 73 to 40; 78 to 40; Appendix 4). Because active shinnery dunes are not contiguous throughout the majority of the range, we are left with the impression that practically all the range of *S. arenicolus* has edge-like characteristics.

Twenty-one survey sites where *S. arenicolus* was not found along the periphery of the range contained shinnery dune habitat suitable for *S. arenicolus*. Most of these sites were located in relatively isolated shinnery dune complexes where persistence of populations may be difficult and where the probability of colonization by *S. arenicolus* is undoubtedly very low. Examination of the distribution map shows the occurrence of *S. arenicolus* is even more patchy at the edges of the range, especially at the northern end (Fig 1). Correspondingly, the

occurrence of *S. arenicolus* was more difficult to predict in shinnery habitat in the northeastern and northwestern regions. In the northern and northeastern regions, 38-40% of sites in suitable habitat within the range were unoccupied, compared to 20-25% in the southern region and the Mescalero Sands (Table 6).

RECOMMENDATIONS

CONSERVING THE RANGE AND DISTRIBUTION OF *SCELOPORUS ARENICOLUS*

We recommend for the long-term conservation of *S. arenicolus*, the view must be embraced that the range, distribution, and even the populations of the lizards themselves are dynamic entities that move across the landscape. Considering together the dynamic nature of the shinnery dunes, the habitat specificity of the lizards, and the finding that they were absent from more than 25% of sites with suitable habitat surveyed within their present range, it is imprudent to consider currently unoccupied patches of suitable habitat within the range or along the edge of the range as useless to *S. arenicolus*.

The viewpoint that the range and distribution of *S. arenicolus* is static is illogical and dangerous not only to sand dune lizards, but also to the unique shinnery dunes environment. Ecosystem engineering by humans, either by default through indirect effects of activities that fragment the landscape (e.g., construction of roads), or directly by removing shinnery oak in areas where *S. arenicolus* does not occur presently can only be justified by a short term and static view of a landscape that is obviously dynamic. We observed ancient drilling sites for potash and oil that are occupied by *S. arenicolus* today, but it is very important to point out those well pads and associated roads were less than half the size of modern drilling pads and new roads. We never observed *S. arenicolus* on paved roads or on wide caliche roads with shoulders. We feel it is prudent to limit the size and location of alterations to shinnery dunes

habitat, and to study the reclamation of shinnery dune habitat from caliche roads and drill pads.

DETECTING *SCELOPORUS ARENICOLUS*

We have great confidence that our survey methods reliably determine the presence or absence of *S. arenicolus*. It is important to point out, however, that trained biologists and technicians could not discern differences in suitable habitat at a site that was occupied from one that was not. For example, the shinnery dunes near the WIPP site extending to Jal appeared more suitable for *S. arenicolus* than many occupied sites within the present range. The finding that *S. arenicolus* was found at 60 - 76 % of sites within suitable habitat within the present range show there is a high probability the lizards will occur there, but also means it is unavoidable that site surveys are required to answer the question whether or not *S. arenicolus* occurs at a site, regardless of probability of presence or absence. Thus it is probably impossible to predict with precision whether *S. arenicolus* should be absent from any areas of active shinnery dunes based on a suite of variables measured from afar, such as with remote sensing data. Remote sensing methods would need to distinguish between shinnery flats and shinnery dunes and reveal topographic differences of < 3 m to account for the characteristic bumpiness of shinnery dunes with blowouts. These considerations imply that habitat mapping based on remote sensing (e.g. LANSAT thematic mapper data) would be somewhat useful for locating patches of suitable habitat, but would not be able to precisely predict whether or not a site were occupied by *S. arenicolus*.

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