Ecology and Conservation of the Imperiled Dunes Sagebrush Lizard: An Ecological Specialist in a Threatened Ecosystem

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Abstract

The Dunes Sagebrush Lizard (*Sceloporus arenicolus*) is endemic to the Mescalero-Monahans Sandhills, in southeastern New Mexico and west Texas. It only lives in dunes with bowl-shaped depressions (blowouts) that are semi-stabilized by shinnery oak (*Quercus havardii*). Meticulous studies reveal population dynamics in these lizards scale from local neighborhoods of individuals up to the geographic distribution. The condition and configuration of the irreplaceable landforms it inhabits are directly linked to population vital rates and persistence of populations. The Mescalero-Monahans Sandhills overlies the Permian Basin, a region beset with increasing and extensive fragmentation from oil and gas development and sand mining for fracking. Fragmentation disrupts both the geomorphologic processes that maintain dunes and the dispersal dynamics that connect lizard neighborhoods. Effective conservation of shinnery oak dunes is a persistent challenge. Conservation agreements facilitate monitoring, land stewardship, and research. However, conservation agreements do not match dynamics of ecological scaling in this system and may not confront the problem of fragmentation that drives disappearance of the Dunes Sagebrush Lizard. The same recommendation has been made since 1997, with increasing precision- there is a clear need to protect extensive and relatively undisturbed areas of shinnery oak dunes that are home to this highly specialized species.

Introduction

Biodiversity is in perilous decline at every scale of organization from loss of genetic variation to loss of populations, to extinction of species, and the dis-assembly of communities, ecosystems, and landscapes. This loss of biodiversity is increasingly referred to as biological annihilation in recognition that annihilation is probably a more realistic representation of the biodiversity crisis than mass extinction (Ceballos et al., 2017; Rogan et al., 2021). The concept recognizes that range contraction, loss of populations, altered ecological communities, ecological homogenization caused by invasive species, and landscape degradation result in the

impoverishment of biodiversity across entire continents regardless of the number of global species' extinctions. While species may persist in small fragments of their former range, their ecological function in ecological communities and across landscapes is all but lost.

What biodiversity is easiest to lose, quickest to decline, and hardest to restore? In many cases it is the species that are endemic to relatively small geographic areas and species that have narrow ecological niches. Endemic species are easily imperiled because large proportions of their entire range can become uninhabitable and never recover. A textbook example of this is the endangerment and outright extinction of species endemic to oceanic islands, which represents the largest proportion of all species extinctions. Island endemics have been lost due to the tragic reason they occurred nowhere else and had nowhere else to go. It is much the same for species with very small geographic ranges on continents, so-called "micro-endemics" that are restricted to a mountain range, a single watershed, or a unique geological formation. Other species that are easily imperiled are often ones that possess behavioral and morphological adaptations that make them "ecological specialists" good at using a narrow subset of resources. Some ecological specialists may depend entirely on just a few food resources that are procured via unique foraging adaptations, others may be adapted to thrive in a very narrowly defined habitat. As such, ecological specialists are sensitive to any sort of change that impacts the resources they require or the unique habitat in which they live.

The Dunes Sagebrush Lizard (*S. arenicolus*: Phrynosomatidae) is a small dune-dwelling lizard that is both a micro-endemic species and an extreme ecological specialist (Fig. 1). It is endemic to a small area of ancient inland dunes, the Mescalero-Monahans Sandhills, located in southeastern New Mexico and adjacent west Texas (Degenhardt and Jones, 1972, Axtell, 1988, Degenhardt and Jones, 1972, Fitzgerald and Painter, 2009, Fitzgerald et al., 2011, Chan et al., 2013, Chan et al., 2020) (Fig. 2). Dunes Sagebrush Lizards are only found in the shinnery oak (*Q. havardii*) dunes of the Mescalero-Monahans Sandhills Ecosystem. The Dunes Sagebrush Lizard is also a remarkable habitat specialist. It is a dune-dwelling lizard that only lives in sand dunes that are semi-stabilized by shinnery oak with characteristic bowl-shaped depressions of sand (blowouts). This dune landform is patchily distributed in the shinnery oak matrix that stabilizes the dune fields and comprises the only habitat of the Dunes Sagebrush Lizard. This species carries out its entire life cycle among interconnected blowouts and the vegetation around the perimeter of interconnected blowouts (Fitzgerald et al., 1997, 2011; Fitzgerald and Painter, 2009; Hibbitts et al., 2013; Walkup et al., 2018).

