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ARTICLE

Fragmentation alters home range and movements of the Dunes Sagebrush Lizard (*Sceloporus arenicolus*)

Megan E. Young, Wade A. Ryberg, Lee A. Fitzgerald, and Toby J. Hibbitts

Abstract: Habitat fragmentation is a major driver of biodiversity loss and among reptiles has been attributed as a cause of species decline. The negative effect of habitat fragmentation has also been shown to be worse for species that are habitat specialists. The Dunes Sagebrush Lizard (*Sceloporus arenicolus* Degenhardt and Jones, 1972) is a species that specializes on the shinnery oak (*Quercus havardii* Rydb.) sand-dune landform of the Mescalero–Monahans Sandhills ecosystem in western Texas and eastern New Mexico, USA. This landform has been fragmented by roads and well pads used for the extraction of oil and gas resources. The effects of fragmentation on the home range and movements of this species can lead to the effective isolation of populations and increased risk of localized extirpations. We showed that home-range size was larger in an unfragmented area and that the mean distance of movements was greater. We also observed that roads in the fragmented areas restricted movements of *S. arenicolus*. We concluded that roads can be barriers to movements even though only narrow strips of habitat are altered.

Key words: habitat loss, species decline, Mescalero–Monahans Sandhills, Phrynosomatidae, oil and gas development, road ecology, *Sceloporus arenicolus*, Dunes Sagebrush Lizard.

Résumé : La fragmentation d'habitats est un important facteur de perte de biodiversité et, chez les reptiles, a été interprétée comme étant une cause du déclin d'espèces. Il a également été démontré que l'effet négatif de la fragmentation d'habitats est plus important pour les espèces spécialistes en ce qui concerne l'habitat. Le lézard des armoises du désert (*Sceloporus arenicolus* Degenhardt et Jones, 1972) est un spécialiste du relief de dunes de sable à chênes de Harvard (*Quercus havardii* Rydb.) de l'écosystème des collines de sable de Mescalero–Monahans de l'ouest du Texas et de l'est du Nouveau-Mexique (États-Unis). Ce relief a été fragmenté par des routes et plateformes d'exploitation utilisées pour l'extraction de ressources pétrolières et gazières. Les effets de la fragmentation sur le domaine vital et les déplacements de cette espèce peuvent mener à l'isolement effectif de populations et un risque accru de disparition locale. Nous montrons que la taille des domaines vitaux est plus grande dans une zone non fragmentée et que la distance moyenne des déplacements y est plus grande. Nous observons également que les routes dans les zones fragmentées restreignent les déplacements de *S. arenicolus*. Nous en concluons que les routes peuvent constituer des barrières aux déplacements même si seules d'étroites bandes d'habitat sont modifiées. [Traduit par la Rédaction]

Mots-clés : perte d'habitat, déclin des espèces, collines de sable de Mescalero–Monahans, phrynosomatidés, mise en valeur des ressources pétrolières et gazières, écologie des routes, *Sceloporus arenicolus*, lézard des armoises du désert.

Introduction

Habitat fragmentation is a process through which a landscape is broken into a number of smaller, more isolated patches, separated by unsuitable habitat and is always associated with habitat loss (Fahrig 2003). Fragmentation may also alter factors such as solar radiation, wind, and hydrologic regimes, perpetually altering the landscape (Saunders et al. 1991). Fragmentation and loss of habitat are different phenomena, but together are a major driver of biodiversity loss (McGarigal and Cushman 2002; Torres et al. 2016). Habitat modification, including fragmentation, loss, and small-scale changes in microhabitat, has also contributed to species declines (Gibbons et al. 2000; Gardner et al. 2007; Whitfield et al. 2007; Leavitt and Fitzgerald 2013; Walkup et al. 2017). Specialist species are acutely susceptible to habitat alteration due in part to their dependence on one, or few, habitat types (Devictor et al. 2008; Hibbitts et al. 2009), and their adaptation to a relatively stable environment (Futuyma and Moreno 1988).

Surprisingly, few studies have been conducted on how habitat fragmentation affects the movements and home range of individuals in vertebrate species (Hinam and St. Clair 2008; Öckinger et al. 2010). Patterns of effects of habitat fragmentation are not clear, in some cases a single species may respond differently to fragmentation (Ewers and Didham 2006). What seems to be important to home-range size is the scale of fragmentation; for example, the distance between suitable habitat patches and sizes of those patches. Species may use multiple patches in their home range if they are close enough, which will increase home-range size compared with continuous habitat. If the habitat patches are small and separated by large areas of unsuitable habitat, then the predation risks or energetic requirements associated with long

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movements may force individuals to maintain smaller home ranges in these isolated patches compared with continuous habitat (Grubb and Doherty 1999). Little evidence exists for the effects of habitat fragmentation on movement and home-range size of specialists, but theory suggests that habitat specialists with their specific habitat requirements would be more susceptible to negative influences of habitat fragmentation (Debinski and Holt 2000; Hibbitts et al. 2013).

Within the Mescalero–Monahans Sandhills ecosystem of western Texas and eastern New Mexico, USA, fragmentation from oil and gas development results in a landscape with fewer, smaller, and more isolated habitat patches (Leavitt and Fitzgerald 2013). In Texas, density of well pads may reach 55 or more well pads per section (1 square mile = 259 ha; Hibbitts et al. 2013), connected by caliche roads (i.e., roads made of calcium carbonate). With a mean well pad size of 13 620 m^2, approximately 30% of native land cover may potentially be converted to caliche well pads in the most densely altered areas. Although habitat fragmentation is a landscape-level process, it can affect processes at the community and population levels, and at the level of individuals' home-range size and movement patterns (Smolensky and Fitzgerald 2011; Leavitt and Fitzgerald 2013; Ryberg et al. 2013; Hibbitts et al. 2017; Walkup et al. 2017). Burt (1943) described home range as the area used by an animal for its normal daily activities, such as locating food, mates, or shelter. In lizards, home-range size can be influenced by myriad factors, including availability of food or mates, habitat quality, body size, sex, reproductive status, or territoriality (Rose 1982; Ruby and Dunham 1987; Hews 1993; Perry and Garland 2002; Haenel et al. 2003; Manteuffel and Eiblmaier 2008). Furthermore, the size of an individual's home range is directly related to the movement necessary to acquire food, mates, or habitat of sufficient quality and quantity. Elucidating patterns of movement and home range within a species can therefore provide insights into its ecological niche. In the case of threatened or imperiled species like the Dunes Sagebrush Lizard (*Sceloporus arenicolus* Degenhardt and Jones, 1972), this knowledge is crucial for making informed conservation decisions.

