
MICROHABITAT SELECTION BY A HABITAT SPECIALIST AND A GENERALIST IN BOTH FRAGMENTED AND UNFRAGMENTED LANDSCAPES

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Abstract.—Habitat loss and fragmentation are leading causes of species declines and extirpations. Such changes to habitat have been shown to negatively affect specialist species more than generalists. The mechanism behind this negative effect is associated with changes to the specific elements of the habitat that specialist species require. Here we focus on the effects of habitat fragmentation on microhabitat selection by specialist and generalist species of lizards in the unique Mescalero/Monahans Sand Dune ecosystem in the southwestern USA. The Dunes Sagebrush Lizard (*Sceloporus arenicolus*) is a specialist species only found in this ecosystem and the Common Side-blotched Lizard (*Uta stansburiana*) is a generalist species found in a variety of ecosystems throughout western North America. We found that fragmentation in this ecosystem altered available microhabitats in that fragmented sites had shallower slopes and more compacted soils than unfragmented sites. Both *S. arenicolus* and *U. stansburiana* selected microhabitats independent of their availability in fragmented versus unfragmented sites, therefore, fragmentation had no effect on microhabitat selection for either species. When comparing the two lizard species, *S. arenicolus* selected steeper, more open sites than *U. stansburiana*, which selected sites with shallower slopes, associated with more vegetation structure. These results show that fragmentation in this ecosystem alters the available microhabitats that are preferred by both species, but because its geographic range is more limited, this will likely have a larger negative impact on the specialist species. These results provide support for the utility of the specialist-generalist concept in predicting extinction risk in this system.

Key Words.—habitat loss; lizard; oil and gas development; *Sceloporus arenicolus*; *Uta stansburiana*

INTRODUCTION

Human-induced habitat loss and fragmentation are the leading causes of global biodiversity declines (Millennium Ecosystem Assessment 2005; Carpenter et al. 2006). Several studies have shown this loss of biodiversity is occurring non-randomly, with specialist species (those species that occupy a small, discrete niche space) experiencing faster rates of population decline relative to generalist species (those species that occupy broad niches; reviewed in Clavel et al. 2011). These results are consistent with the long-standing prediction that specialists should be more affected by habitat loss and fragmentation than generalists (Levins 1968; Futuyma and Moreno 1988; Devictor et al. 2008). Consequently, many authors have concluded that the specialist-generalist concept is useful for predicting which species' populations are at greatest risk of extinction in the current biodiversity crisis (reviewed in Devictor et al. 2010).

Although many studies using the specialist-generalist concept to investigate the effects of habitat loss and fragmentation focus on trends between populations (Clavel et al. 2011), the utility of the specialist-generalist

concept in predicting extinction risk should extend to other scales as well. For example, it is logical that specialist populations will decline when their habitats are lost, but the degradation of remaining habitats may also affect specialists more than generalists. In many cases specialists are utilizing habitat elements that are unique features of their ecosystems (Henle et al. 2004), and these elements might be lost in remaining degraded habitats even though the habitat appears intact. For this reason, it is important to measure habitat selection by individuals to determine what habitat elements specialists are using and whether or not habitat loss and fragmentation degrades those habitat elements upon which specialists are dependent.

In this study, we explore the utility of the specialist-generalist concept, applied at the scale of individual habitat selection, using two species of lizards that co-occur in an ecosystem threatened by habitat loss and fragmentation, the Mescalero/Monahans Sand Dune ecosystem of southeastern New Mexico and west Texas. The Dunes Sagebrush Lizard (*Sceloporus arenicolus*) is a habitat specialist restricted to Shinnery Oak sand dune habitat and is endemic to this ecosystem (Degenhardt et al., 1996). This habitat is comprised of sand dunes

stabilized by Shinnery Oak (*Quercus havardii*) and wind-hollowed, open sandy depressions called blowouts. The configuration of sand dunes and wind-hollowed blowouts within this habitat is dynamic and generates micro-topographic variation that gives this habitat a “bumpy” appearance (Ryberg et al. 2013). The Common Side-blotched Lizard (*Uta stansburiana*), which co-occurs with *S. arenicolus* in Shinnery Oak sand dune habitats, is a habitat generalist found throughout this ecosystem and several other ecosystems from the Pacific coast of North America to western Texas and northwest Mexico (Davis and Verbeek 1972; Parker and Pianka 1975; Smith 1995).

