POPULATION VARIATION IN DUNE-DWELLING LIZARDS IN RESPONSE TO PATCH SIZE, PATCH QUALITY, AND OIL AND GAS DEVELOPMENT

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ABSTRACT—We studied relationships between quality and quantity of habitat and conversion of land to caliche roads and well pads associated with oil and gas development. We asked how these factors affected abundance of dune-dwelling lizards, with emphasis on a habitat specialist, the dunes sagebrush lizard *Sceloporus arenicolus*. Open depressions in dune complexes are a critical landscape feature for *S. arenicolus*, and extensively used by all species; thus, size and total area of open depressions in a study site were our measures of habitat quality and quantity. There were significant differences in habitat quality among sites, and habitat quality and quantity were correlated significantly. Abundances of all lizards, including *S. arenicolus*, varied significantly among sites and this variation could be explained by amount of habitat at a given site. Relationships between oil and gas development, quantity and quality of habitat, and abundances of lizards likely occur on different spatial scales constraining our ability to detect direct effects of oil and gas development alone. Our research is the first to investigate effects of oil and gas development on an assemblage of dune-dwelling lizards.

RESUMEN—Se estudiaron las relaciones entre la calidad y la cantidad de hábitat y la conversión de hábitat a caminos y plateas de caliche para pozos petroleros asociados al desarrollo petrolero. Preguntamos cómo dichos factores afectan la abundancia de lagartijas que habitan dunas, con énfasis en una especie especialista *Sceloporus arenicolus*. Las depresiones abiertas en los complejos de dunas de arena son una característica importante del paisaje para *S. arenicolus* y son usadas mucho por todas las especies, entonces el tamaño y área total de estas depresiones en un sitio fueron nuestras medidas de calidad y cantidad de hábitat. Se encontraron diferencias significativas en la calidad de hábitat entre los sitios, y la calidad y cantidad de hábitat estuvieron significativamente correlacionadas entre sí. Las abundancias de lagartijas de todas las especies, inclusive *S. arenicolus*, variaron significativamente entre sitios, y tal variación podría estar explicada por la cantidad de hábitat en un sitio determinado. Las relaciones entre el desarrollo petrolero, la calidad y cantidad de hábitat, y las abundancias de lagartijas probablemente ocurren a distintas escalas espaciales, limitando nuestra capacidad de detectar los efectos directos de desarrollo petrolero exclusivamente. Este trabajo es el primero en investigar algunos efectos del desarrollo petrolero en un ensamblaje de lagartijas de dunas.

The association between availability of habitat and persistence of species is clear, and recent work elucidates how cumulative loss of habitat at large spatial scales erodes capacity of the landscape to sustain biodiversity (Pope et al., 2000; Gaston et al., 2003). Farming croplands, extraction of timber, urban development, and construction of roads all contribute to loss of habitat and result in variable configuration of remaining patches of habitat and associated effects on biodiversity (Andren, 1994; Hokit et al., 1999; Fahrig, 2003). For example, with agricultural or urban development, large tracts of land may be converted leading to a few patches of habitat that are relatively isolated. Habitat also is lost to road construction or timber extraction, but the resulting fragmentation may lead to an increase in number of patches and variation in size and isolation of patches. Thus, it is important to understand how land-management practices influence availability and quality of habitats across landscapes.

Oil and gas exploration and development began in the 1800s and occurs on large spatial scales spanning hundreds of thousands of hectares (Bureau of Land Management, http://www.blm.gov/nm/st/en/prog/energy/oil_and_gas/lease_sale_notices.html). Yet there are few studies that discuss loss of habitat, scarring of land, and fragmentation caused by this type of land management (Fiori and Zalba, 2003; Schneider et al., 2003; Linke et al., 2005, 2008). During oil and gas development in the Southwest, natural habitat is lost and fragmented by networks of caliche (decomposed limestone) roads and well pads. The pattern of landscape fragmentation from oil and gas development is distinct from that caused by farming croplands, clear-cutting, and cattle grazing, and its effects on different forms of biodiversity are even less understood. Consequently, investigating responses of species to oil and gas development is warranted.