Sceloporus arenicolus is a small phrynosomatid lizard endemic to the Mescalero–Monahans Sandhills ecosystem (Degenhardt et al. 1996). The species is a psammophilic habitat specialist restricted to shinnery oak (*Quercus havardii* Rydb.) sand-dune landforms, which consist of parabolic dunes and depressions called blowouts that are created from an interaction between wind, sand, and the dune-stabilizing shinnery oaks (Fitzgerald and Painter 2009; Laurencio and Fitzgerald 2010; Ryberg et al. 2015). Across these landforms, the spatial configuration of blowouts constrains or facilitates movements of *S. arenicolus*. Within an area, groups of interacting individuals occur in neighborhoods, whose size is a function of population density and movements (Ryberg et al. 2013). Larger neighborhoods exhibit higher recruitment and population diffusion rates, acting as sources for smaller neighborhood sinks with negligible recruitment. Thus, population persistence in this species depends on diffusion dispersal throughout interconnected habitat patches (Ryberg et al. 2013; Walkup et al. 2017). Dispersal among isolated habitat patches is effectively zero over both short and long time frames (Chan et al. 2009; Leavitt 2012).

We undertook the present study to evaluate the prediction, based on previous work, that fragmentation of shinnery oak sand dunes by well pads interconnected with roads would restrict movements of *S. arenicolus* with concordant effects on home-range size. Our objectives for this study were threefold. First, we analyzed variation in movements and home-range size between male and female *S. arenicolus*. Second, we analyzed variation in movement and home range between lizards in fragmented and unfragmented areas. Third, we evaluated the specific role of caliche roads as barriers to localized movements.

Materials and methods

Study site

The study area was located near Andrews, Texas (975–1010 m elevation). We chose sites known from previous surveys to contain *S. arenicolus* (Hibbitts et al. 2013). We selected three independent sites that varied in the degree of landscape fragmentation and their proximity to, or distance from, caliche roads. One site was approximately 7 ha in area, bisected by a caliche road, and abutted three caliche well pads. It was located in a section with 61 well pads, among the highest density of roads and well pads in the area. We note that this degree of fragmentation was not replicated in our study design. It has been well studied that populations of *S. arenicolus* are depressed or locally extinct in fragmented landscapes, and it is difficult to find extant populations to study in fragmented habitats (Smolensky and Fitzgerald 2011; Leavitt and Fitzgerald 2013; Ryberg et al. 2013; Hibbitts et al. 2017; Walkup et al. 2017). The site in the fragmented area was located in the same dune system and was within 7.5 km of two unfragmented sites more distant from roads. Although we recognized the lack of a fully replicated study design could limit our conclusions, our results do allow meaningful conclusions to be made as to how landscape characteristics, especially roads and well pads, affect behaviors and movements of individuals. A second site was approximately 4.5 ha in area and 100 m from the nearest road, which was a small dirt two-track road used for ranch vehicles. The third site was approximately 1 ha, within a larger chain of dune blowouts. The nearest road was another small two-track road, located 50 m away. The latter two sites were located in a square mile section with only six well pads, which is considered a relatively low degree of fragmentation based on other research on the species (Leavitt and Fitzgerald 2013).

Radiotelemetry

We captured 36 lizards by noose or pitfall trap to use as subjects for radio-tracking. Upon capture, we marked all lizards with a unique toe clip and affixed a 0.3 g radio transmitter (model R614; Advanced Telemetry Systems, Inc., Isanti, Minnesota, USA) directly to the middle of the back of each lizard using cyanoacrylate glue, with the whip antenna extending posteriorly (Sabo 2003). We relocated lizards using a scanning receiver (model R410; Advanced Telemetry Systems, Inc.) and a three-element Yagi antenna. Alternative methods to toe clipping for identifying individual lizards were investigated. The only reasonable alternative method that would not cause distress would be photo identification, but this species is mostly patternless making the identification of individuals using this method difficult. Toe clipping is a method of permanent marking for lizards that has been systematically reviewed (Perry et al. 2011) and approved by the Society for the Study of Amphibians and Reptiles. We had approval from Texas A&M University's Institutional Animal Care and Use Committee (AUP 2012-105).