Construction of caliche roads and well pads for oil and gas development within this ecosystem has resulted in the loss and fragmentation of Shinnery Oak sand dune habitat. Caliche is a limestone rock used to cover roads and well pads for vehicular travel. Previous research has identified potential correlates between oil and gas development and *S. arenicolus* and *U. stansburiana* abundances (Smolensky and Fitzgerald 2011; Leavitt 2012). Using data from visual transect surveys and measurements of oil pad densities, Sias and Snell (unpubl. report) found a significant, negative correlation between *S. arenicolus* abundance and oil pad density. Additionally, Smolensky and Fitzgerald (2011) identified a positive association between *S. arenicolus* abundances and the amount or extent of blowouts within the surrounding habitat, two habitat elements known to decrease with oil and gas development (Endangered Status for Dunes Sagebrush Lizard, Proposed Rule, 75 Fed. Reg. 77801-77817, 14 December 2010). Finally, in a mark-recapture study, Leavitt (2012) found reduced *S. arenicolus* abundance and higher *U. stansburiana* abundance in areas fragmented by networks of caliche roads and well pads versus areas that are not fragmented.

While these observed relationships between oil and gas development and *S. arenicolus* and *U. stansburiana* abundances are consistent with predictions of the specialist-generalist concept, the processes by which oil and gas development alters Shinnery Oak, sand dune habitat and whether or not those changes include habitat elements upon which *S. arenicolus* and *U. stansburiana* are dependent is unknown. Thus, the purpose of this study is to answer the following questions: (1) how are Shinnery Oak, sand dune habitats different in fragmented and unfragmented landscapes?; (2) what habitat elements are *S. arenicolus* and *U. stansburiana* dependent upon in both fragmented and unfragmented landscapes?; and (3) do the potential changes in habitat driven by oil and gas development include elements upon which the habitat specialist, *S. arenicolus*, is dependent? Answers to this last question would provide a potential mechanism for the observed changes in abundance of *S. arenicolus* and *U. stansburiana* in fragmented habitats and also provide support for the

utility of the specialist-generalist concept in predicting extinction risk in this system.

MATERIALS AND METHODS

We selected six sites for surveys, all of which were within a three km radius of Latitude 32.1442°, Longitude -102.7576° on University of Texas Lands (20 km west and 20 km south by air of Andrews, Texas). Museum records indicated that this area contained populations of *S. arenicolus* and *U. stansburiana* as recently as 2006–07 and 2011 (museum tags: TCWC 91402, 95359, 95369, 95375, and 95413). We chose three fragmented and three unfragmented sites, to compare differences in microhabitat selection for each species. The unfragmented sites were as close as possible to the fragmented sites while still within habitat (range = 0.5–0.8 km). The fragmented sites were located in areas with the highest density of well pads in Shinnery Oak, sand dune habitat in Texas (55 well pads/section). Each site was 500 × 500 m (total area = 250,000 m²) and contained a grid of 49 points (7 × 7) spaced 83.33 m apart. The total area of all six grids was 1,500,000 m² of which half was in fragmented and half in unfragmented areas.

During the summer of 2012, we took microhabitat measurements within a one meter square quadrat centered at each of the 49 points within each grid. Within each quadrat, we determined the dominant slope by visual inspection and then measured the slope using a 0.5-m metal t-bar equipped with a magnetic angle locator. We also measured soil compaction with a soil penetrometer. We calculated soil compaction at each point as the median of soil penetrometer readings from three haphazardly selected locations within the quadrat. We also took a photograph of the quadrat while it was centered on the point. These photographs were visually analyzed to determine the percent cover of open sand, caliche, Shinnery Oak, forbs, grass, and leaf litter (dead plant material).

During the summer of 2012, we conducted three visual encounter surveys for *S. arenicolus* on 14–16 June, 27–29 July, 18–20 August and one visual encounter survey for *U. stansburiana* on 21–23 July. More surveys were required for *S. arenicolus* to ensure that a statistically meaningful sample size could be reached. Only one survey per site was conducted for *U. stansburiana*, because this species was very abundant and provided a large sample size with less effort. Although individual *S. arenicolus* were not marked and the potential for pseudoreplication exists, we believe that this was rare within our sample because most *S. arenicolus* observations were in different blowouts on subsequent surveys and *S. arenicolus* are known to have small home range sizes (847 m² for males and 401 m² for females; Megan Young, unpubl. data). Our visual encounter

