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Effects of habitat fragmentation on population structure of dune-dwelling lizards

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Abstract. Landscape fragmentation alters biotic and abiotic characteristics of landscapes, variously affecting the size and demographic structure of species' populations. Fragmentation is predicted to negatively impact habitat specialists because of perturbations to their habitat, whereas generalists should be less sensitive to fragmentation. Differences in life history among the lizards in this community should partly explain some of the variation in generalist species' responses to fragmentation. During five seasons (2009–2013), we captured eight species of lizards on 27 independent trapping grids located in unfragmented ($N = 18$) and fragmented ($N = 9$) grids in the Mescalero-Monahans Sandhills ecosystem in southeastern New Mexico. Using a two-way ANOVA, we tested for effects of fragmentation and year on capture rates for each species. To test for effects of fragmentation on demographic structure, we used contingency tables with expected frequencies computed from the demographic structure on unfragmented grids. Capture rates of the endemic habitat specialist *Sceloporus arenicolus* (dunes sagebrush lizard) decreased to zero in fragmented sites. The demographic structure of *S. arenicolus* and *Holbrookia maculata* (common lesser earless lizard) was severely disrupted at fragmented sites, with proportions of juveniles, adult males, or adult females being over- or underrepresented during sample months. Variable responses of five generalist species could be attributed to life history patterns, habitat affinity, and breeding phenology. This is the first empirical study we are aware of that describes and quantifies the demographic effects of fragmentation on populations of multiple lizard species in a replicated study. Our findings lend important insights into how habitat specialization and differences in life history influence the susceptibility of species to the impacts of fragmentation.

Key words: *Aspidoscelis;* demography; ecological specialist and generalist; *Holbrookia maculata;* oil and gas development; *Sceloporus arenicolus; Uta stansburiana.*

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INTRODUCTION

Habitat loss and landscape fragmentation are considered primary drivers of biodiversity loss (Brooks et al. 2002, Dirzo and Raven 2003, Bellard et al. 2014). However, studies of vertebrate and invertebrate communities show that individual species respond to landscape fragmentation differently; some species thrive, while others decline (Haila 2002, Fahrig 2003). Fragmentation can cause population declines in vulnerable species by disrupting processes such as dispersal, gene flow, recruitment, and survival (Hokit and Branch 2003, Henle et al. 2004, Mitrovich et al. 2009). However, broad variations in species' specific responses to fragmentation have made it difficult to identify general trends that predict how a species may respond to fragmentation (Betts et al. 2014).

In an attempt to identify general trends in species' responses to fragmentation, Andrén et al. (1997) and Henle et al. (2004) predicted that habitat specialists would be more sensitive to fragmentation because they are dependent upon relatively restricted habitat types. Alternatively, habitat generalists are likely to be less sensitive to fragmentation and may even thrive in disturbed and changing landscapes because of their broader habitat tolerances, benefitting from the increased landscape heterogeneity, more edge habitat, and competitive relaxation associated with fragmentation (Henle et al. 2004, Devictor et al. 2008). This prediction has been supported in taxonomic groups, such as birds and insects (Warren et al. 2001, Kotze and O'Hara 2003, Goulson et al. 2005, Devictor et al. 2008), and has been identified as a good predictor for some reptile species (Mac Nally and Brown 2001, Hibbitts et al. 2009). However, this dichotomy does not describe all the variation seen in the responses of lizards to fragmentation, and generalist species can also show declines in fragmented areas (e.g., Driscoll 2004, Attum et al. 2006). As such, the contrast between habitat specialists and generalists could be a useful framework, if integrated with other characteristics of the species, in predicting the likelihood of lizard species being sensitive to fragmentation.

Theory predicts that a typical population is characterized by a relatively stable age structure and sex ratio, with natural seasonal fluctuation (Fitzgerald 1994, Gotelli 1995, Caswell 2001, Le Galliard et al. 2005). In species that experience seasonal birth pulses, including many lizard species in temperate areas, the age structure corresponds to a predictable yearly phenology, with relatively high proportions of adults and young-of-year at the beginning of the breeding season, a peak in the proportion of adults during the middle of the breeding season as juveniles mature, and a peak in proportions of juveniles near the end of the breeding season as hatchlings emerge (Bustard 1969, Fitzgerald et al. 1999). Over many years, the age structure is expected to be stable, despite the seasonal changes.

However, age or stage structure varies among species and is strongly associated with their life history strategies. Populations of species with early maturation, short life span, and high fecundity have relatively high proportions of juveniles after reproduction has occurred, which reverts to very low proportions of juveniles the next spring (Alcala and Brown 1967, Tinkle 1973, Dunham and Miles 1985, Barbault and Mou 1988). Alternatively, some species maintain higher proportions of juveniles throughout the year which may be attributed to a still relatively high fecundity, slower maturation, and longer life spans (Turner et al. 1969). Species with longer life spans, later age at maturity, and lower fecundity are characterized by population structures with almost equal proportions of adults and juveniles (Ballinger 1973, Stearns 1992). We propose that small populations are susceptible to disruptions of age or stage structure of both sexes (hereafter, demographic structure) as a result of landscape fragmentation. However, because of the interplay between life history, breeding phenology, and habitat affinity among species, effects of fragmentation should manifest differently for the different species in an ecological community.