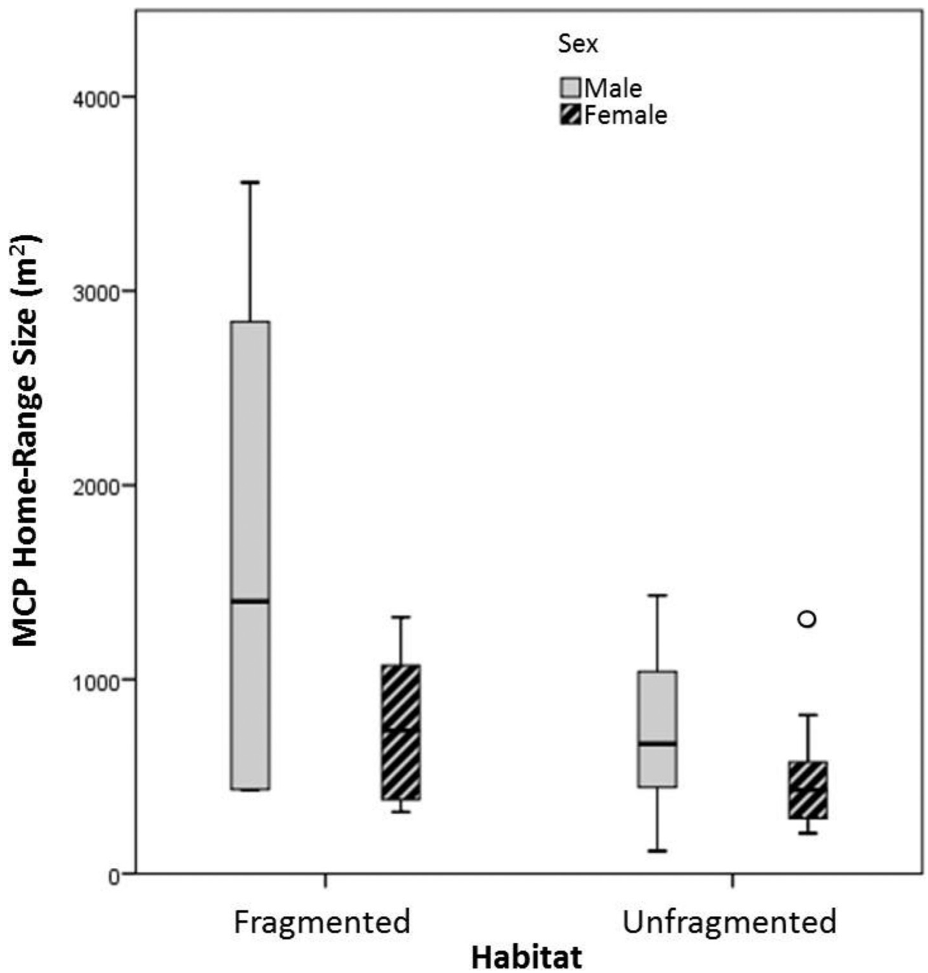
During June–August 2012 and May–August 2013, we tracked lizards three times per day for 30 days, or until transmitters were lost due to shedding or predation. The mean number of locations per day did not differ by sex (male: $n = 20$, mean = 2.69, SD = 0.28; female: $n = 16$, mean = 2.69, SD = 0.30) or by fragmentation treatment (unfragmented: $n = 24$, mean = 2.66, SD = 0.29; fragmented: $n = 12$, mean = 2.75, SD = 0.28) We located lizards during their prime activity period (0900–1100), during the hottest part of the day (1400–1600), and in the evenings (1800–2000). During each relocation, we attempted to visually locate the lizard to confirm its position and to record its behavior. We recorded locations in the field using a handheld GPS unit (Garmin Model 60csx) with an accuracy of ±3 m.

Table 1. Measures of mean (±SD) home-range size and mean (±SD) distance moved per day for radio-tracked Dunes Sagebrush Lizards (*Sceloporus arenicolus*) in unfragmented and fragmented sites, as well as for males and females.

	MCP (m^2)	95% KDE	50% KDE	Daily distance moved (m/day)
Unfragmented (*n* = 24)	633.6±364.9	1154.0±646.2	253.0±159.3	21.6±6.3
Fragmented (*n* = 12)	1219.6±1044.4	2061.5±2046.7	393.0±402.5	26.7±6.7
Females (*n* = 16)	614.8±362.6	1009.9±580.1	176.0±93.2	20.8±6.1
Males (*n* = 20)	1000.3±874.1	1813.8±1646.1	398.5±320.5	25.3±6.8

Note: MCP, minimum convex polygons; KDE, fixed kernel density estimators.

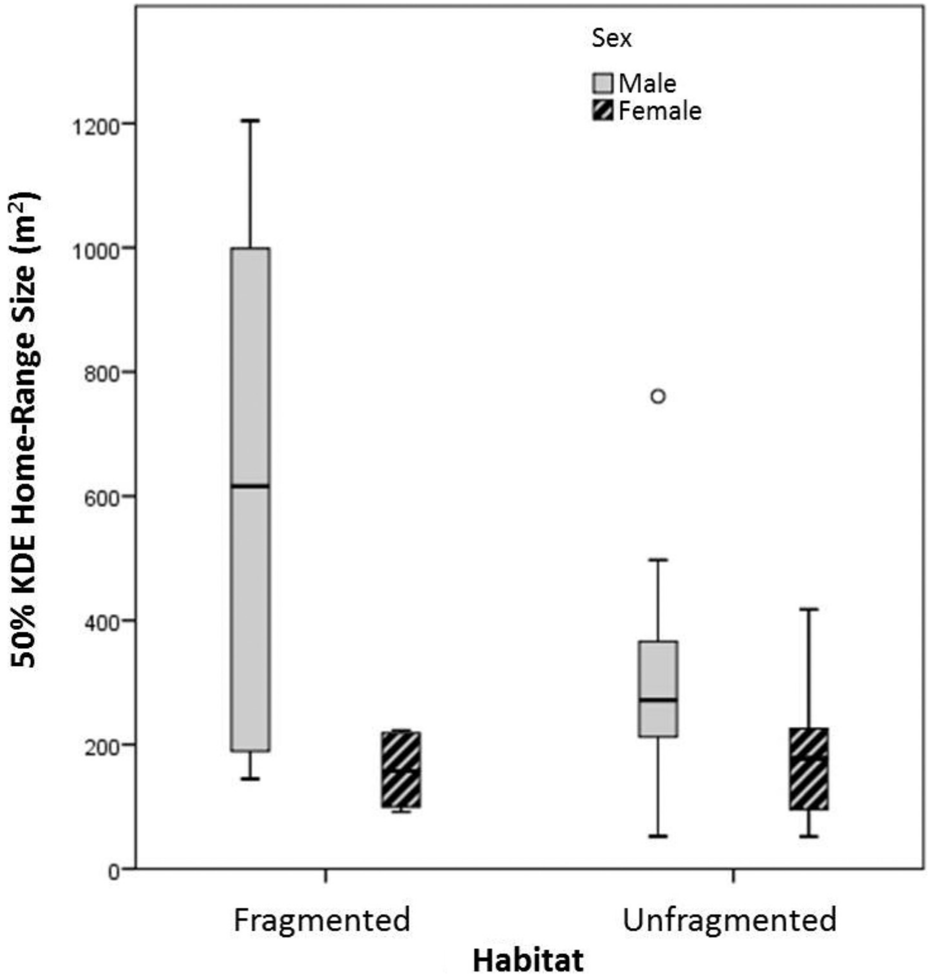
Fig. 1. Male and female Dunes Sagebrush Lizard (*Sceloporus arenicolus*) home-range size (minimum convex polygons (MCP)) in fragmented and unfragmented habitats.