Among squamate reptiles, various forms of habitat loss and fragmentation are considered to be primary drivers of declines in populations (Shine, 1991; Gibbons et al., 2000; Collins and Storfer, 2003; Gardner, 2007). Although farming croplands, deforestation, and cattle grazing were discussed in these reviews, none addressed the potential effects of oil and gas development on reptiles. Possible direct and indirect effects of oil and gas development have been documented on other species of invertebrates and vertebrates. For example, changes in community structure of ground beetles (Carabidae) were attributed to fragmentation of forest by installation of an oil pipeline (Silverman et al., 2008). Birds have been trapped in oil pits, causing mortalities numbering in the thousands (Trail, 2006). Initiation of nesting by sage grouse (*Centrocercus urophasianus*) was reduced due to disturbance from oil wells and activity on roads (Lyon and Anderson, 2003), and mule deer (*Odocoileus hemionus*) shifted selection of habitat as a result of oil and gas development (Sawyer et al., 2006, 2009). Although it is intuitive that oil and gas development will affect reptiles, it also is apparent that species vary in response to change in landscape (Andren, 1992; Bender et al., 1998; Hokit et al., 1999; Vega et al., 2000). Herein, we investigate the response of an assemblage of lizards to various levels of oil and gas development. The goal of our research was to gain insight into thresholds of landscape degradation that elicit responses from habitat specialists versus from an entire assemblage of lizards.

The Mescalero Sands ecosystem of southeastern New Mexico and adjacent Texas supports an assemblage of lizards consisting of generalists and specialists that occupy a sand-dune system that is semi-stabilized by shinnery-oak (*Quercus havardii*). This ecosystem is best described as a restricted system of dune complexes that vary in size and connectivity. Dune complexes themselves are patchy, consisting of open sand-dune depressions, called blowouts, in a matrix of shinnery-oak. Size and density of blowouts vary as does topographic complexity of the dunes. Among the seven species of lizards that inhabit the shinnery-oak and sand-dune habitat is the endemic habitat specialist *Sceloporus arenicolus* (dunes sagebrush lizard). *Sceloporus arenicolus* has a restricted range (Degenhardt et al., 1996; Fitzgerald and Painter, 2009; Laurencio and Fitzgerald, 2010) and is a candidate for listing as endangered or threatened (United States Fish and Wildlife Service, 2009). This species occurs exclusively in and around sand-dune blowouts and it prefers relatively large blowouts based on availability in the landscape (Chan et al., 2009; Fitzgerald and Painter, 2009). Other species of lizards use both sand-dune blowouts and the surrounding matrix of shinnery-oak. Conservation status of *S. arenicolus* has drawn attention of natural-resource agencies, the oil and gas industry, conservation organizations, private landowners, and other stakeholders. All stakeholders are interested in knowing more about natural variation in populations of *S. arenicolus*, both temporally and spatially, especially in the context of oil and gas development.

The patchy nature of this shinnery-oak-sand-dune habitat, the species of lizards that use it, and the ongoing development of oil and gas resources within the Mescalero Sands ecosystem present an excellent system for studying relationships between quality and quantity of habitat patches, abundance of lizards, and effects of land conversion to caliche roads and well pads on both habitat and abundance of lizards. As such, we asked, what is the association between patch size (blowouts) and total patch area on abundance of lizards, especially for the specialist *S. arenicolus*, and what are the effects of networks of caliche roads on sand-dune blowouts? Blowouts represent important patches of habitat in the shinnery-oak, sand-dune matrix that are used by various dune-dwelling lizards, and size of individual blowouts (patch size) is a measure of habitat quality. Based on occupation by *S. arenicolus*, dune complexes with a high density of large, deep, sand-dune blowouts is presumed superior habitat to areas with small numbers of small blowouts. In addition to loss of habitat due to outright conversion of the surface from natural habitat to packed caliche, the network of roads and well pads may also influence quality of remaining habitat by disrupting geomorphologic processes that create and maintain blowouts. For example, after fragmentation, remaining blowouts may be smaller in size and, thus, poorer quality for lizards. We predicted that abundance of lizards would increase with greater numbers of sand-dune blowouts and larger size of blowouts. We also predicted a decrease in number of lizards at sites with more oil and gas development. We tested these predictions by counting lizards and quantifying variation in size of individual blowouts and total area of blowouts at multiple study sites with varying amounts of caliche roads and well pads, then correlating number of lizards to quality and quantity of blowouts, and to amount of caliche. Because oil and gas development may affect *S. arenicolus* and other species of lizards that occupy the Mescalero Sands ecosystem, results of this research are directly applicable to land management and conservation (Mac Nally et al., 2002). This study is the first to provide insight into effects of alteration of habitat associated with oil and gas development on herpetofauna.