The consequences of landscape fragmentation may be exacerbated in ecosystems that are naturally patchy and may affect the population dynamics or persistence of species adapted to living in patchy habitats (Ryberg et al. 2013, 2015). The Mescalero-Monahans Sandhills ecosystem, located in southeastern New Mexico and adjacent west Texas, overlying the Permian Basin, is comprised of ancient parabolic dunes maintained by wind, moving sand, and partially stabilized by *Quercus havardii* (shinnery oak; Hall and Goble 2008). The system is characterized by a patchy arrangement of open dune blowouts (bowl-shaped depressions formed when sand is blown against the leeward slope with vegetated arms extending around the sides) in a matrix of shinnery oak flats (Fitzgerald and Painter 2009, Ryberg et al. 2015). Networks of roads built for oil and gas development result in persistent landscape fragmentation (Smolensky and Fitzgerald 2011, Leavitt and Fitzgerald 2013; Fig. 1), and these fragmented areas have more compact soils, shallower slopes, and less shinnery oak, which are strong indicators of degraded dune blowout landforms in this habitat (Hibbitts et al. 2013). The lizard community in this system is composed of species ranging from widespread generalists to an endemic habitat specialist (Table 1). To date, much work has focused on *Sceloporus arenicolus* (dunes sagebrush lizard), an endemic habitat specialist threatened by loss and

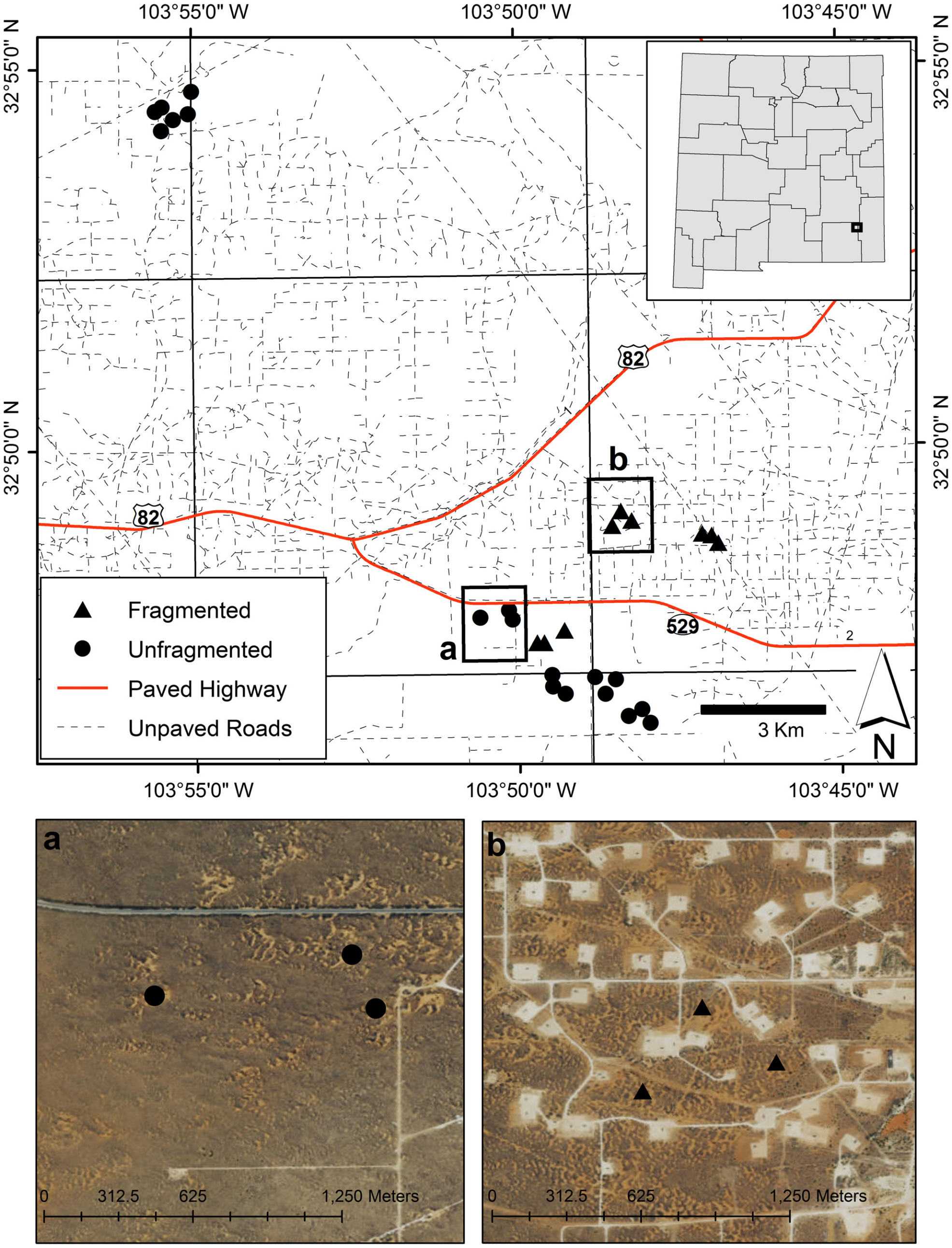

Fig. 1. Map of the study area identifying the location of 27 trapping grids in southeastern New Mexico. The aerial images show trapping sites. Sites were classified as fragmented when the density of oil well pads was >13.0 well pads/section (259 ha). (a) An unfragmented site with one well pad and (b) a fragmented site with 61 well pads.

degradation of shinnery oak dunes. This habitat specialist requires dune blowouts, which are an emergent landform maintained by complex interactions among wind, sand, and the shinnery oak (Ryberg et al. 2015). While previous work has shown population dynamics of *S. arenicolus* are particularly sensitive to configuration and condition of the dune blowout landforms (Smolensky and Fitzgerald 2011, Ryberg et al. 2013, 2015), they are not the only species in this lizard

Table 1. Total captures and capture rates (mean captures/trap-day/grid) of eight species of lizard sampled on 27 trapping grids in unfragmented and fragmented sites during 2009–2013.