Data analyses

We used ArcInfo version 10.1 (ESRI, Inc., Redlands, California, USA) and the adehabitatHR package in R version 2.15.1 to calculate the following home-range estimators and movement parameters: 100% minimum convex polygons (MCP), 50% and 95% fixed kernel density estimators (KDE), and mean distance moved per day (i.e., average of total path length per day). Because home-range estimators are sensitive to the number of relocations, we only included lizards with at least 25 locations in the analyses (Schoener 1981; Stone and Baird 2002). We found no relationship between number of sightings and home-range estimates by sex (male — MCP: $y = 9.05x + 443.02$, $r^2 = 0.04$; 95% KDE: $y = -10.34x + 2198.4$, $r^2 = 0.02$; 50% KDE: $y = -2.56x + 476.48$, $r^2 = 0.03$; female — MCP: $y = 6.08x + 209.39$, $r^2 = 0.12$; 95% KDE: $y = -23.05x + 2734.8$, $r^2 = 0.19$; 50% KDE: $y = -5.05x + 582.48$, $r^2 = 0.17$) or by fragmentation treatment (unfragmented — MCP: $y = 13.10x + 386.63$, $r^2 = 0.04$; 95% KDE: $y = -4.42x + 1295.6$, $r^2 = 0.04$; 50% KDE: $y = -2.83x + 407.43$, $r^2 = 0.26$; fragmented — MCP: $y = 5.55x + 304.57$, $r^2 = 0.09$; 95% KDE: $y = -16.51x + 2674.6$, $r^2 = 0.04$; 50% KDE: $y = -3.36x + 537.91$, $r^2 = 0.04$), indicating that the minimum number of sightings per individual was sufficient for home-range estimation and comparison. The least-squares cross validation (LSCV) method of selecting the smoothing parameter, recommended by Seaman et al. (1999), failed to minimize the mean integrated squared error (MISE) for most lizards; therefore, we used the reference bandwidth instead. Kernel methods are known to perform poorly in home ranges that contain distinct boundaries (e.g., cliffs, rivers, ponds) (Getz and Wilmers 2004; Getz et al. 2007). Our study site contained no physical barriers to lizard movements. Sampling lizards three times a day results in spatial autocorrelation; however, attempting to remove autocorrelation through subsampling may reduce the biological relevance of the home-range estimates, as well as remove

Fig. 2. Male and female Dunes Sagebrush Lizard (*Sceloporus arenicolus*) core-area home ranges based on 50% fixed kernel density estimators (KDE) estimation in fragmented and unfragmented habitats.



information about movement patterns (De Solla et al. 1999; Börger et al. 2006; Fieberg 2007; Kuhn et al. 2014; Melville et al. 2015). Therefore, we decided to include all of our data in our analysis of home range.

We conducted two-way ANOVA tests in R version 2.15.1 to assess the effects of sex and habitat type (fragmented versus unfragmented) on each of the parameters listed above. Home-range variables were not normally distributed, so they were log transformed before conducting the ANOVA. Data were homoscedastic according to Box's M test for equal variances among groups. To determine the effect of caliche roads and well pads on movements, we used a χ^2 test with Yates' correction. We used satellite imagery (DigitalGlobe 2015) to calculate the amount of caliche versus noncaliche soil surface at our fragmented site and compared expected versus observed movements that crossed caliche or ended on caliche.

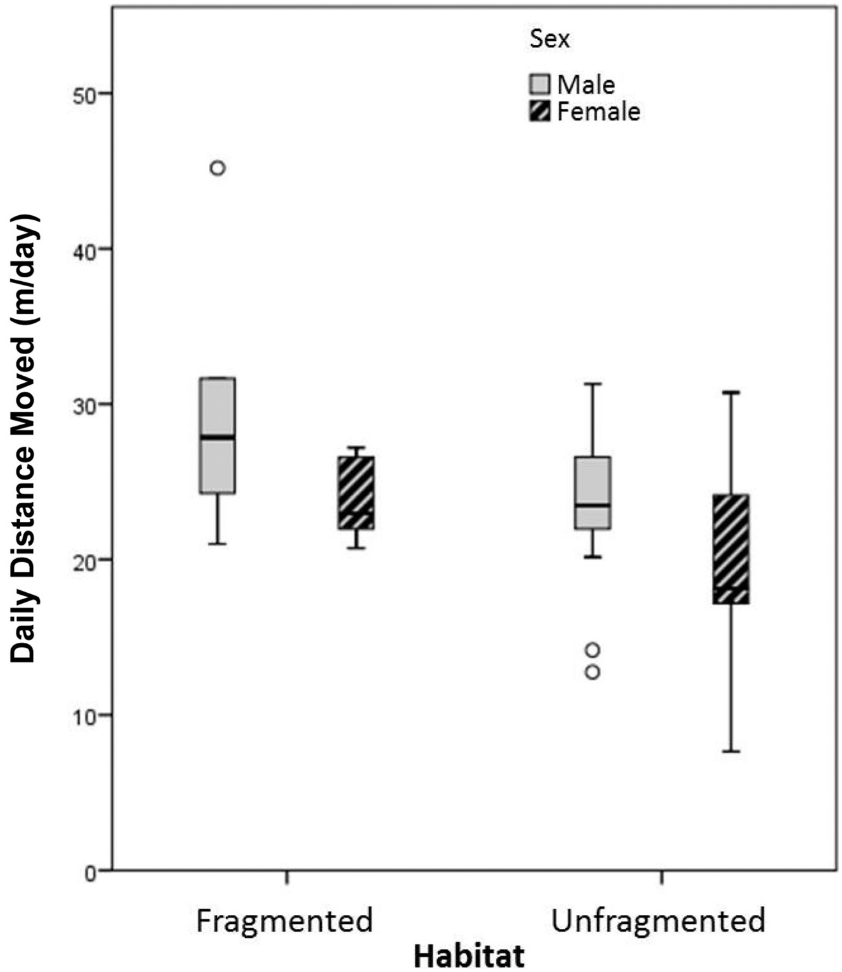
Results

We tracked lizards for a mean of 28.0 days (range: 10–36 days) and collected a mean of 60.2 relocations per lizard (range: 26–90 relocations per lizard) (Supplementary Table S1).[1] During the study, 4 of the 36 lizards were lost to snake predation (one Glossy Snake (*Arizona elegans* Kennicott in Baird, 1859), three Coachwhip (*Coluber* (*Masticophis*) *flagellum* (Shaw, 1802))) and 10 others shed their radios prior to the end of the 30 day tracking period. Throughout the duration of the study, we observed that one lizard crossed a caliche road in a spot that was covered with wind-blown sand.