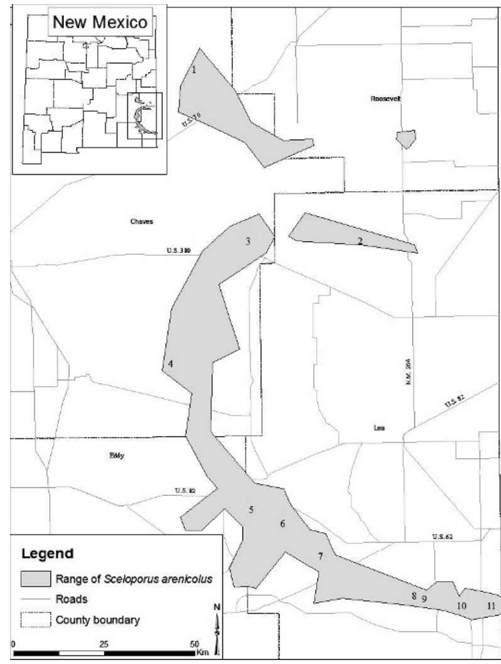

Fig. 1—Geographic range of the dunes sagebrush lizard *Sceloporus arenicolus* in New Mexico. Also shown are locations of 11 sites where survey transects were conducted and where habitat variables were quantified in the Mescalero Sands ecosystem of southeastern New Mexico during May–July 2005 and 2006.

Materials and Methods—Study sites in the Mescalero Sands ecosystem were in Chaves, Eddy, and Lea counties, New Mexico. This ecosystem is characterized by stabilized and semi-stabilized dunes interspersed with shinnery-oak, sand sagebrush (*Artemisia filifolia*), bunchgrasses (*Aristida, Schizachyrium, Andropogon*), and sandy hummocks with honey mesquites (*Prosopis glandulosa*). We quantified abundance of lizards at 11 sites (Fig. 1) based on presence of shinnery-oak-sand-dune habitat, presence of *S. arenicolus*, and amount of oil and gas development.

Our indicator of oil and gas development on the landscape was total surface area of caliche, which was the total area of oil-well pads and roads in a 259-ha area of shinnery-oak-sand-dune habitat surrounding transects at each study site. This spatial scale was large enough to include caliche-covered well pads and roads that immediately surrounded transects. We used ArcMap, version 9.0 (Environmental Systems Research Institute, Inc., Redlands, California) to quantify total surface area of caliche. The New Mexico State Land Office (in litt.) provided GIS data that included locations of oil wells and roads. Size of well pads was standardized at 6,400 m^2 and roads were standardized at 4 m wide. The 4-m width of roads was conservative based on guidelines for construction of caliche roads suggested by the New Mexico Commission of Public Records (http://www.nmcpr.state.nm.us/NMAC/parts/title19/19.002.0020.htm) and the Chaves County Commission (http://co.chaves.nm.us/agendas/2006/101906/101906-A3.pdf m).

Total area of blowouts at sites was our measure of quantity of habitat because blowouts are integral to the shinnery-oak-sand-dune habitat, they are used by multiple species of lizards, they are a critical feature of habitat for *S. arenicolus*, and they provide thermoregulatory sites for other species of lizards (Sartorius et al., 2002). *Sceloporus arenicolus* inhabits larger blowouts based on availability in occupied habitat; thus, larger blowouts are considered to be better quality of habitat than smaller blowouts. Many small blowouts can provide the same total area of blowouts as a few large blowouts; for this reason, quantity of habitat does not necessarily equal quality of habitat. We measured area of each blowout within the 11,259-ha sites in ArcMap 9.0 (Environmental Systems Research Institute, Inc., Redlands, California) to determine average size of blowout available to dune-dwelling lizards. A polygon shape file of all blowouts was created from aerial photographs taken in 2004 and obtained from the New Mexico State Land Office (in litt.). Mean size of blowout for the entire site was our index of site-wide quality of habitat.