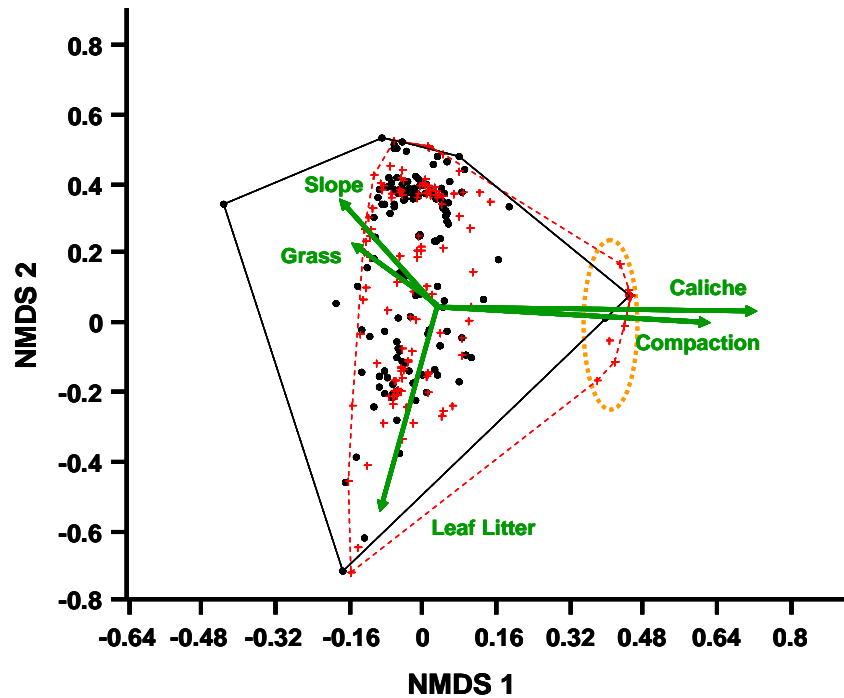


FIGURE 1. Nonmetric multidimensional scaling (NMDS) ordination of all survey points characterizing microhabitats available in fragmented (red pluses with dashed lines) and unfragmented (black dots with solid lines) sites (stress = 0.3029). Green arrows show significant correlations of habitat variables to NMDS axes. The orange dashed oval circumscribes the 34 points falling on caliche roads and well pads that were removed from the multivariate analyses (29 from fragmented, 5 from unfragmented sites) to show that the effects of fragmentation go beyond the caliche roads and well pads themselves and extend into the remaining microhabitats available to lizards (see text).

surveys were designed as time constrained searches. We used the grid of 49 points, which split each site into 36 squares (6943.89 m² each) to frame our time constrained searches. We surveyed each of these squares for 5 minutes on each visit for a total survey time of 180 person-minutes per site. This method helped us to survey the total area of the site without biasing our search to a particular habitat. We marked the location of each lizard observed with a pin flag, used a GPS to georeference the location, and recorded the time. We

returned to the point of each lizard observation after the survey was complete and recorded microhabitat data as described above.

After inspecting microhabitat variables for multicollinearity (pair-wise correlation matrix), we determined that no habitat variables were highly correlated (Spearman’s correlation coefficient, $-0.35 < \rho < 0.35$). Next, we evaluated assumptions of multivariate normality using the Mardia (1974) estimate of multivariate skewness (skew = 31.28, $Z = 1533$, $df = 84$,

TABLE 1. Univariate, non-parametric tests (Wilcoxon rank-sum) comparing microhabitat differences between random unfragmented (*u*) and fragmented (*f*) sites. Sample sizes (*n*) and means (*x*) are listed for each variable. Because multiple comparisons are made, significance is noted at the $\alpha = 0.05$ (*), 0.01 (**), and 0.006 (***) levels. See text for interpretation.

Microhabitat Variables	Unfragmented vs. Fragmented			
	n_u/n_f	x_u/x_f	Z	P
Slope	147/147	7.6/5.6	3.1	0.002***
Compaction	147/147	3.1/6.3	2.5	0.013*
Open Sand	147/147	34.1/34.1	1.8	0.079
Leaf Litter	147/147	24.9/18.1	3.3	0.001***
Shinnery Oak	147/147	7.7/6.5	0.8	0.449
Grass	147/147	3.1/0.2	5.4	< 0.001***
Caliche	147/147	2.9/20.6	4.6	< 0.001***
Forbs	147/147	27.4/20.5	1.8	0.070

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TABLE 2. Univariate non-parametric tests (Wilcoxon rank-sum) comparing microhabitat differences between lizard locations (*l*) and random points within unfragmented (*u*) sites within fragmented (*f*) sites for *Sceloporus arenicolus* and *Uta stansburiana*. Sample sizes (*n*) and means (*x*) are listed for each variable. Because multiple comparisons are made, significance is noted at the $\alpha = 0.05$ (*), 0.01 (**), and 0.006 (***) levels. See text for interpretation.