When using MCP, 95% KDE, or 50% KDE, males had higher mean home-range size than females and moved greater distances per day (Table 1). Habitat significantly affected MCP size (fragmented versus unfragmented) (Fig. 1; $F_{[1,32]}$ = 5.23, p = 0.028), with individuals in fragmented habitat exhibiting larger home ranges than those in unfragmented habitat. Although male MCP sizes tended to be larger than those of females, the difference was not significant ($F_{[1,32]}$ = 2.05, p = 0.162), nor was there any interaction between habitat and sex ($F_{[1,32]}$ = 0.52, p = 0.477). We did not observe a significant effect of sex ($F_{[1,32]}$ = 3.89, p = 0.057), habitat ($F_{[1,32]}$ = 2.86, p = 0.100), or an interaction effect ($F_{[1,32]}$ = 1.70, p = 0.201) on 95% KDE size. Males had significantly larger 50% KDE home ranges than females ($F_{[1,32]}$ = 9.07, p = 0.005), but no effect of habitat ($F_{[1,32]}$ = 1.43, p = 0.241) or interaction effect ($F_{[1,32]}$ = 1.70, p = 0.201) was observed (Fig. 2). Males moved significantly greater distances per day than females ($F_{[1,32]}$ = 4.90, p = 0.030), and lizards in fragmented areas moved significantly greater distances per day than those in unfragmented areas ($F_{[1,32]}$ = 6.34, p = 0.017), but no interaction was observed between habitat type and sex ($F_{[1,32]}$ = 0.11, p = 0.746) (Fig. 3).

[1]Supplementary Table S1 is available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2017-0048.

Fig. 3. Male and female Dunes Sagebrush Lizard (*Sceloporus arenicolus*) distance moved per day in fragmented and unfragmented habitats.



We observed three movements by the same *S. arenicolus* (individual #32) at the same location on one caliche road (Fig. 4). The road at the crossing location had a thin (approximately 5 cm) covering of wind-blown sand over the caliche. This crossing rate, 3 out of the total 799 movements made by all lizards in the fragmented site, was significantly less than the expected crossing rate based on the total percentage of available habitat that had a caliche substrate ($\chi^2 = 46.534$, $p < 0.001$).

Discussion

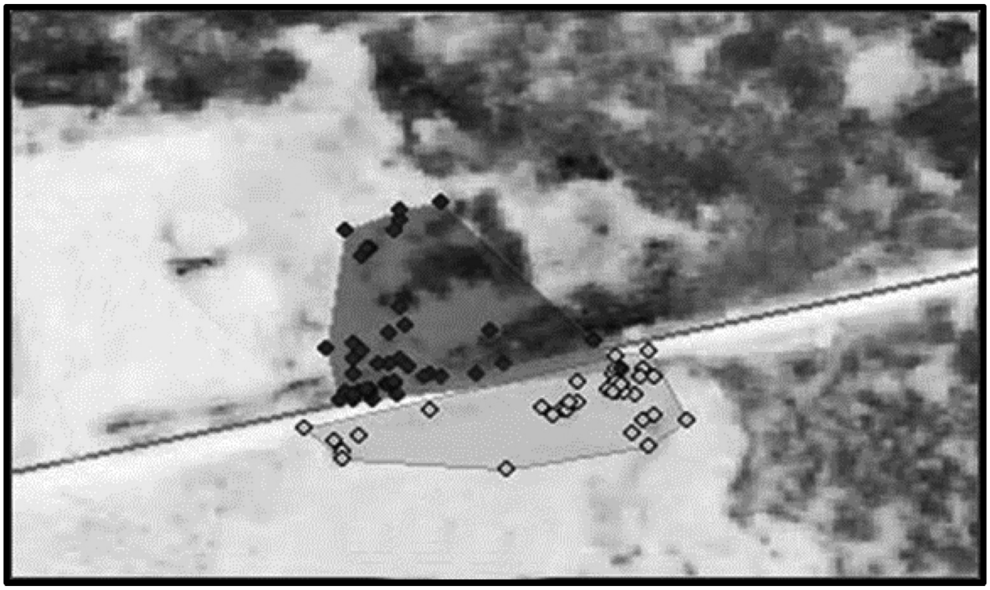
Our results illustrated that home-range size and length of daily movements of *S. arenicolus* were altered at a site that was fragmented from oil and gas development. Specifically, lizards at the fragmented site exhibited larger MCP home ranges and moved greater distances on a daily basis. Additionally, we found differences between the sexes, with males having significantly larger core home ranges and moving significantly greater distances than females.

At the 50% KDE level, which is representative of an individual's core area of use (White and Garrott 1990), males had significantly larger home ranges than females across all sites. Among many lizard species, males have larger home ranges than females (Perry and Garland 2002). This is particularly true among species in the genus *Sceloporus* Wiegmann, 1828 (Ferner 1974; Smith 1985; Abell 1999); Abell (1999) reported home ranges of male Striped Plateau Lizards (*Sceloporus virgatus* H.M. Smith, 1938) to be four times larger than those of females. This has been attributed to female home ranges being primarily determined by energetic requirements, whereas males must also gain access to mates (Hews 1993; Perry and Garland 2002). Abell (1997) found that a male *S. virgatus* in close spatial proximity to a female was more likely to sire most, or all, of the female's clutch; therefore, a larger male home range may correlate with greater reproductive success. Although we did not examine the specific reasons for larger male home ranges in *S. arenicolus*, it is clear that this observation conforms to a larger pattern among species of *Sceloporus.*

Movements of *S. arenicolus* also varied between sexes, with males moving significantly greater distances per day than females. This result might also be related to reproductive activity. All of our observations took place during the breeding season, and we assumed that most, if not all, of the females were gravid at some point during the study. The added mass of eggs can hinder speed and mobility (Shine 2003) and affect behavior. Female *S. arenicolus* have been observed to bask more frequently as they approached time of nesting (M.T. Hill, personal communication). In contrast, male lizards may move more to increase their likelihood of encountering a mate or to defend territory.