We quantified encounters of lizards per unit effort by time from line transects conducted in May–July 2005 and 2006. Number of transects at a site was 8–48 due to availability of personnel. We standardized data on abundance of lizards by converting raw counts to encounters per unit effort for each transect and for all transects at a site (site-wide encounters of lizards per unit effort). To compute site-wide encounters of lizards per unit effort we divided total minutes of searching effort by total number of lizards counted at a site. All transects were 25 min in duration. Transects were standardized by time because in studies of lizards, the correlation between number of individuals seen and time spent searching might be more meaningful than number of individuals seen over distance. All transects were surveyed during 0800–1300 h. Transects were not surveyed during rain or when substrate temperature was (<20 or >50°C). Transects were located randomly within shinnery-oak-sand-dune habitat after presence of *S. arenicolus* was verified. We did not consider other types of habitats, because *S. arenicolus* does not use them. As such, our results only apply to effects of oil and gas development on lizards in the shinnery-oak-sand-dune habitat.

We used a Kruskall-Wallis test to search for differences in quality of habitat (size of blowout) among sites, with size of individual blowouts as the sample unit. This was followed by a Nemenyi test (nonparametric Tukey test) for post-hoc multiple comparisons, with the standard error adjusted for unequal samples (Zar, 1999). Quality and quantity of habitat may be correlated and consequently confound our conclusions regarding the relationship between total area of blowouts, mean size of blowout, total surface area of caliche, and abundance of lizards. Thus, we used linear regression to test for a relationship between mean size of blowout (site-wide quality of habitat) and total area of blowouts (quantity of habitat), with total area of blowouts as the independent variable.

We analyzed pooled encounters of lizards per unit effort for all lizards combined, and separately for *S. arenicolus.* We used analysis of variance and a Kruskal-Wallis test to compare encounters of lizards per unit effort collectively and of *S. arenicolus* among sites. Encounters of lizards per unit effort for each transect was the sample unit in these tests. We used a Tukey test and an adjusted Nemenyi test for post-hoc multiple comparisons.

We computed linear regressions on site-wide encounters of lizards per unit effort against total surface area of caliche, total area of blowouts, and mean size of blowout for *S. arenicolus* and lizards collectively to test the null hypotheses of no relationship between abundance of lizards and oil and gas development, quantity of habitat, and quality of habitat. When necessary, data for encounters of lizards per unit effort were log-transformed prior to analysis to homogenize variances of groups and to meet assumptions of normality (Zar, 1999).

RESULTS—Range for total surface area of caliche among the 11 sites was 1.32–23.88 ha (mean = 9.23, *SD* = 8.24, *n* = 11; Table 1). A site that contained 23.88 ha of total surface area of caliche had ≤9% of the area comprised of oil and gas development. Range for total area of blowouts among the 11 sites was 14.47–50.82 ha (mean = 31.31, *SD* = 10.50, *n* = 11). A site that contained ≤50.82 ha of total area of blowouts

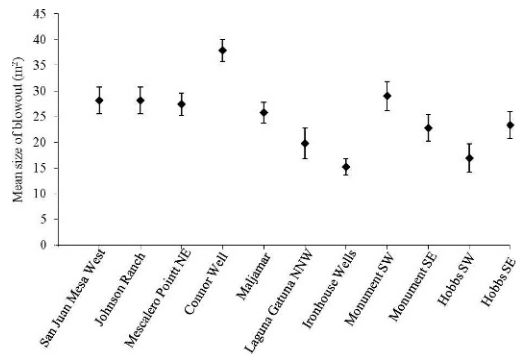

FIG. 2—Quality of habitat measured by mean size of blowout at 11 sites within shinnery-oak and sand-dune habitat in the Mescalero Sands ecosystem of southeastern New Mexico. Error bars indicate ±1 *SE.*