Microhabitat Variables	<i>Sceloporus arenicolus</i>				<i>Uta stansburiana</i>			
	n_l/n_u	x_l/x_u	Z	P	n_l/n_u	x_l/x_u	Z	P
Lizard vs. Unfragmented								
Slope	11/147	27.7/7.6	2.9	0.003***	16/147	11.1/7.6	3.8	0.001***
Compaction	11/147	0.7/3.1	-2.7	0.008**	16/147	2.6/3.1	0.7	0.474
Open Sand	11/147	62.7/34.0	1.6	0.113	16/147	62.2/34.0	6.7	< 0.001***
Leaf Litter	11/147	9.1/24.9	-0.5	0.609	16/147	17.2/24.9	3.3	< 0.001***
Shinnery Oak	11/147	18.6/7.7	1.1	0.260	16/147	4.7/7.7	2.9	0.004***
Grass	11/147	0.9/3.1	-2.7	0.007**	16/147	1.6/3.1	2.7	0.008**
Caliche	11/147	0/2.9	0.0	1.000	16/147	0/2.9	2.4	0.014*
Forbs	11/147	8.6/27.4	-1.7	0.082	16/147	14.4/27.4	4.6	< 0.001***
Lizard vs. Fragmented								
Slope	14/147	21.8/5.6	3.1	0.002***	24/147	8.8/5.6	4.7	< 0.001***
Compaction	14/147	3.3/6.3	-1.8	0.075	24/147	3.5/6.3	1.6	0.132
Open Sand	14/147	76.6/34.0	3.0	0.003***	24/147	56.3/34.0	4.7	< 0.001***
Leaf Litter	14/147	5.8/18.1	-2.2	0.027*	24/147	10.6/18.1	1.1	0.277
Shinnery Oak	14/147	7.9/6.5	-0.9	0.357	24/147	11.3/6.5	2.7	0.007**
Grass	14/147	0.4/0.2	1.0	0.317	24/147	3.3/0.2	6.9	< 0.001***
Caliche	14/147	0.0/20.6	-1.7	0.083	24/147	0.0/20.6	5.7	< 0.001***
Forbs	14/147	9.4/20.5	-1.3	0.192	24/147	20.5/18.5	0.9	0.357

$P < 0.001$) and kurtosis (kurtosis = 89.50, $Z = 20.24$, $df = 84$, $P < 0.001$), and the Doornik and Hansen (1994) omnibus test ($E_p = 2395$, $P < 0.001$). Given these significant departures from multivariate normality, we used a two-group permutation (non-parametric) method to distinguish among multivariate data sets. This permutation test is an alternative to Hotelling's test when the assumptions of multivariate normal distributions and equal covariance matrices do not hold. The basic idea behind permutation methods is to generate a reference distribution by recalculating a statistic for many permutations of the data. With this method, we tested for equality of means of two groups using permutation (2000 replicates) to estimate the Mahalanobis squared distance (MSD), a measure that gauges the similarity of sample sets (Mahalanobis 1936). Specifically, we used this test and statistic to make the following separate microhabitat comparisons: (1) Shinnery Oak sand dune microhabitat in fragmented landscapes to that in unfragmented landscapes; (2) microhabitat of *S. arenicolus* sites to the microhabitat available in unfragmented landscapes; (3) microhabitat of *S. arenicolus* sites to the microhabitat available in fragmented landscapes; (4) microhabitat of *S. arenicolus* sites in fragmented and unfragmented landscapes; (5) microhabitat of *U. stansburiana* sites to the microhabitat available in unfragmented landscapes; (6) microhabitat of *U. stansburiana* sites to the microhabitat available in fragmented landscapes; (7) microhabitat of *U. stansburiana* sites in fragmented and unfragmented

landscapes; and (8) microhabitat of *S. arenicolus* sites to that of *U. stansburiana* sites.