Observations collected at the fragmented site showed the MCP of home range size was larger, and movements were greater there than in the other sites. The apparent, and striking, difference between the sites was the presence of the road and well pads, which impeded movements of individual lizards. We did not test for specific mechanisms that may explain greater home-range size in this context; however, the literature points to the role of density-dependent interactions and resource availability. In many species, home-range size is negatively correlated with lizard den-

Fig. 4. Home range (minimum convex polygons (MCP)) of Dunes Sagebrush Lizard (*Sceloporus arenicolus*) individuals #32 (solid diamonds) and #37 (open diamonds). Individual #32 was the only *S. arenicolus* to cross a caliche road (dark line). This crossing was made at a sand-covered portion of the caliche road. Individual #37 moved directly parallel to the road, but never crossed it. No individuals were observed on caliche surfaces.



sity (Whiting 1999; Haenel et al. 2003). However, no single factor adequately explained variation in home-range size in those studies. Similarly, Manteuffel and Eiblmaier (2008) experimentally manipulated density in *S. virgatus* populations and found smaller home ranges within the high-density group. As *S. arenicolus* abundance has been shown to be lower in fragmented habitat than in unfragmented habitat (Leavitt and Fitzgerald 2013; Walkup et al. 2017), it is likely that larger *S. arenicolus* home ranges at our fragmented site were related to the low lizard densities observed there.

An alternative, nonexclusive, hypothesis to explain larger home-range size in the fragmented area is that quality and quantity of resources may be diminished there (food, refugia, cover, thermally favorable sites), forcing lizards to range over larger areas and move greater distances to access resources. Hews (1993) observed female San Pedro Side-blotched Lizards (*Uta palmeri* Stejneger, 1890) shifting their home ranges in response to supplemented food resources, suggesting that individual space use can be directly linked to resource availability. In this study, we believe that *S. arenicolus* may have had larger MCP home ranges in fragmented habitat due to habitat alteration caused by fragmentation, which essentially reduces the availability of preferred microhabitats (Hibbitts et al. 2013). This may have forced individuals to traverse nonpreferred microhabitats to reach preferred microhabitats (e.g., steep slopes: Hibbitts et al. 2013; coarse sand-grain size: Ryberg and Fitzgerald 2015; high soil moisture: Ryberg et al. 2012). In contrast, results from the core-area analysis (50% KDE) were not significantly different between fragmented and unfragmented areas, suggesting that adequate resources were available in the habitat patches being used by the lizards. This apparent contradiction could be explained by virtue of the fact that the MCP derives its shape from the outermost locations and can often include areas not actually used by an individual (Worton 1987). The core-area (50% KDE) estimates likely excluded outermost locations where individuals crossed nonpreferred microhabitats without spending substantial time in those areas. This hypothesis is supported by the fact that lizards at our fragmented site moved greater distances than in the other two unfragmented areas.

As mentioned, we only verified through telemetry one individual *S. arenicolus* crossing a caliche road during this study, which included 799 relocations of 14 lizards in the fragmented site. To the best of our knowledge, this individual only crossed the road in a place where sand had covered the caliche road surface. Moreover, at this site the shinnery oak sand-dune habitat, which is required by *S. arenicolus*, was touching the road on both sides. This observation is consistent with the results of an experimental study of road-crossing behavior in *S. arenicolus*, which demonstrated that individuals avoid the caliche road surface, even when the road is small, flat, and immediately adjacent to dune blowouts in occupied habitat (Hibbitts et al. 2017). This observation is worth emphasizing because in many areas of oil and gas extraction within the Mescalero–Monahans Sandhills ecosystem, caliche roads are constructed in a grid-like network. This network of roads is the major source of fragmentation of the habitat used by *S. arenicolus* (Hibbitts et al. 2017), and it also disrupts the self-organized shinnery oak sand-dune blowout landforms (Ryberg et al. 2015). In general, roads are frequently cited as being barriers to dispersal that can have a significant effect on populations and may increase the chances of localized extinctions through the effective isolation of populations within smaller and lower quality habitat patches (e.g., Torres et al. 2016). In our study, it was clear that road-crossing movements did not occur regularly and would likely not be sufficient to sustain the population size (Leavitt and Fitzgerald 2013), demographic structure (Walkup et al. 2017), and resulting source–sink diffusion–dispersal dynamics (Ryberg et al. 2013) necessary to prevent localized extinction of *S. arenicolus* in areas fragmented by roads.

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References

Abell, A.J. 1997. Estimating paternity with spatial behaviour and DNA fingerprinting in the striped plateau lizard, *Sceloporus virgatus* (Phrynosomatidae). Behav. Ecol. Sociobiol. **41**(4): 217–226. doi:10.1007/s002650050382.

Abell, A.J. 1999. Male–female spacing patterns in the lizard, *Sceloporus virgatus*. Amphib.-Reptilia, **20**(2): 185–194. doi:10.1163/156853899X00196.

Börger, L., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A., Lovari, S., and Coulson, T. 2006. Effects of sampling regime on the mean and variance of home range size estimates. J. Anim. Ecol. **75**(6): 1393–1405. doi:10.1111/j.1365-2656.2006.01164.x. PMID:17032372.

Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. J. Mammal. **24**(3): 346–352. doi:10.2307/1374834.

Chan, L.M., Fitzgerald, L.A., and Zamudio, K.R. 2009. The scale of genetic differentiation in the dunes sagebrush lizard (*Sceloporus arenicolus*), an endemic habitat specialist. Conserv. Genet. **10**(1): 131–142. doi:10.1007/s10592-008-9537-x.

Debinski, D.M., and Holt, R.D. 2000. A survey and overview of habitat fragmentation experiments. Conserv. Biol. **14**(2): 342–355. doi:10.1046/j.1523-1739.2000.98081.x.

Degenhardt, W.G., and Jones, K.L. 1972. A new sagebrush lizard, *Sceloporus graciosus* from New Mexico and Texas. Herpetologica, **28**(3): 212–217.