The Dunes Sagebrush Lizard has been a species of conservation concern to government agencies and many stakeholder groups for at least two decades because in addition to having a very restricted and naturally disjunct distribution, land use practices have caused fragmentation and loss of habitat (Smolensky and Fitzgerald, 2011; Leavitt and Fitzgerald, 2013; Ryberg and Fitzgerald, 2016). Meticulous ecological research has demonstrated how and why land use, especially development of oil and gas fields, has led to loss of populations and irreversible changes to the unique shinnery oak dune blowout landforms on which the species is

Fig. 1 The Dunes Sagebrush Lizard (*Sceloporus arenicolus*: Phrynosomatidae) is endemic to the Mescalero-Monahans Sandhills Ecosystem, where it utilizes shinnery oak dunes with blowouts as its habitat. Image on left is an adult male, a gravid female is shown on right.

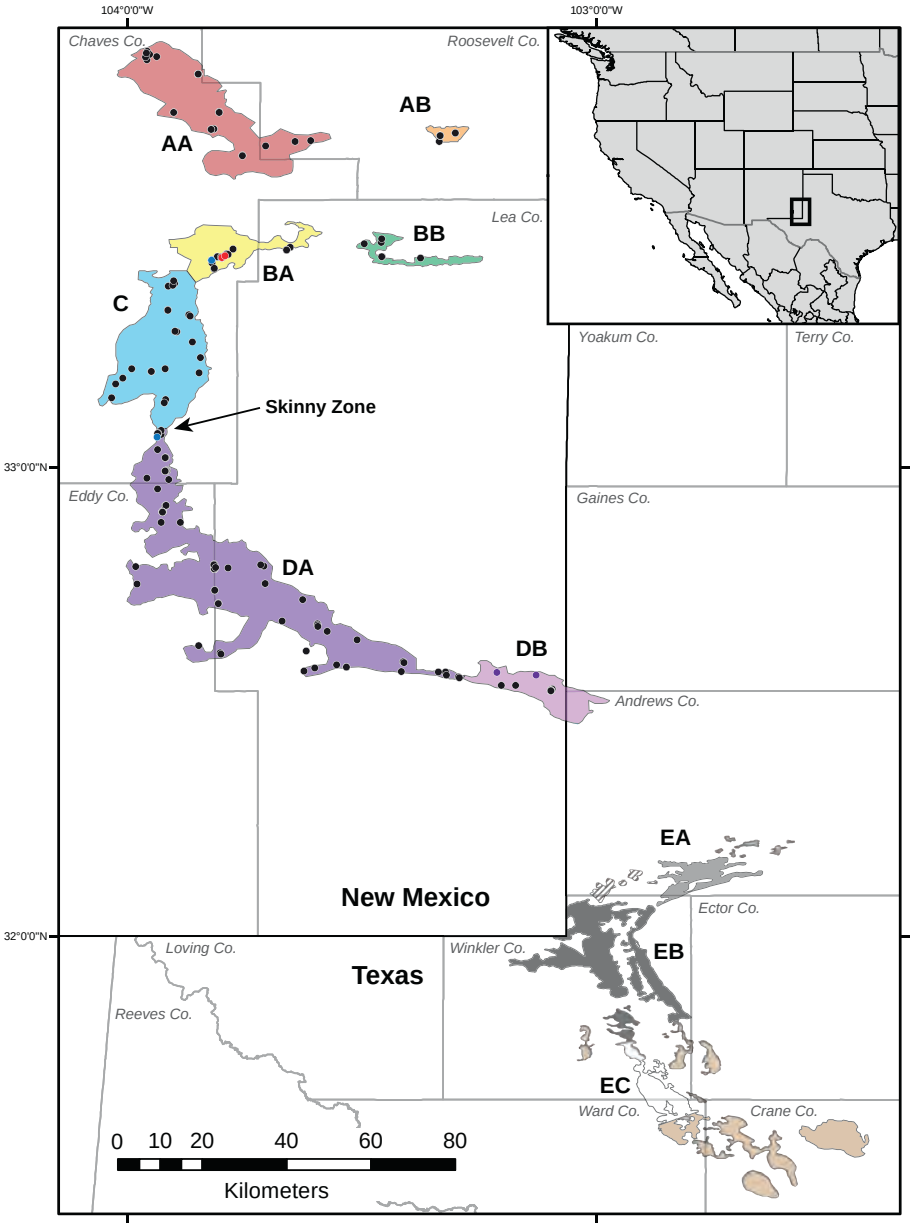

Fig. 2 The geographic distribution and areas of suitable shinnery oak-sand dune habitat for the Dunes Sagebrush Lizard (*Sceloporus arenicolus*) (from Chan LM, Painter CW, Hill M, Hibbitts TJ, Leavitt DJ, Ryberg WA, Walkup DK and Fitzgerald LA (2020) Phylogeographic structure of the dunes sagebrush lizard, an endemic habitat specialist. *PLoS One* **15**: e0238194. doi: 10.1371/journal.pone.0238194). Shaded areas delineate potentially suitable habitat for *S. arenicolus* with colored portions of the landscape corresponding to genetically identifiable phylogroups. Striped areas have not been surveyed, but contain suitable habitat. Brown indicates areas with potentially suitable habitat where *S. arenicolus* has not been found. One locality exists in Crane County from 1970, but the species has not been found there since then. Collection localities for samples of *S. arenicolus* from New Mexico included in this study are indicated with points. Specific localities are not shown for Texas due to legal confidentiality agreements with landowners. Collection localities indicated by colored (non-black) points are samples with mitochondrial haplotypes more closely related to haplotypes from other regions.

dependent. Our purpose is to review and synthesize the ecology and conservation of this imperiled species. This is a compelling case for understanding how habitat change directly affects populations leading to local extinction because of the direct linkages between the species' population dynamics and the habitat it requires. The case of the Dunes Sagebrush Lizard reveals important lessons for conservation of ecological specialists.

Ecology and conservation of the Dunes Sagebrush Lizard