translated to 10% of the area comprised of blowouts. The rest of the area within our 259-ha sites was shinnery-oak vegetation. There were significant differences in quality of habitat (size of blowout) among sites (χ^2_{10} = 3,348.39, $P <$ 0.01; Fig. 2). Quality and quantity of habitat were significantly and positively correlated. Of the variation in quality of habitat among sites, 41% was explained by quantity of habitat (total area of blowout; $R^2 = 0.41$, $P < 0.03$; Fig. 3), suggesting that quality of habitat is linked to amount of habitat. The prediction that oil and gas development should be associated with fewer and smaller sand-dune blowouts was not supported. There was no significant correlation between total surface area of caliche and total area of blowouts nor between total surface area of caliche and mean size of blowout ($r = -0.32$, $P < 0.34$; $r = -0.08$, $P < 0.82$). All sites were chosen because they were in shinnery-oak-sand-dune habitat, and sites with the most area converted to packed caliche still had moderate (10%) total area of blowouts (Table 1).

We encountered 1,321 lizards (0.232 lizards/min) of seven species on 227 transects at the 11 sites. The Texas horned lizard *Phyrnosoma cornutum* was seen only on two transects; thus, it was excluded from analyses. These six species made up the collective dataset; the side-blotched lizard *Uta stansburiana* (0.081 lizards/min) was the most frequently detected followed by *S. arenicolus* (0.046 lizards/min), the marbled whiptail *Aspidoscelis marmoratus* (0.036 lizards/min), the lesser earless lizard *Holbrookia maculata* (0.016 lizards/min), the six-lined race runner *Aspidoscelis*

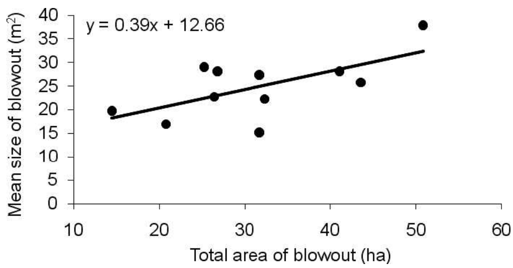

FIG. 3—Results of a linear regression showing the relationship between mean size of blowout and total area of blowout among 11 sites in the Mescalero Sands ecosystem of southeastern New Mexico.

sexlineatus (0.009 lizards/min), and the prairie lizard *Sceloporus consobrinus* (0.006 lizards/min). Mean encounters of lizards per unit effort varied significantly among sites for lizards collectively and nearly so for *S. arenicolus* ($F_{10,215} = 8.78$, $P < 0.01$; $\chi^2_{10} = 57.35$, $P < 0.06$, respectively; Fig. 4, Tables 2 and 3). Site-wide encounters of lizards per unit effort was correlated with total area of blowouts for lizards collectively ($R^2 = 0.59$, $\beta = 0.77$, $P < 0.01$; Fig. 5a) indicating a positive relationship between abundance of lizards and quantity of habitat. We did not detect a significant relationship between site-wide encounters of *S. arenicolus* per unit effort and total area of blowouts ($R^2 = 0.27$, $\beta = 0.57$, $P < 0.12$; Fig. 5b). Large variation in encounters of *S. arenicolus* per unit effort among sites with large total area of blowouts reduced the ability of linear regression to detect a relationship between the two variables. Interestingly, there was no strong relationship between quality of habitat (mean size of blowout) and abundances for lizards collectively or for *S. arenicolus* ($R^2 = 0.10$, $P < 0.33$; $R^2 = 0.01$, $P < 0.76$, respectively).

We did not detect significant relationships between encounters of lizards per unit effort and total surface area of caliche for lizards collectively or for *S. arenicolus* ($R^2 = 0.05$, $P < 0.50$; $R^2 = 0.07$, $P < 0.45$, respectively). Sites with 9% of the surface area converted to caliche had similar mean encounters of lizards per unit effort to sites that had 1% of the area converted (Table 1). The lack of significant predictive relationships between total surface area of caliche and encounters of lizards per unit effort of lizards collectively and *S. arenicolus* indicated that differences in abundance of lizards among sites could not be attributed to total surface area of caliche.

DISCUSSION—Our results clearly showed that abundance of lizards varied significantly and in complex ways across the landscape of the Mescalero Sands ecosystem. Total amount of blowout and mean size of blowout in the habitat also varied across the landscape. Quantity and quality of habitat were positively correlated. There was a significant predictive relationship between total area of blowouts and mean size of blowout, indicating that quality of habitat (i.e.,

TABLE 1—Total surface area of caliche, total area of blowout, mean size of blowout, and site-wide encounters per unit effort of lizards collectively and the dunes sagebrush lizard *Sceloporus arenicolus* at 11 sites (numbers correspond to Fig. 1) in the Mescalero Sands ecosystem of southeastern New Mexico. The proportion of each 259-ha site comprised of caliche well pads and roads is in parentheses.