We visualized multivariate groups that were significantly different based on MSD using nonmetric multidimensional scaling (NMDS) in two-dimensional coordinate space. The NMDS method is an approach to ordination in which scatters of points representing samples in a low-dimensional ordination space are iteratively allowed to evolve until the Euclidean distances among the points resemble an observed dissimilarity matrix as closely as possible (Kruskal 1964a, 1964b). The NMDS method is nonmetric because stress, the measure of closeness of fit, is based on a monotonic regression of ordination distances plotted in rank-order against dissimilarities calculated from the data matrix. Like other ordination approaches, it is always possible in NMDS to achieve a lower stress or better fit with an increase in dimensionality (e.g., more principle components in PCA). In this study, we used a scree diagram to describe how stress values changed with increasing dimensionality, and we identified that dimensions beyond two did not substantially lower the stress value. The “rule of thumb” for interpreting stress presented by Kruskal (1964a, 1964b) and subsequent researchers is that stresses up to 0.2 can be ecologically interpretable and useful (Clarke 1993; MjM Software Design, Gleneden Beach, Oregon, USA and references therein). Because some of our stress values for the NMDS were above 0.2 (see below), we have incorporated additional statistical procedures in

TABLE 3. Univariate non-parametric tests (Wilcoxon rank-sum) comparing microhabitat differences between *Sceloporus arenicolus* (*sa*) and *Uta stansburiana* (*us*) locations. Sample sizes (*n*) and means (\bar{x}) are listed for each variable. Because multiple comparisons are made, significance is noted at the $\alpha = 0.05$ (*), 0.01 (**), and 0.006 (***) levels. See text for interpretation.

Microhabitat Variables	<i>Sceloporus arenicolus</i> vs. <i>Uta stansburiana</i>			
	n_{sa}/n_{us}	$\bar{x}_{sa}/\bar{x}_{us}$	Z	P
Slope	25/40	24.4/9.7	4.6	< 0.001***
Compaction	25/40	2.2/3.2	1.5	0.130
Open Sand	25/40	70.5/58.6	1.6	0.110
Leaf Litter	25/40	7.2/13.3	1.9	0.024*
Shinnery Oak	25/40	12.6/8.6	1.0	0.336
Grass	25/40	0.6/2.6	2.7	0.007**
Forbs	25/40	9.0/16.9	3.1	0.002***

our analysis of microhabitat selection. For example, we also used Wilcoxon rank-sum tests (non-parametric) with Bonferroni corrections to estimate univariate differences among groups. We report significant differences at $\alpha = 0.05$, 0.01, and Bonferroni corrected 0.006 levels (Tables 1–3). However, because the Bonferroni correction is sometimes considered too conservative in its control for multiple comparisons (Hochberg and Tamhane 1987), we interpret statistical significance for all $P < 0.05$. All together, the answers to the questions above and our conclusions were drawn by using a “strength of evidence” approach that incorporates the results from each of the different statistical procedures described above. None of our conclusions were drawn from a single statistical result.

RESULTS

We found significant differences between Shinnery Oak sand dune habitats in fragmented and unfragmented sites (Fig. 1; MSD = 0.079, $P < 0.001$). Shinnery Oak sand dune habitats in fragmented sites had shallower slopes, higher soil compaction, less leaf litter and grass, and more caliche than the same habitats in unfragmented sites (Table 1). These significant differences between fragmented and unfragmented sites remained even when those microhabitat points falling on caliche roads and well pads were removed from the multivariate analyses (figure not shown; MSD = 0.047, $P = 0.002$). Given these observed differences in the Shinnery Oak sand dune habitats available to *S. arenicolus* and *U. stansburiana* in fragmented and unfragmented sites, we next compared microhabitat selection of *S. arenicolus* and *U. stansburiana* in both fragmented and unfragmented sites. We found that *S. arenicolus* selected microhabitats within Shinnery Oak sand dune habitats that differed significantly from random microhabitats available in both fragmented and unfragmented sites (Fig. 2A and B; MSD = 0.271, $P < 0.001$; MSD = 0.205, $P < 0.001$, respectively). Specifically, *S. arenicolus* selected microhabitats with steeper slopes, less compact soils, and less grass within

habitats found in unfragmented sites, and they selected microhabitats with steeper slopes, less compact soils, more open sand, and less leaf litter and caliche within habitats found in fragmented sites (Table 2). However, we found no significant differences in *S. arenicolus* microhabitat selection within Shinnery Oak sand dune habitats found in fragmented and unfragmented sites (MSD = 0.3238, $P = 0.331$).

For *U. stansburiana*, we also found that lizards selected microhabitats within Shinnery Oak sand dune habitats that differed significantly from random microhabitats available in both unfragmented and fragmented sites (Fig. 2C and D; MSD = 0.108, $P = 0.003$; MSD = 0.131, $P < 0.001$, respectively). Specifically, *U. stansburiana* selected microhabitats with steeper slopes, more open sand, and less leaf litter, shinnery, grass, caliche, and forbs in unfragmented sites, and they selected microhabitats with steeper slopes, more open sand, shinnery, and grass, and less caliche in fragmented sites (Table 2). However, we found no significant differences in *U. stansburiana* microhabitat selection within Shinnery Oak sand dune habitats found in fragmented and unfragmented sites (MSD = 0.173, $P = 0.197$).