Family Species	SVL at maturity (mm)	Max SVL (mm)	Clutch size† (eggs per clutch)	Clutches per season	Max age (yr)	Habitat affinity†	Total captures Capture rates ± SD	
							Unfragmented (n = 18)	Fragmented (n = 9)
Phrynosomatidae								
Holbrookia maculata	44†	75†	2.98–6.1	1–2‡	5†	Generalist: Grasslands Sand dunes	231 0.0045 ± 0.0042	34 0.0012 ± 0.0019
Phrynosoma cornutum	68†	86	23–30	>1†	10†	Generalist§: Deserts Grasslands Sand dunes	34 0.0006 ± 0.0005	23 0.0008 ± 0.0009
Sceloporus arenicolus	43	63	5.1	1–2‡	4‡	Specialist: Sand dunes	1390 0.0148 ± 0.0198	31 0.0011 ± 0.0014
Sceloporus consobrinus	44	62	7.2–9.9	1–3‡	4†	Generalist: Woodlands Deserts Grasslands	173 0.0027 ± 0.0022	59 0.0020 ± 0.0016
Uta stansburiana	39	59	2–5	2–3†	3†	Generalist: Grasslands Woodlands Sand dunes	11,650 0.2028 ± 0.0367	6871 0.2356 ± 0.0384
Teiidae								
Aspidoscelis marmorata	69	98	2.2	1–2†	8†	Generalist: Woodlands Grassland Sand dunes	1012 0.0171 ± 0.0114	508 0.0174 ± 0.0128
Aspidoscelis sexlineata	54	81	2.9	1–2‡	4†	Generalist: Grasslands Deserts	168 0.0031 ± 0.0011	90 0.0031 ± 0.0008
Scincidae								
Plestiodon obsoletus	77	130†	12.3	0–1‡	8†	Generalist: Grasslands Riparian Woodlands	3 0.0001 ± 0.0002	2 0.00007 ± 0.0001

Notes: SVL, snout-vent length; SD, standard deviation. Size at maturity, maximum size, and life span for females were estimated for the populations in our study area from our data unless otherwise indicated by symbols.

† Degenhardt et al. (1996).

‡ Jones and Lovich (2009).

§ Dietary Specialist.

community that may be impacted by fragmentation (Leavitt and Fitzgerald 2013).

Several studies have addressed the effects of landscape or habitat fragmentation on community composition, species presence, and gene flow (Driscoll 2004, Hoehn et al. 2007, Munguia-Vega et al. 2013). In some cases, fragmentation per se did not affect most species (Schutz and Driscoll 2008); other studies concluded fragmentation appeared to drive species loss and changes in abundance (Driscoll 2004, Russildi et al. 2016). Species loss can lead to disassembly of structured communities (Leavitt and Fitzgerald 2013). In the Mescalero-Monahans Sandhills ecosystem, there is a pattern of nested community structure in lizards throughout the ecosystem (Ryberg and Fitzgerald 2016). In fragmented areas, community structure is random compared to the nested structure of lizard communities in unfragmented areas (Leavitt and Fitzgerald 2013). Although these studies provide important information on effects of fragmentation on community structure, we are not aware of any studies that have quantified the effects of fragmentation on the demographic structure of multiple lizard species in a community.

Here, we evaluate the effects of landscape fragmentation on capture rates and the demographic structure of species in a dune-dwelling lizard community. We predict that (1) the specialist species will have lower capture rates in fragmented areas, while generalist species capture rates will be similar across fragmented and unfragmented areas; (2) the demographic structure of the endemic specialist in fragmented areas will deviate strongly from that in unfragmented (control) areas; and (3) the demographic structure of generalist species will show no effect of fragmentation. This is the first empirical study we are aware of that describes and quantifies the demographic effects of fragmentation in a community of lizards. This work provides important insights into how landscape fragmentation disrupts population structure of ecological specialist species, and how species in ecological communities vary in their response to fragmentation.

METHODS

From May 2009 to September 2013, we trapped lizards on 27 pitfall grids in the Mescalero Sands ecosystem in Lea and Eddy Counties, New Mexico (Fig. 1). Nine grids were located in areas classified as fragmented treatments, while another 18 grids were located in unfragmented areas as controls. Landscapes were classified as fragmented if there were 13 or more oil well pads in a section (259 ha), based on prior research that demonstrated a negative correlation between lizard densities and oil well density (Sias and Snell 1998, Leavitt 2012, Leavitt and Fitzgerald 2013). We selected this criterion for fragmentation because the value of 13 well pads per section has become implemented as a management threshold for conservation of *Sceloporus arenicolus* (Leavitt and Fitzgerald 2013). Well densities where the 18 unfragmented grids were located ranged from 0 to 12.95 well pads/section, and from 31.08 to 64.75 well pads/section in fragmented treatments. The network of roads connecting well pads creates a grid-like pattern of fragmentation (Fig. 1b). Fragmentation can cause habitat degradation as well as loss of connectivity. Across sites in the Mescalero Sands ecosystem, the quality and quantity of shinnery dune habitat were significantly correlated (Smolensky and Fitzgerald 2011). Previous work also showed that fragmented sites had fewer, smaller, and more dispersed dune blowouts than unfragmented sites (Leavitt and Fitzgerald 2013).