Concern over the future of the Dunes Sagebrush Lizard and the unique inland dune ecosystem that it occupies has been the impetus for research on the species. Essentially all research on the species was the result of targeted projects aimed at producing scientifically

defensible knowledge needed to inform conservation priorities. These included multi-year projects on: effects of herbicide spraying to kill shinnery oak; geographic distribution; habitat selection; interdune dispersal; nesting ecology; population dynamics; movement ecology; systematics, taxonomy and phylogeography; conservation genetics; landscape ecology; and habitat suitability mapping. Findings from these studies led to an integrated understanding of the ecology of the Dunes Sagebrush Lizard at ecological scales ranging from population genetics to populations to ecological communities to persistence and extinction of the species. This long-term directed research program has provided a thorough and synthetic understanding of the ecology of the Dunes Sagebrush Lizard. Research has revealed mechanisms that determine how and why habitat disturbance and landscape fragmentation leads to loss of populations.

Life history

Description

The Dunes Sagebrush Lizard is a member of the Phrynosomatidae, which consists of small to medium sized lizards distributed mainly in North America. The genus *Sceloporus* is known as the spiny lizards with all species having over lapping dorsal scales with a pronounced keel that ends in a spine posteriorly on each scale. Species of this genus most often exhibit territoriality, with males maintaining larger home ranges than females. In general, species in the genus *Sceloporus* use a sit and wait strategy of foraging.

The Dunes Sagebrush Lizard is small with males averaging 54.5 mm snout-vent length (SVL) with a maximum of 75 mm, and females averaging 53.8 mm with a maximum of 63 mm SVL (Degenhardt and Jones, 1972). The dorsal coloration is light brown with an ill-defined pair of longitudinal lighter stripes extending down the sides of the torso. Males have large paired blue belly patches and occasionally have scattered blue scales on the throat. Females develop orange markings on the sides of the face, neck, and body when they become gravid (Hibbitts and Hibbitts, 2015). *S. arenicolus* has 8 or more scales separating the medial ends of the femoral pores, which is an identifying characteristic of this species. Enlarged scales partially cover the ear openings and the front digits are relatively long, traits that are probably adaptive in this sand-diving and sand-burrowing species.