Given that *S. arenicolus* and *U. stansburiana* appeared to be selecting microhabitats with many of the same attributes, we also compared differences in microhabitat selection between them. We found significant differences in microhabitat selected between *S. arenicolus* and *U. stansburiana* within Shinnery Oak sand dune habitats (Fig. 3; MSD = 0.301, $P = 0.001$). Specifically, *S. arenicolus* selected microhabitats with steeper slopes, more open sand, and less leaf litter, grass, and forbs than *U. stansburiana* (Table 3).

DISCUSSION

We found that fragmentation, in this case oil and gas development, had a significant effect on microhabitats available to *S. arenicolus* and *U. stansburiana*. Fragmented sites had significantly more caliche, which

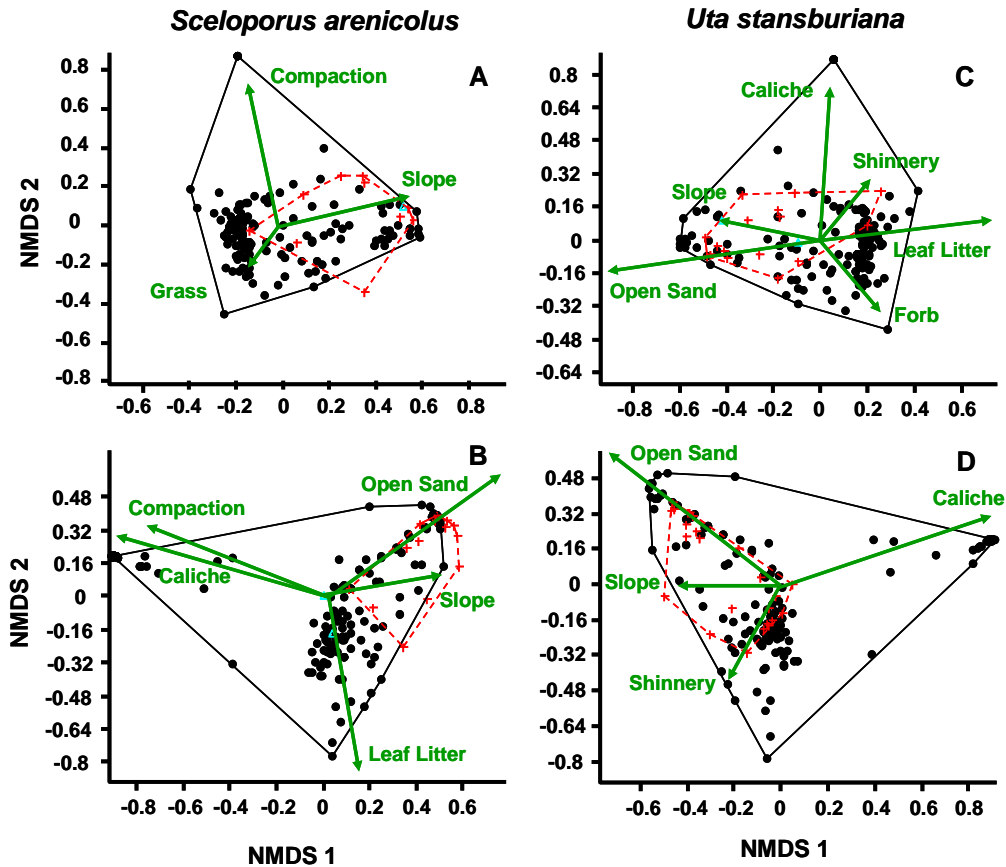


FIGURE 2. Nonmetric multidimensional scaling (NMDS) ordination characterizing the difference between microhabitats selected by *Sceloporus arenicolus* and those available in (A) unfragmented (stress = 0.1941) and (B) fragmented sites (stress = 0.1941), and the difference between microhabitats selected by *Uta stansburiana* and those available in (C) unfragmented (stress = 0.2122) and (D) fragmented sites (stress = 0.1551). Microhabitats selected by lizards of both species are shown with red pluses and dashed lines. Microhabitats available to lizards in both unfragmented and fragmented sites are shown with black dots and solid lines. Green arrows show significant correlations of habitat variables to NMDS axes.