Pairwise distances among trapping grids ranged from 164 to 19,054 m. The closest fragmented grids were 164 m apart, and the closest unfragmented grids were 193 m apart. All other fragmented grids were >235 m apart, while all other unfragmented grids were >244 m apart. The nearest fragmented grid to an unfragmented grid was 806 m. All the trapping grids were located in shinnery oak dunes with blowouts that were known to be occupied by *S. arenicolus* (Laurencio and Fitzgerald 2010). By design, the 27 independent sites were similar in landscape characteristics. The shinnery oak dune habitat that is required by *S. arenicolus* was similar among all trapping grids regardless of their spatial distribution and distances among them. This design allowed for statistically independent capture data, while testing for effects of landscape fragmentation in replicated similar habitat patches.

Each trapping grid consisted of 30 pitfall traps spaced 20 m apart in a 5 × 6 array, covering a total area of 1.2 ha. Traps were 20-L buckets buried with the rim level to the substrate with a 0.165-m^2 (16 × 16 in) plywood cover. Sampling took place from May to August in 2009, from April to August in 2010, and from April to September in 2011–2013. Trapping grids were opened in four-day sessions. Each grid was opened for three sessions in 2009, and six sessions each in 2010 through 2013. This yielded a total of 9720 trap-days in 2009 and 19,440 trap-days each season during 2010–2013.

For each lizard captured, we recorded species, trap number, sex, snout-vent length (SVL), and assigned a unique permanent mark by toe-clipping. We classified individuals as adult male, adult female, or juvenile based on sex and reported either the minimum SVL at reproductive maturity for each species or the smallest recorded gravid female in our data set (whichever was smaller; Table 1).

To calculate capture rates (captures/trap-day), species captures were standardized by trap-days and stratified by treatment and year. Standardizing by capture rate controlled for differences in the number of trapping grids in unfragmented and fragmented sites. Although lizards were individually marked, we had very few captures on fragmented grids for some species (Table 1), and did not have enough recaptures on fragmented grids to use capture–mark–recapture methods to test for differences in population abundance in unfragmented and fragmented sites. Thus, we assumed that any difference in captures was dependent only on trapping effort, and used capture rates as a proxy for abundance. We tested for differences in mean capture rates by treatment and year for each species separately using two-way ANOVA. The arcsine transformation reduced heteroscedasticity and was appropriate given our question and the simple arrangement of yearly capture rates among treatments (Zar 1999). Significant interaction between treatment and year indicated whether species responded to annual environmental variability similarly in both treatments.

Monthly captures were pooled across years for each demographic, and then contingency tables were used to test the hypothesis of no difference in demographic structure of each species between fragmented and unfragmented treatments (Fitzgerald et al. 1999). We assumed that the frequencies of captures of each demographic on unfragmented sites represented the baseline demographic structure of the lizard populations in this ecosystem. Based on that assumption, we calculated the expected frequencies for captures of each demographic on fragmented grids, using the observed frequencies on unfragmented sites. Those expected frequencies were then tested against observed frequencies for the fragmented sites for the contingency tables. For *Uta stansburiana* (common side-blotched lizard) and *Aspidoscelis marmorata* (marbled whiptail), we subdivided the contingency tables and performed chi-square tests for differences in monthly proportions of each demographic on fragmented grids; the other species had such low frequencies (multiple cells with less than two expected captures) on fragmented grids each month that the assumptions of the chi-square test were violated and the tests were not performed (Fitzgerald et al. 1999, Zar 1999).

RESULTS

From 2009 to 2013, we had a total of 22,279 captures of eight species of lizards. *Uta stansburiana* was the most common (18,521 total captures), followed by *Aspidoscelis marmorata* (1520) and *Sceloporus arenicolus* (1421). Three species, *Holbrookia maculata* (common lesser earless lizard), *Aspidoscelis sexlineata* (six-lined racerunner), and *Sceloporus consobrinus* (prairie lizard), were captured in much lower frequencies. We excluded *Phrynosoma cornutum* (Texas horned lizard) and *Plestiodon obsoletus* (Great Plains skink) from statistical analyses because of very few captures of these species (Table 1).

We observed statistically significant differences in annual mean capture rates in unfragmented and fragmented treatments for *U. stansburiana* ($F_{1,125}$ = 9.77, $P < 0.01$), *S. arenicolus* ($F_{1,125}$ = 111.91, $P < 0.01$), and *H. maculata* ($F_{1,125}$ = 25.70, $P < 0.01$; Fig. 2). *Sceloporus arenicolus* and *H. maculata* were captured significantly more in unfragmented areas (unfragmented mean = 0.015, standard deviation [SD] = 0.020; fragmented mean = 0.001, SD = 0.001, unfragmented mean = 0.005, SD = 0.004; fragmented mean = 0.001, SD = 0.002, respectively). Captures of the specialist *S. arenicolus* were remarkably low in the fragmented areas, with only 31 of 1421 captures from five of the nine fragmented grids (range 1–11 individuals captured on each fragmented grid). We did not capture *S. arenicolus* on four of the nine fragmented grids in five years of trapping, despite deliberate placement of grids in close proximity to recent museum records of *S. arenicolus*. The generalist species, *U. stansburiana,* had higher capture rates in fragmented areas (fragmented mean = 0.24, SD = 0.04; unfragmented mean = 0.20, SD = 0.04). There were no differences in mean capture rates for *A. marmorata*, *A. sexlineata*, and *S. consobrinus* between treatments ($F_{1,\ 125}$ = 0.14, P = 0.71, $F_{1,\ 125}$ = 1.04, P = 0.31, $F_{1,\ 125}$ = 0.96, P = 0.33, respectively).