Reproduction and nesting

The Dunes Sagebrush Lizard can be found throughout the year with two activity peaks in late spring and mid-summer (Leavitt, 2019). Like most lizards, onset of reproduction is cued by increasing temperatures and day length in spring. Courtship and mating occur mostly during May and June, which also corresponds to the peak of activity in the third week of June (Leavitt, 2019). Like other members of their genus and family, female Dunes Sagebrush Lizards tend to migrate out of their core home range to nest (Hill and Fitzgerald, 2007). During a radio-tracking study of 20 females, 10 nesting sites were found and two nests were discovered with eggs. Nesting females dispersed to adjacent blowouts or other portions of larger blowout areas immediately before nesting. Nesting occurred at night and was often characterized by a late afternoon movement outside of the normal range of the lizard. Females dug nest tunnels into the steep side of a blowout until they reached moist soil at a depth of 11 or 19 cm. Another nest was found in 2011 in a blowout (Ryberg et al., 2012). The observations, taken together, indicated females select nest sites close to the moisture horizon in the sandy soil and choose sites where sand grain size composition is relatively coarse compared to surrounding areas in their home range (Ryberg et al., 2012). Females may reproduce once or twice in a season, laying an average of 5 eggs per clutch in mid-June, and again in late July or early August (Fitzgerald and Painter, 2009; Ryberg et al., 2015). Hatchlings appear in early July and a portion will reach sexual maturity in their first spring (about 10 months of age). Individuals that hatch later or grow slower may not breed until their second spring. The lifespan of the Dunes Sagebrush Lizard is typically 3 years and rarely 5 or more years.

The Dunes Sagebrush Lizard is adept at burrowing and diving into sand. Individuals dive into the sand to hide or escape predation and may wait for prey while mostly buried. Typically, individuals bury themselves just under the surface of the sand to spend the night. In many cases a small portion of their back and tail are still visible from the surface. The nesting excavations made by females are arduous, and the females may stay beneath the surface for hours and move around underneath the surface. Coarse sand probably makes nesting, burrowing, and sand-diving easier. Sand that is too fine or too compact may interfere with breathing and may not allow sufficient diffusion of oxygen (Ryberg and Fitzgerald, 2015).

Diet and predators

The Dunes Sagebrush Lizard is a sit-and-wait ambush forager, and its diet is typical of small North American lizard species, consisting mostly of ants, grasshoppers and crickets, spiders, beetles, and other arthropods (Fitzgerald and Painter unpublished data). Several predators may take Dunes Sagebrush Lizards as prey, including a variety of snake species (e.g., Young et al., 2018), avian predators such as Loggerhead Shrikes (*Lanius ludovicianus*) and Greater Roadrunners (*Geococcyx californianus*) (Hathcock and Hill, 2019), and mammalian predators. One radio-tracking study found Coachwhip Snakes (*Masticophis flagellum*) consumed 20% of radio-tagged gravid females (Hill and Fitzgerald, 2007). In a separate radio-tracking study of 36 individuals, one was preyed on by a Glossy Snake (*Arizona elegans*) and three others by Coachwhip Snakes (Young et al., 2018).

Evolutionary history, systematics, and taxonomy

The Dunes Sagebrush Lizard is a classic "peripheral isolate", which refers to its ancestral populations that were isolated on the periphery of its ancestral species' range. The species, *S. arenicolus*, was originally described as a subspecies of the Sagebrush Lizard, *Sceloporus graciosus*, which inhabits the Great Basin. It was formally described as a new subspecies, *S. graciosus arenicolus* (Degenhardt and Jones, 1972), but elevated to species status (*S. arenicolus*) by Collins (1991) because it was identified as a morphologically distinct, allopatric subspecies. Later studies of phylogenetic systematics of lizards in the genus *Sceloporus* supported the identity of *S. arenicolus*, but finer scale resolution of relationships among the sagebrush lizards, including *S. arenicolus* was still lacking (Wiens and Reeder, 1997; Wiens et al., 2010). Chan et al. (2013) later completed phylogenetic analyses of mitochondrial DNA sequence data for multiple populations of sagebrush lizards and reviewed taxonomic literature on the morphology of the Dunes Sagebrush Lizard. They emphasized that the species is morphologically and genetically distinct from its nearest relatives and should be considered a species. An estimate of divergence times showed the Dunes Sagebrush Lizard, together with its most closely related sagebrush lizard relatives, was about 2,330,000 years old, and the median age estimate of dunes sagebrush lizard clade was about 490,000 years old. A more recent intraspecific analysis using DNA sequence data and microsatellite data estimates the clade age of the Dunes Sagebrush Lizard to be closer to 34,800 years old (Chan et al., 2020). While uncertainty surrounds the exact age of dunes sagebrush lizards, it is believed that the Dunes Sagebrush Lizard co-evolved with formation of the Mescalero-Monahans Sandhills ecosystem during the Pleistocene (Chan et al., 2009), presumably becoming specialized to live in the dune environment where it diverged in isolation from its sagebrush lizard ancestors.