Degenhardt, W.G., Painter, C.W., and Price, A.H. 1996. Amphibians and reptiles of New Mexico. University of New Mexico Press, Albuquerque.

De Solla, S.R., Bonduriansky, R., and Brooks, R.J. 1999. Eliminating autocorrelation reduces biological relevance of home range estimates. J. Anim. Ecol. **68**(2): 221–234. doi:10.1046/j.1365-2656.1999.00279.x.

Devictor, V., Julliard, R., and Jiguet, F. 2008. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. Oikos, **117**(4): 507–514. doi:10.1111/j.0030-1299.2008.16215.x.

Ewers, R.M., and Didham, R.K. 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biol. Rev. **81**(1): 117–142. PMID:16318651.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Evol. Syst. Camb. Philos. Soc. **34**(1): 487–515. doi:10.1146/annurev.ecolsys.34.011802.132419.

Ferner, J.W. 1974. Home-range size and overlap in *Sceloporus undulatus erythrocheilus* (Reptilia: Iguanidae). Copeia, **1974**(2): 332–337. doi:10.2307/1442527.

Fieberg, J. 2007. Kernel density estimators of home range: smoothing and the autocorrelation red herring. Ecology, **88**(4): 1059–1066. doi:10.1890/06-0930. PMID:17536721.

Fitzgerald, L.A., and Painter, C.W. 2009. Dunes sagebrush lizard (*Sceloporus arenicolus*). *In* Lizards of the American Southwest: a photographic field guide. *Edited by* L.L.C. Jones and R.E. Lovich. Rio Nuevo Publishers, Tucson, Ariz. pp. 198–201.

Futuyma, D.J., and Moreno, G. 1988. The evolution of ecological specialization. Annu. Rev. Ecol. Evol. Syst. **19**(1): 207–233. doi:10.1146/annurev.es.19.110188.001231.

Gardner, T.A., Barlow, J., and Peres, C.A. 2007. Paradox, presumption and pitfalls in conservation biology: the importance of habitat change for amphibians and reptiles. Biol. Conserv. **138**(1–2): 166–179. doi:10.1016/j.biocon.2007.04.017.

Getz, W.M., and Wilmers, C.C. 2004. A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. Ecography, **27**: 489–505. doi:10.1111/j.0906-7590.2004.03835.x.

Getz, W.M., Fortmann-Roe, S., Cross, P.C., Lyons, A.J., Ryan, S.J., and Wilmers, C.C. 2007. LoCoH: nonparametric kernel methods for constructing home ranges and utilization distributions. PLoS ONE, **2**: e207. doi:10.1371/journal.pone.0000207. PMID:17299587.

Gibbons, W., Scott, D.E., Ryan, T.J., Buhlmann, K.A., Tuberville, T.D., Metts, B.S., Greene, J.L., Mills, T., Leiden, Y., Poppy, S., and Winne, C.T. 2000. The global decline of reptiles, déjá vu amphibians. BioScience, **50**(8): 653–666. doi:10.1641/0006-3568(2000)050[0653:TGDORD]2.0.CO;2.

Grubb, T.C., and Doherty, P.F. 1999. On home-range gap crossing. Auk, **116**(3): 618–628. doi:10.2307/4089323.

Haenel, G.J., Smith, L.C., and John-Alder, H.B. 2003. Home-range analysis in *Sceloporus undulatus* (eastern fence lizard). I. spacing patterns and the context of territorial behavior. Copeia, **2003**(1): 99–112. doi:10.1643/0045-8511(2003)003[0099:HRAISU]2.0.CO;2.

Hews, D.K. 1993. Food resources affect female distribution and male mating opportunities in the iguanian lizard *Uta palmeri*. Anim. Behav. **46**(2): 279–291. doi:10.1006/anbe.1993.1189.

Hibbitts, T.J., Painter, C.W., and Holycross, A.T. 2009. Ecology of a population of the narrow-headed garter snake (*Thamnophis rufipunctatus*) in New Mexico: catastrophic decline of a river specialist. Southwest. Nat. **54**(4): 461–467. doi:10.1894/GC-195.1.

Hibbitts, T.J., Ryberg, W.A., Adams, C.S., Fields, A.M., Lay, D., and Young, M.E. 2013. Microhabitat selection by a habitat specialist and a generalist in both fragmented and unfragmented landscapes. Herpetol. Conserv. Biol. **8**(1): 104–113.

Hibbitts, T.J., Fitzgerald, L.A., Walkup, D.K., and Ryberg, W.A. 2017. Why didn't the lizard cross the road? Dunes Sagebrush Lizards exhibit road avoidance behaviour. Wildife Res. **44**(3): 194–199. doi:10.1071/WR16184.

Hinam, H.L., and St. Clair, C.C. 2008. High levels of habitat loss and fragmentation limit reproductive success by reducing home range size and provisioning rates of northern saw-whet owls. Biol. Conserv. **141**(2): 524–535. doi:10.1016/j.biocon.2007.11.011.

Kuhn, C.E., Ream, R.R., Sterling, J.T., Thomason, J.R., and Towell, R.G. 2014. Spatial segregation and the influence of habitat on the foraging behavior of northern fur seals (*Callorhinus ursinus*). Can. J. Zool. **92**(10): 861–873. doi:10.1139/cjz-2014-0087.

Laurencio, L.R., and Fitzgerald, L.A. 2010. Atlas of distribution and habitat of the dunes sagebrush lizard (*Sceloporus arenicolus*) in New Mexico. Texas Cooperative Wildlife Collection, Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station.

Leavitt, D.J. 2012. Ecological consequences of landscape fragmentation on the lizard community in the Mescalero–Monahans Shinnery sands. Ph.D. dissertation, Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station.

Leavitt, D.J., and Fitzgerald, L.A. 2013. Disassembly of a dune-dwelling lizard community due to landscape fragmentation. Ecosphere, **4**(8): 1–15. doi:10.1890/ES13-00032.1.

Manteuffel, V.M., and Eiblmaier, M. 2008. The influence of competitor density on space use in juvenile striped plateau lizards (*Sceloporus virgatus*). Acta Oecol. **33**(3): 365–371. doi:10.1016/j.actao.2008.01.006.