Capture rates varied significantly across years for *U. stansburiana* ($F_{4,125}$ = 36.47, $P < 0.01$), *S. arenicolus* ($F_{4,125}$ = 6.23, $P < 0.01$), *H. maculata* ($F_{4,125}$ = 5.89, $P < 0.01$), *A. sexlineata* ($F_{4,125}$ = 16.73, $P < 0.01$), and *S. consobrinus* ($F_{4,125}$ = 6.69, $P < 0.01$; Fig. 2). The highest capture rates for these five species occurred in 2011, while the lowest capture rates occurred in 2013 for *S. arenicolus*, *H. maculata*, *S. consobrinus*, and *A. sexlineata* and in 2009 for *U. stansburiana*. *Aspidoscelis marmorata* capture rates did not vary significantly across years ($F_{4,125}$ = 1.43, P = 0.23).

There was a significant statistical interaction between treatment (fragmented vs. unfragmented) and year for *U. stansburiana* ($F_{4,125}$ = 4.36, $P < 0.01$) and *A. sexlineata* ($F_{4,125}$ = 3.24, P = 0.01), revealing a pattern of inter-annual variation in capture rates among unfragmented and fragmented grids (Fig. 2). *Uta stansburiana* capture rates were higher on unfragmented grids than on

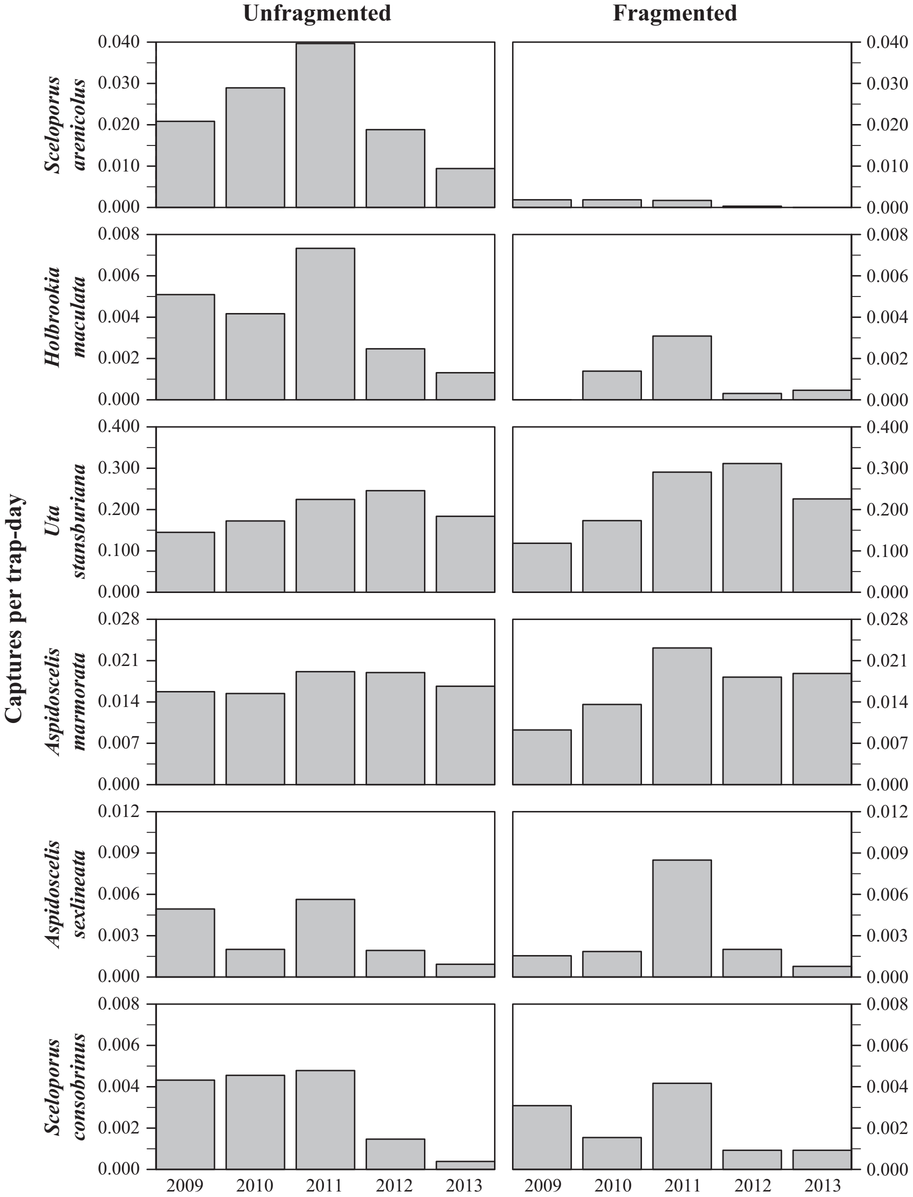

Fig. 2. Yearly capture rates (captures/trap-days) for each species on unfragmented and fragmented trapping grids. The scale of the *y*-axis is different for each species relative to their abundance.

fragmented grids in 2009 and higher on fragmented grids in 2010–2013. *Aspidoscelis sexlineata* capture rates were higher on unfragmented grids in 2009, 2012, and 2013 and higher on fragmented grids in 2010 and 2011. There was no interaction between year and treatment for the specialist *S. arenicolus*, nor for *H. maculata*, which were both significantly less numerous on fragmented grids ($F_{4,125} = 1.19$, $P = 0.32$, and $F_{4,125} = 1.38$, $P = 0.25$, respectively). There was also no significant interaction for *S. consobrinus* and *A. marmorata*, species that were not dependent on dune blowout landforms ($F_{4,125} = 0.84$, $P = 0.51$, and $F_{4,125} = 0.72$, $P = 0.58$, respectively).