Site	Total surface area of caliche (ha)	Total area of blowout (ha)	Mean size of blowout (m^2)	Site-wide encounters of lizards per unit effort	Site-wide encounters of *S. arenicolus* per unit effort
1. San Juan Mesa West	1.32 (1)	26.76 (10)	28.15	0.232	0.056
2. Johnson Ranch	6.96 (3)	41.06 (16)	28.15	0.183	0.059
3. Mescalero Point NE	1.52 (1)	31.37 (12)	27.42	0.197	0.064
4. Connor Well	2.47 (1)	50.82 (20)	37.85	0.383	0.000
5. Maljamar	12.24 (5)	43.54 (17)	25.78	0.330	0.035
6. Laguna Gatuna NNW	14.45 (6)	14.47 (6)	19.80	0.107	0.011
7. Ironhouse Well	4.20 (2)	31.71 (12)	15.25	0.277	0.030
8. Monument South W	23.28 (9)	25.23 (10)	29.04	0.188	0.036
9. Monument South E	23.88 (9)	26.40 (10)	22.78	0.245	0.023
10. Hobbs SW	3.73 (1)	20.78 (8)	16.96	0.230	0.033
11. Hobbs SE	7.52 (3)	32.35 (12)	22.33	0.282	0.105

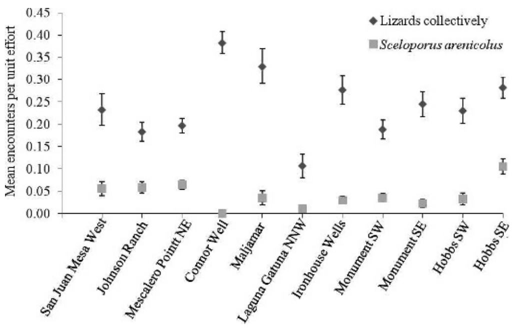

FIG. 4—Abundances of all seven species of lizards collectively and of the dunes sagebrush lizard *Sceloporus arenicolus* at 11 sites in the Mescalero Sands ecosystem of southeastern New Mexico. Abundances are mean encounters per unit effort (±1 *SE*) computed from 227 transects.

size of patch) for lizards in shinnery-oak sand-dunes depended on extent of habitat. Moreover, abundance of lizards also was associated positively with extent of habitat.

Abundances of *S. arenicolus* also varied across the landscape, and our results suggest that extent of sand-dune blowouts in the surrounding landscape was an important determinant of these abundances, although total area of blowouts could not explain entirely the observed pattern among sites. The relationship between total area of blowouts and encounters of *S. arenicolus* per unit effort was positive and explained 27% of variance in the dataset (Fig. 5b), but this relationship was not significant. Lack of a stronger statistical pattern for *S. arenicolus* was due to small mean encounters per unit effort and considerable variation among sites. For example, mean values were zero at one

TABLE 2—Results from Tukey's test with unequal samples on mean encounters per unit effort of all species of lizards collectively at 11 sites in the Mescalero Sands ecosystem of southeastern New Mexico. Sites that do not share the same letter are significantly different.

Site	*n*	Mean	Rank
Laguna Gatuna NNW	18	0.107	1 a
Johnson Ranch	28	0.183	2 ab
Monument SW	27	0.188	3 ab
Mescalero Point NE	48	0.197	4 abc
Hobbs SW	16	0.230	5 abc
San Juan Mesa West	10	0.232	6 abc
Monument SE	16	0.245	7 bc
Ironhouse Wells	12	0.277	8 bcd
Hobbs SE	22	0.282	9 bcd
Maljamar	8	0.330	10 cd
Connor Well	21	0.383	11 d

TABLE 3—Results from Nenyemi's test (nonparametric Tukey's test) with unequal samples for mean encounters of *Sceloporus arenicolus* per unit effort at 11 sites in the Mescalero Sands ecosystem of southeastern New Mexico. Sites that do not share the same letter are significantly different.