McGarigal, K., and Cushman, S.A. 2002. Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. Ecol. Appl. **12**(2): 335–345. doi:10.1890/1051-0761(2002)012[0335:CEOEAT]2.0.CO;2.

Melville, H.I.A.S., Conway, W.C., Morrison, M.L., Comer, C.E., and Hardin, J.B. 2015. Home-range interactions of three sympatric mesopredators in east Texas. Can. J. Zool. **93**(7): 547–557. doi:10.1139/cjz-2014-0322.

Öckinger, E., Schweiger, O., Crist, T.O., Debinski, D.M., Krauss, J., Kuussaari, M., Petersen, J.D., Pöyry, J., Settele, J., Summerville, K.S., and Bommarco, R. 2010. Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. Ecol. Lett. **13**(8): 969–979. PMID:20482577.

Perry, G., and Garland, T., Jr. 2002. Lizard home ranges revisited: effects of sex, body size, diet, habitat, and phylogeny. Ecology, **83**(7): 1870–1885. doi:10.1890/0012-9658(2002)083[1870:LHRREO]2.0.CO;2.

Perry, G., Wallace, M.C., Perry, D., Curzer, H., and Muhlberger, P. 2011. Toe clipping of amphibians and reptiles: science, ethics, and the law. J. Herpetol. **45**(4): 547–555. doi:10.1670/11-037.1.

Rose, B. 1982. Lizard home ranges: methodology and functions. J. Herpetol. **16**(3): 253–269. doi:10.2307/1563718.

Ruby, D.E., and Dunham, A.E. 1987. Variation in home range size along an elevational gradient in the iguanid lizard *Sceloporus merriami*. Oecologia, **71**(3): 473–480. doi:10.1007/BF00378723. PMID:28312997.

Ryberg, W.A., and Fitzgerald, L.A. 2015. Sand grain size composition influences subsurface oxygen diffusion and distribution of an endemic, psammophilic lizard. J. Zool. (Lond.), **295**(2): 116–121. doi:10.1111/jzo.12184.

Ryberg, W.A., Hill, M.T., Lay, D., and Fitzgerald, L.A. 2012. Observations on the nesting ecology and early life history of the Dunes Sagebrush Lizard (*Sceloporus arenicolus*). West. N. Am. Nat. **72**(4): 582–585. doi:10.3398/064.072.0413.

Ryberg, W.A., Hill, M.T., Painter, C.W., and Fitzgerald, L.A. 2013. Landscape pattern determines neighborhood size and structure within a lizard population. PLoS ONE, **8**(2): e56856. doi:10.1371/journal.pone.0056856. PMID:23441217.

Ryberg, W.A., Hill, M.T., Painter, C.W., and Fitzgerald, L.A. 2015. Linking irreplaceable landforms in a self-organizing landscape to sensitivity of population vital rates for an ecological specialist. Conserv. Biol. **29**(3): 888–898. doi:10.1111/cobi.12429. PMID:25472888.

Sabo, J.L. 2003. Hot rocks or no hot rocks: overnight retreat availability and selection by a diurnal lizard. Ecophysiology, **136**(3): 329–335. doi:10.1007/s00442-003-1292-6.

Saunders, D.A., Hobbs, R.J., and Margules, C.R. 1991. Biological consequences of ecosystem fragmentation: a review. Conserv. Biol. **5**(1): 18–32. doi:10.1111/j.1523-1739.1991.tb00384.x.

Schoener, T.W. 1981. An empirically based estimate of home range. Theor. Popul. Biol. **20**(3): 281–325. doi:10.1016/0040-5809(81)90049-6.

Seaman, D.E., Millspaugh, J.J., Kernohan, B.J., Brundige, G.C., Raedeke, K.J., and Gitzen, R.A. 1999. Effects of sample size on kernel home range estimates. J. Wildl. Manage. **63**(2): 739–747. doi:10.2307/3802664.

Shine, R. 2003. Effects of pregnancy on locomotor performance: an experimental study on lizards. Oecologia, **136**(3): 450–456. doi:10.1007/s00442-003-1281-9. PMID:12750993.

Smith, D.C. 1985. Home range and territory in the striped plateau lizard (*Sceloporus virgatus*). Anim. Behav. **33**(2): 417–427. doi:10.1016/S0003-3472(85)80066-X.

Smolensky, N.L., and Fitzgerald, L.A. 2011. Population variation in dune-dwelling lizards in response to patch size, patch quality, and oil and gas development. Southwest. Nat. **56**(3): 315–324. doi:10.1894/F03-MLK-21.1.

Stone, P.A., and Baird, T.A. 2002. Estimating lizard home range: the Rose model revisited. J. Herpetol. **36**: 427–436. doi:10.1670/0022-1511(2002)036[0427:ELHRTR]2.0.CO;2.

Torres, A., Jaeger, J.A.G., and Alonso, J.C. 2016. Assessing large-scale wildlife responses to human infrastructure development. Proc. Natl. Acad. Sci. U.S.A. **113**(30): 8472–8477. doi:10.1073/pnas.1522488113. PMID:27402749.

Walkup, D.K., Leavitt, D.J., and Fitzgerald, L.A. 2017. Effects of habitat fragmentation on population structure of dune-dwelling lizards. Ecosphere, **8**(3): e01729. doi:10.1002/ecs2.1729.

White, G.C., and Garrott, R.A. 1990. Analysis of wildlife radio-tracking data. Academic Press Inc., San Diego, Calif.

Whitfield, S.M., Bell, K.E., Philippi, T., Sasa, M., Bolaños, F., Chaves, G., Savage, J.M., and Donnelly, M.A. 2007. Amphibian and reptile declines over 35 years at La Selva, Costa Rica. Proc. Natl. Acad. Sci. U.S.A. **104**(20): 8352–8356. doi:10.1073/pnas.0611256104. PMID:17449638.

Whiting, M.J. 1999. When to be neighbourly: differential agonistic responses in the lizard *Platysaurus broadleyi*. Behav. Ecol. Sociobiol. **46**(3): 210–214. doi:10.1007/s002650050611.

Worton, B.J. 1987. A review of models of home range for animal movement. Ecol. Model. **38**(3–4): 277–298. doi:10.1016/0304-3800(87)90101-3.