Tests of contingency tables identified important differences in demographic proportions for some species (Fig. 3). Overall for *U. stansburiana*, significantly more juveniles and fewer adults

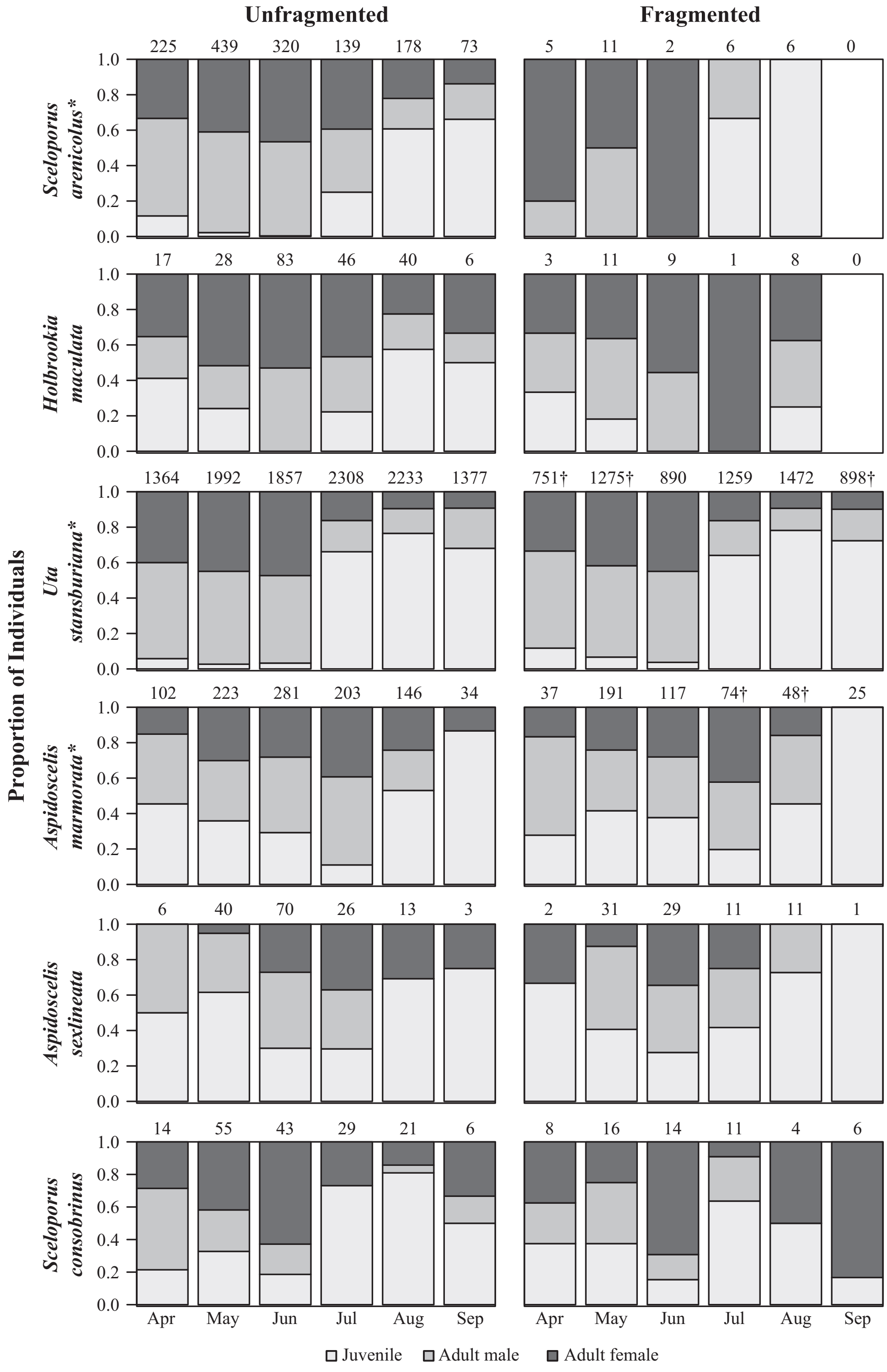

Fig. 3. Demographic structures of each species on unfragmented and fragmented trapping grids from April to September, corresponding to the active season for lizards. Bars represent the proportion of juveniles, adult males, and adult females captured each month. All five years of sampling are combined; sample sizes for each month

(*Fig. 3. Continued*)
are above the bars. The asterisk (*) next to the species name indicates that on the fragmented grids that population had significantly different overall demographic proportions than expected compared to the baseline unfragmented grids. The dagger (†) next to the monthly sample sizes for *Uta stansburiana* and *Aspidoscelis marmorata* indicates that on the fragmented grids that population had significantly different demographic proportions that month than expected compared to the baseline unfragmented grids.

were captured on fragmented grids ($\chi^2 = 43.91$, df = 2, $P < 0.0001$). Subdivided contingency tables revealed significantly fewer adult females and more juveniles were captured in April and May ($\chi^2 = 53.40$, df = 2, $P < 0.0001$, and $\chi^2 = 79.69$, df = 2, $P < 0.0001$, respectively). In September, we captured significantly larger proportions of juveniles and smaller proportions of adult males ($\chi^2 = 12.37$, df = 2, $P = 0.0021$). There were no significant differences in demographic proportions for this species in June, July, and August on fragmented sites ($P > 0.05$).

The overall contingency table for *A. marmorata* showed there were significantly more juveniles and fewer adults captured on fragmented grids ($\chi^2 = 7.18$, df = 2, $P = 0.0276$; Fig. 3). The subdivided contingency table showed July had significantly fewer adult males and more juveniles ($\chi^2 = 7.03$, df = 2, $P = 0.0297$) and in August there were significantly more adult males ($\chi^2 = 6.64$, df = 2, $P = 0.0362$). There were no statistically significant differences in demographic proportions in April, May, June, and September ($P > 0.05$).