is used to make well pads and roads. Additionally, fragmented sites had more compact soils and shallower slopes than unfragmented sites. These significant differences between fragmented and unfragmented sites remained even when those microhabitat points falling on caliche roads and well pads were removed from the analyses. This shows that the effects of fragmentation go beyond the caliche roads and well pads themselves and extend into remaining habitats. Some of these extended effects could be attributed to the construction of holding ponds next to well pads. These ponds are created during the drilling process and then covered with sand post-drilling. Vegetation is allowed to colonize these open spaces naturally. Microhabitats within these disturbed spaces have very shallow slopes, higher compaction, and are devoid of Shinnery Oak (at least for several years post disturbance). We also believe that other factors may have contributed to the microhabitat differences observed between fragmented and

unfragmented sites. One of these potential factors is changes in the wind patterns across fragmented sites. Wind plays a major role in the creation and maintenance of these habitats in the Mescalero/Monahans Sand Dunes ecosystem, and changes to the way wind moves through the landscape could cause the degradation of habitat as sand is deposited in different areas and as targets of wind erosion shift in space (Rich and Stokes 2011).

We found that both the generalist *U. stansburiana* and the specialist *S. arenicolus* selected microhabitats with specific characteristics, and that these microhabitats were significantly different than what was available in both fragmented and unfragmented sites. We also found no evidence that fragmentation alters microhabitat selection in either species. *Sceloporus arenicolus* selected sites with steeper slopes, less compact soils, more open sand and less leaf litter. These characteristics are associated with the edges of blowouts, which have

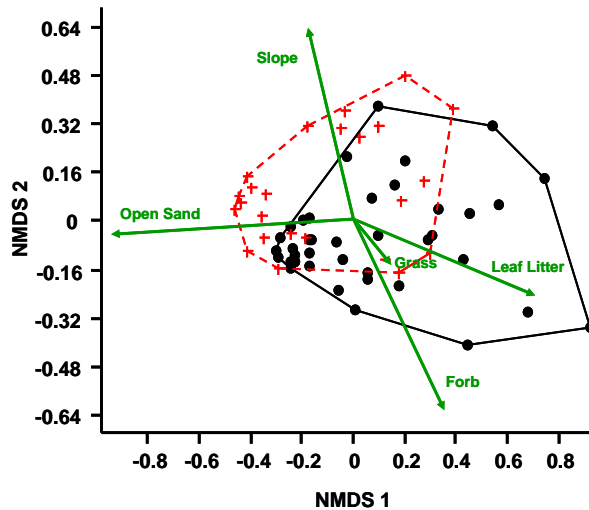


FIGURE 3. Nonmetric multidimensional scaling (NMDS) ordination characterizing the difference between microhabitats selected by *Sceloporus arenicolus* (red pluses with dashed lines) and *Uta stansburiana* (black dots with solid lines; stress = 0.1179) in the southwestern USA. Green arrows show significant correlations of habitat variables to NMDS axes.

been identified as essential habitat for *S. arenicolus* (Degenhardt et al. 1996; Smolensky and Fitzgerald 2011); however, these habitat characteristics can also be found in other formations within the Mescalero/Monahans Sand Dunes ecosystem. *Uta stansburiana* selected sites with more open sand, steeper slopes, less caliche, and more leaf litter. Both species avoided microhabitats associated with flat patches of Shinnery Oak, which commonly occur in areas known as shinnery flats. In many cases, Shinnery Oak in the shinnery flat areas formed a closed canopy which could make it difficult for these ectothermic species to thermoregulate.

Both species also avoided microhabitats with caliche. The caliche surface forms an impermeable barrier that neither species of lizard can dig or burrow through. Caliche also inhibits the growth of plants that both species use for refuge to avoid predation (Tinkle et al. 1962) and for thermoregulation (Sartorius et al. 2002). Both species selected microhabitats with steeper slopes and more open sand than would be expected from available microhabitats. However, *S. arenicolus* utilized steeper slopes than *U. stansburiana* (Fig. 3) and also showed a stronger affinity for open sand than *U. stansburiana*, which was more associated with vegetation structure (e.g., grass, forbs, leaf litter; Fig. 3). A habitat generalist may be expected to utilize all or most of the microhabitat sites that are available, but even a generalist species will have constraints on what microhabitats they can use due to many other factors like thermoregulatory requirements, foraging mode, and predator avoidance (Tinkle et al. 1962).