Site	*n*	Mean	Rank
Connor Well	21	55.50	1 a
Laguna Gatuna NNW	18	72.69	2 a
Monument SE	16	91.16	3 ab
Hobbs SW	16	98.09	4 ab
Monument SW	27	105.46	5 ab
Ironhouse Wells	12	107.13	6 ab
Maljamar	8	107.44	7 ab
Johnson Ranch	28	128.64	8 ab
Mescalero Point NE	48	135.58	9 ab
San Juan Mesa West	10	136.30	10 ab
Hobbs SE	22	167.43	11 b

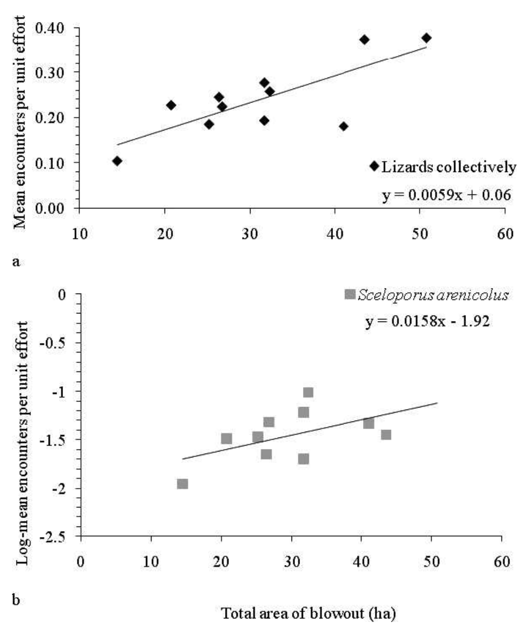

FIG. 5—Relationship between total area of blowout and site-wide encounters per unit effort for a) lizards collectively and for b) the dunes sagebrush lizard *Sceloporus arenicolus* among 11 sites in shinnery-oak and sand-dune habitat in the Mescalero Sands ecosystem of southeastern New Mexico. Mean encounters per unit effort for *S. arenicolus* were log-transformed.

site and close to zero at several sites (Fig. 5b). Other factors associated with fragmentation (e.g., isolation of patch) or meta-population dynamics (Hanski and Gilpin, 1991; Hokit et al., 1999) may also have influenced the patterns of abundance that we observed. Populations of lizards studied in other patchy environments showed responses similar to what we detected. Area of habitat was correlated with abundances of nine species of squamates in the patchy Florida scrub (McCoy and Mushinsky, 1999). In a coastal-dune system in Argentina, a habitat specialist, the sand dune lizard *Liolaemus multimaculatus*, nearly disappeared within 7 years after construction of a road reduced its habitat by 90% (Vega et al., 2000). Thus, it is likely that populations of *S. arenicolus* exhibit similar responses and were correlated with area of blowouts in the habitat.

Despite specialization of *S. arenicolus* on sand-dune blowouts and its presence in relatively large patches (Chan et al., 2009; Fitzgerald and Painter, 2009), we did not find a significant relationship between average size of patch (mean size of blowout) and encounters of *S. arenicolus* per unit effort, or for all lizards combined. Although there is evidence that abundance of *S. arenicolus* and other species of lizards increase with size of patch (Fitzgerald and Painter, 2009), the form of the relationship is not clear, e.g., the relationship may be curvilinear or a step-function. Understanding size of populations and demographic variation among dune-dwelling lizards in relation to size of patch is a topic currently being studied.

We demonstrated that area of habitat and size of patch co-varied, but it was difficult to disentangle effects of size of patch from quantity of habitat. Size of patch is correlated with abundance, survivorship, and recruitment in other lizards studied at single sites (Hokit and Branch, 2003*a*, 2003*b*). Thus, we predict both features probably are important to lizards in the Mescalero Sands ecosystem. Importantly, effects of area and size of patch on abundance of lizards probably also are scale-dependent. Sandel and Smith (2009) pointed out three basic observations from which scale-dependence arises: abundance increases with area, environmental conditions vary across space, and the effect of an organism on its environment is spatially limited. Our analyses demonstrated the first two conditions clearly exist for lizards in shinnery-oak-sand-dune habitats, and we may presume that environmental effects on local populations of lizards, especially the specialist *S. arenicolus*, were independent among our study sites. Interestingly, because of scale-dependence between area of habitat (total area of blowouts) and size of patch (mean size of blowout) among geographically dispersed sites in the Mescalero Sands ecosystem, effects of patch size at individual sites probably were not detected in our study. At the regional scale, habitat area (total area of blowouts) apparently drives abundance, whereas patch size may determine local abundance of lizards.