The contingency table for *S. arenicolus* showed there were significantly fewer adult males and more juveniles on fragmented sites ($\chi^2 = 6.15$, df = 2, $P = 0.0462$; Fig. 3). There were no significant differences in demographics for *H. maculata*, *S. consobrinus*, and *A. sexlineata* on fragmented and unfragmented grids ($\chi^2 = 1.25$, df = 2, $P = 0.5353$; $\chi^2 = 0.79$, df = 2, $P = 0.6737$; and $\chi^2 = 0.34$, df = 2, $P = 0.8437$, respectively).

DISCUSSION

Our results strongly supported our predictions and those of Andrén et al. (1997) and Henle et al. (2004) that species with the strongest habitat preferences should show the greatest response to landscape fragmentation. While the habitat specialist was strongly affected by fragmentation, with negative consequences for both abundance and demographic structure, we also showed generalist species exhibited a range of responses to fragmentation. Some generalists responded negatively, in particular *Holbrookia maculata*, while others appeared to prosper, namely *Uta stansburiana* and *Aspidoscelis marmorata*. A similar pattern was described by Vega et al. (2000), who showed strong reduction in habitat area and population density in a habitat specialist lizard following construction of a road through coastal dunes and little response by the generalists.

The endemic and threatened habitat specialist, *Sceloporus arenicolus*, merits careful discussion, because it lends insight as to how specialist species are affected by isolation and habitat degradation following fragmentation. *Sceloporus arenicolus* disappeared from fragmented sites and its demographic structure was clearly disrupted compared to unfragmented sites, where we observed a typically structured sequence of demographic cohorts across months during all sample years. Capture rates of *S. arenicolus* were very low on fragmented sites compared to unfragmented sites, and consistently declined across the five years of trapping, until we captured no *S. arenicolus* on any fragmented grid in the final year of the project. Meanwhile, in the 18 unfragmented sites, capture rates of *S. arenicolus* increased from 2009 to 2011 and then decreased from 2011 to 2013, a pattern that was not statistically significant and was not unexpected for healthy fluctuating populations. There was at least one demographic life stage (adult males, adult females, or juveniles) missing each month overall, and in each of the five seasons of the study. The demographic structure was skewed toward females on fragmented grids, albeit with few captures. We did not capture adults later in the trapping periods, with males captured only during April through June, and females captured in April, May, and July. Young-of-year were not captured during April to May on fragmented sites, so it is reasonable to assume juveniles from the prior reproductive season on fragmented sites either emigrated or died. While low numbers on the fragmented grids could play some role in our ability to accurately assess demographic structure of *S. arenicolus*, we are confident, given the five years of intensive trapping, these results strongly suggest this specialist species has a relatively high susceptibility to local extinction following fragmentation. Taken together, we interpret these results to mean there were too few *S. arenicolus* on fragmented grids necessary to maintain the demographic structure of a self-sustaining population (Figs. 2, 3).

We also documented significantly fewer captures and disrupted demographic structure in *H. maculata* in the fragmented sites, indicating the changed landscape of the fragmented treatments had a detrimental effect on their populations. For example, on fragmented grids, only males were captured in July, where we expected to capture adult females and hatchlings as well. Also, we captured no *H. maculata* in September on fragmented grids despite having captured them on unfragmented grids during this month. In this ecosystem, *H. maculata* occurs along roads, basks on roads, and uses several vegetation types in sandy areas (Degenhardt et al. 1996). It remains unclear why this species should be susceptible to fragmentation. Leavitt and Fitzgerald (2013) examined the effects of changes in habitat structure on community structure in this system and also found *S. arenicolus* and *H. maculata* were sensitive to fragmentation and consistently were the first two species to disappear from fragmented sites. Leavitt (2012) showed the abundance of these two species was not associated with the same landscape features. *Sceloporus arenicolus* abundance was associated with steep slopes and relatively hard soils, while *H. maculata* abundance was positively associated with flat slopes and relatively hard soils, suggesting they were affected by fragmentation for different reasons. Even though the mechanisms of how these species responded to fragmentation may have differed, their populations showed similar patterns of demographic disruption.

The super-abundant (18,521 captures) short-lived generalist, *U. stansburiana,* had both higher capture rates and more variable demographics in fragmented areas. Capture rates were higher in unfragmented grids in some years, and higher in fragmented grids in others. Our interpretation of this significant interaction between year and treatment pattern was that stochastic responses to the environment among years in this abundant, short-lived generalist varied locally and were not strongly influenced by fragmentation. On the fragmented grids, there were more juveniles captured than expected in April, May, and September with all years combined.

Aspidoscelis marmorata capture rates were consistent across treatments and showed no effect of inter-annual variation. This species is longer-lived than the other generalist species, uses many habitats, and is also the most wide-ranging, active forager in this lizard community. Despite the generalist nature of *A. marmorata*, contingency tests revealed juveniles were captured at significantly higher frequencies than expected on fragmented grids in July and August. These differences later in the breeding season may have resulted from either more nesting in the fragmented areas or hatchlings having higher survival rates in fragmented areas.

Two generalists, *Sceloporus consobrinus* and *Aspidoscelis sexlineata,* both with relatively moderate life spans, moderate body sizes, and moderate to high fecundity, showed no significant differences in the demographic structure at unfragmented and fragmented sites. In addition, *S. consobrinus* showed no significant response in capture rates by year or treatment. The lack of response by this species is consistent with predictions; in this area, *S. consobrinus* tends to use only the extensive matrix of shinnery oak flats surrounding dune areas. *Aspidoscelis sexlineata* is a wide-ranging active forager that occurs within and outside dunes, similar in life history to its congener *A. marmorata.* Although for *A. sexlineata* we found a significant year-by-treatment interaction in capture rates (with higher capture rates on fragmented grids in 2010–2011), there were no clear differences between fragmented and unfragmented treatments. In the end, it is likely these two species, which use habitats surrounding the dunes, were less affected by fragmentation.