Slope was the only microhabitat variable that was significant in each test. This indicates that the micro-topographic variation of stabilized dunes within the Mescalero/Monahans Sand Dunes ecosystem is important to both species of lizards studied but especially important to *S. arenicolus*. From these data and previous research, we infer that *S. arenicolus* is a habitat specialist at multiple scales. At landscape scales, *S. arenicolus* is restricted to Shinnery Oak sand dune habitats with blowouts (Degenhardt et al. 1996; Smolensky and Fitzgerald 2011), and at local scales within these habitats, *S. arenicolus* prefers the steepest slopes associated with blowouts. Previous research at local scales also suggests that nesting females prefer sandy soils with high moisture content and large sand grain size composition (Ryberg et al. 2012). Because micro-topography and soil characteristics appear to be important microhabitat elements for *S. arenicolus*, we infer that this lizard is a topo-edaphic microhabitat specialist at local scales within Shinnery Oak sand dune habitats. *Uta stansburiana*, on the other hand, thrives in many habitats across western North America (i.e., it is a habitat generalist) and likely selects microhabitats with steeper slopes than available in all of those habitats regardless of other microhabitat features (such as soil type, soil compaction and plant associations; Tinkle et al. 1962; Davis and Verbeek 1972; Parker and Pianka 1975).

Our results confirm that the way in which oil and gas development fragments Shinnery Oak sand dune habitat does indeed alter microhabitat elements upon which the habitat specialist, *S. arenicolus*, is dependent. As mentioned above, fragmentation increased the amount of flat caliche surfaces within habitats, which decreased the availability of preferred microhabitats with steep slopes. In our fragmented study areas specifically, at least 25% (55 wells/640-ac section with 3-ac well pads, road area not calculated) of the surface was converted to caliche and an additional acre of surface was made level for the construction of retention ponds. The loss of these micro-topographic features represents one direct ecological mechanism by which fragmentation of habitat could lead to observed decreases in the abundance of *S. arenicolus* (Leavitt 2012). Another potential indirect ecological mechanism that would support the observed decrease in *S. arenicolus* abundance also exists. Given that the slopes available to *S. arenicolus* in blowouts are constrained on the upper end by the angle of repose for the slipface of sand dunes (approximately 35 degrees, Strahler and Archibold 2008), *S. arenicolus* appears to select a very narrow range of slopes bound by physics on the high end and potentially niche segregation with *U. stansburiana* on the low end. Under such conditions, it is possible that *S. arenicolus* experiences competition with *U. stansburiana* for steep microhabitats in areas with shallower slopes available. By extension, it is

therefore also possible that competitive interactions between these species increase in areas fragmented by oil and gas development, because such disturbances decrease available habitat with steep slopes (Fig. 1). This mechanism represents a potential indirect way for fragmentation of habitat by oil and gas development to result in the observed reduction of *S. arenicolus* abundance (Leavitt 2012). The potential effect of fragmentation on the habitat generalist, *U. stansburiana*, is more complicated. *Uta stansburiana* also showed a preference for steeper microhabitats and should therefore exhibit a negative response to fragmentation. However, as described above, the net effect of losing steep slopes on *U. stansburiana* will depend on whether these two species compete for steep slopes within Shinnery Oak sand dune habitats and whether observed decreases in *S. arenicolus* abundance in fragmented habitats alleviate such interactions. If these two conditions are true, then they provide one ecological mechanism by which observed *U. stansburiana* abundances might have increased in fragmented habitats (Leavitt 2012). Alternatively, *U. stansburiana* also preferred areas that were open and steep slopes are naturally associated with open areas in unfragmented Shinnery Oak sand dune habitats. After fragmentation, more open areas exist that can be occupied by *U. stansburiana* that would not be suitable for *S. arenicolus*, which could also explain why *U. stansburiana* abundances increased and *S. arenicolus* abundances decreased in fragmented habitats (Leavitt 2012).

Altogether these results highlight several ecological mechanisms by which habitat fragmentation by oil and gas development might lead to the observed changes in *S. arenicolus* and *U. stansburiana* abundances via decreases in the preferred microhabitats available to the habitat specialist, *S. arenicolus*. As such, these results also provide support for the utility of the specialist-generalist concept in predicting extinction risk in this system. With regard to habitat management, our observations that *S. arenicolus* prefers steep slopes and avoids caliche surfaces suggests that minimizing the disturbance to areas with naturally steep, open slopes would benefit *S. arenicolus* persistence. Exact placement of caliche well pads and roads can minimize this disturbance, but caution should be taken because the effects of fragmentation reach beyond the edges of the caliche well pads and roads. Thus, until research can identify the appropriate buffer distances from habitat that prevent such degradation, the best practice for oil and gas development would be to avoid Shinnery Oak sand dune habitats whenever possible.

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