Furthermore, variation in abundances of lizards across the Mescalero Sands ecosystem probably did not correspond to only two habitat variables and one measure of landscape alteration. Changes in vegetation, for example, affect abundances of lizards (Jellinek et al., 2004). Abundances of *S. undulatus* and *H. maculata* remained relatively stable during initial years of brush encroachment on a dune landscape, but then declined after the open vegetation on dunes was significantly reduced (Ballinger and Watts, 1995). We did not quantify vegetative cover in patches of sand-dune blowouts, but we could see differences in diversity of grasses and plants in blowouts at the study sites. Thus, it is reasonable to speculate that vegetative differences also were associated with abundances of *S. arenicolus* and other species of lizards. Indeed, there is evidence that *S. arenicolus* is sensitive to changes in cover and type of vegetation. Numbers of *S. arenicolus* decreased by 78% within 5 years at sites where shinnery-oak was removed by spraying with herbicide compared to paired control sites (H. L. Snell et al., in litt.). Since the time when shinnery-oak was killed at those study sites >15 years ago, dune blowouts became vegetated with grasses and forbs, blowouts became smaller and flatter, and *S. arenicolus* was no longer present.

Despite the observation that areas of the landscape in the Mescalero Sands ecosystem have been fragmented extensively by oil and gas development, we did not find clear statistical evidence to support our hypotheses that oil and gas development at our study sites had a direct negative effect on quantity of habitat, quality of habitat, and populations of lizards. Thus, we did not detect a threshold for which oil and gas development correlated to reduced abundances of dune-dwelling lizards, or of *S. arenicolus* specifically. Among the 11 sites scattered throughout the Mescalero Sands ecosystem, total area of blowouts and mean size of blowout were variable, and we could not control for natural variation in habitats in our analyses. For example, the two sites with greatest total area of blowouts, Maljamar and Connor Well, had low abundance of *S. arenicolus* (Table 1). These sites also had relatively low total surface area of caliche (5 and 1%, respectively). In contrast, Hobbs SE had relatively low total surface area of caliche, total area of blowouts, and mean size of blowout, yet had the highest encounters of *S. arenicolus* per unit effort.

In addition to natural variation in area of habitat and patchiness among sites, stochastic variation in populations of lizards among sites further confounded our ability to detect effects of conversion of land to caliche, if such effects exist. All studies of lizard populations have documented spatial and temporal variation in vital rates that determine population growth and size. A classic 11-year study of the sagebrush lizard *Sceloporus graciosus* (closest relative of *S. arenicolus*) documented two-fold differences in population size between two sites and among years at each site (Tinkle et al., 1993). Distinguishing variation in natural populations from variation caused by anthropogenic mechanisms can be challenging, especially when long-term data on populations are not available (Tinkle, 1979; Pechmann et al., 1991; Tilman et al., 1994). In the face of demographic stochasticity such as this, it becomes extremely difficult to ascertain the cause of differences in populations among multiple sites, even with long-term data (Fitzgerald, 1994).

Our work represents the first attempts to enumerate lizard populations in the Mescalero Sands ecosystem (Smolensky, 2008; Smolensky and Fitzgerald, 2010; this study). This is the first study to investigate effects of oil and gas development on a dune-dwelling assemblage of lizards, and our results provide insights for future research and establishment of monitoring protocols. What is the next step? Research on landscape fragmentation and connectivity, and on associations among landscape metrics and occurrence of *S. arenicolus* at multiple scales is needed to gain better insight into what factors, and at which spatial scale, best predict persistence of this species and other lizards. A good approach to directly elucidate effects of oil and gas development, or other disturbances on populations of lizards at individual sites, would be long-term studies coupled with before-after-control-intervention experiments (Murtaugh, 2002; Stewart-Oaten, 2003).

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