The variable response seen among these five generalist species in this lizard community can be at least partly explained by differences in habitat affinity, breeding phenology, and life history of the species (Fitzgerald et al. 1999). For example, the pattern in the demographic structure of *U. stansburiana* (a small, short-lived, highly fecund phrynosomatid) reflected its breeding phenology. There were high proportions of juveniles in July through September after emergence of abundant hatchlings, and very low proportions of juveniles the next spring, as the young grew quickly to adult size. In contrast, in *S. consobrinus* and *H. maculata* (phrynosomatids that are larger and longer-lived, with relatively high fecundity), we observed high proportions of juveniles during a prolonged breeding season, which we attributed to their relatively high fecundity and longer life spans. Finally, the active-foraging teiids *A. marmorata* and *A. sexlineata* are larger, longer-lived, and slower maturing than other species in this assemblage. Their life history and breeding phenology help explain why we observed juveniles of these species throughout the activity season, as young continue to grow to adult size throughout the following year. Two species whose life history strategies were considered intermediate, *S. consobrinus* and *A. sexlineata*, showed no changes in either capture rates or demographic structure in fragmented sites. Finally, the two species on the opposite end of the life history gradients among the species we studied, *U. stansburiana* (short-lived, habitat generalist) and *A. marmorata* (long-lived, large, wide-ranging forager), appeared to benefit at the fragmented sites.

Although the effects of habitat loss and fragmentation are tightly intertwined, studies that have tried to isolate the effects of both of these landscape changes have found habitat loss generally has a stronger effect on populations than does habitat fragmentation per se (Fahrig 1997). In our study system, the network-like development of well pads and their connecting roads both isolates populations and disrupts the underlying geomorphologic processes that maintain the shinnery oak dune blowout formations (Ryberg et al. 2015). In comparison with other drivers of fragmentation, such as deforestation, this road-network type of fragmentation directly converts a relatively smaller percentage of the landscape surface (e.g., Smolensky and Fitzgerald 2011), but drives processes that result in large-scale degradation of irreplaceable landforms on which the habitat specialist depends (Ryberg et al. 2015). Accordingly, we believe the disrupted demography and declines observed in *S. arenicolus* and *H. maculata* were driven by the effect of fragmentation on landscape integrity and habitat quality.

Fragmentation theory has previously treated the matrix of vegetation that lies between habitat patches as an inhospitable ocean (i.e., patch-isolation model), but more recently a viewpoint has emerged that there is a continuum of matrix and patch-level configurations (Didham et al. 2012). In the case of the Mescalero-Monahans Sandhills ecosystem, it has been demonstrated that the extensive network of roads and well pads degrades the dune blowout landform, changes landscape configuration, and isolates patches of shinnery oak dunes (Hibbitts et al. 2013, Leavitt and Fitzgerald 2013, Ryberg et al. 2015). As such, for species like *S. arenicolus* that have very specific habitat requirements, the concept of the inhospitable matrix may be more relevant. *Sceloporus arenicolus* occurs only in and around interconnected blowouts in relatively large expanses of shinnery oak dunes (Fitzgerald and Painter 2009, Laurencio and Fitzgerald 2010). Movements among disconnected patches have never been observed. This study gives insight into the mechanism of how fragmentation results in disruption of demographic structure in isolated populations of *S. arenicolus*. Previous studies of this habitat specialist showed that areas of poor dune quality were population sinks. Persistence in poor-quality habitat relied on diffusion dispersal of juveniles through interconnected dune blowouts to offset the imbalance between natality and mortality in sink neighborhoods (Ryberg et al. 2013). Landscape condition, which is negatively affected by fragmentation, and population impacts go hand-in-hand. There are tight linkages between condition of shinnery dune blowouts and vital rates of *S. arenicolus*; elasticities in adult survival, juvenile survival, and fertility of *S. arenicolus* were strongly and significantly associated with fractal dimension of interconnected dune blowouts (Ryberg et al. 2015). Moreover, fragmentation of the shinnery dune landscape leads to disassembly of the entire lizard community, largely because of the loss of the habitat specialist (Leavitt and Fitzgerald 2013). The incredibly low capture rates we observed in isolated fragmented sites compared to unfragmented sites over five years reflect the disruption of demographic structure in populations that have become isolated with no rescue effect from immigration. The end result for small, isolated populations of *S. arenicolus* is localized extinctions.

This study also lends insight into the linkages between disturbance of landscape features and the consequences for populations. In short, fragmentation disrupts both the landscape features and the lizard populations. This is the first study to link empirically derived patterns of demographic structure to landscape fragmentation in a lizard community that contains specialist and generalist species. We were able to make direct comparisons of population structure at unfragmented and fragmented sites, and we demonstrated deterioration of demographic structure could be a sign of impending extirpation of species affected by fragmentation. As such, this study enhances previous work on the effects of fragmentation on this lizard community, and demonstrates how populations that are sensitive to fragmentation may begin to deteriorate through the loss of specific components (adult males, adult females, or juveniles) of their population structure. Future work could build on the relationships we have drawn between life history traits and habitat affinity of species, and how these may serve as predictors of how species may respond to fragmentation. This research enhances the picture of how fragmentation may cause demographic disruption and decline of some species while having little effect on others.

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