Geographic distribution

At the time the Dunes Sagebrush Lizard was described, its known distribution in Texas and New Mexico was restricted to only a few locations. Extensive surveys conducted at hundreds of sites over >20 years at hundreds of sites have determined the extent of the geographic range of the Dunes Sagebrush Lizard (Fitzgerald et al., 1997, 2011; Laurencio and Fitzgerald, 2010; Johnson et al., 2016; Hardy et al., 2018; Walkup et al., 2018). A 3-year distribution study in New Mexico was the first effort to document the geographic range in that state (Fitzgerald et al., 1997). Surveys were conducted to better understand the distribution of Dunes Sagebrush Lizard in Texas in 2006 and 2007 (Laurencio and Fitzgerald, 2010). In 2011, a major survey of the range of the Dunes Sagebrush Lizard in Texas was undertaken that documented presence of Dunes Sagebrush Lizards at 28 of 50 sites surveyed (Fitzgerald et al., 2011). After the 2011 Texas survey, a likelihood of occurrence map was developed by expert opinion, based on Dunes Sagebrush Lizard presences, the extent of the dune landform, and connectivity of the occupied habitat patches and dune landscape quality (Fitzgerald et al., 2011). While the extent of the range has not changed markedly, several additional occupied and unoccupied locations within and immediately adjacent to the initially estimated range have been documented providing a very accurate picture of the distribution of the species (Laurencio and Fitzgerald, 2010; Walkup et al., 2018). During 2014–2016, 336 surveys at 100 sites were carried out both in and outside of the previously defined range; no Dunes Sagebrush Lizards were located outside the previously defined range boundaries (Walkup et al., 2018). Various maps and atlases have also been produced that visualize the distribution of the Dunes Sagebrush Lizard in relation to the habitat it occupies (Laurencio and Fitzgerald, 2010; Johnson et al., 2016; Hardy et al., 2018; Walkup et al., 2018). For the purposes of a conservation plan, Hardy et al. (2018) developed a habitat map based on remotely sensed vegetation profiles, similar to a map for the species' range in New Mexico developed by Johnson et al. (2016). Ongoing habitat modeling research is using Dunes Sagebrush Lizard presence points along with remotely sensed landscape covariates to produce another map for conservation planning purposes, in the Texas portion of the species' range. This long-term research on the species' distribution has led to the conclusion that habitat quality and historical patterns of occurrence strongly influence the likelihood of occupancy or occurrence of Dunes Sagebrush Lizards and that it is very strictly tied to the patchy distribution of shinnery oak dunes with blowouts that occur in the Mescalero-Monahans Sandhills Ecosystem.

The habitat of the Dunes Sagebrush Lizard

The shinnery oak sand dunes

The Mescalero Sands of New Mexico and the Monahans Sandhills in Texas, referred to here as the Mescalero-Monahans Sandhills Ecosystem, is an expansive area of sand deposits in the Southern High Plains, or Llano Estacado. This area occurs from north of Lubbock, Texas south along the Texas-New Mexico border region, to Crane County, Texas. Much of the area is covered by sand deposits more than 2 m thick, with dunes or extensive sand sheets present. Major dune belts are referred to as the Muleshoe Dunes, Lea-Yoakum Dunes, Mescalero Dunes and Monahans Dunes (Muhs and Holliday, 2001). The geological history of the area is complex, with multiple periods of sand deposition since the mid-Pleistocene. Dunes were formed 20,000–30,000 years ago, with eolian sand deposited about 15,000 years ago. During the Holocene, dune-building also occurred between 3000 and 7000 years ago (Rich and Stokes, 2011).

Within this broader ecosystem, the entire range of the Dunes Sagebrush Lizard occurs only in the Mescalero and Monahans dunes in Andrews, Crane, Gaines, Ward and Winkler counties in Texas and in Chaves, Eddy, Lea and Roosevelt counties in New Mexico (Fitzgerald and Painter, 2009; Laurencio and Fitzgerald, 2010).

Sand dune blowouts are characteristic of the Mescalero-Monahans Sandhills landscape. Dune blowouts are emergent landforms that are formed and sustained by the complex feedbacks between wind, sand, and the shinnery oak that stabilizes the dunes. Blowouts are formed in vegetated dunes by wind that hollows out open patches of sand in the rugose dune topography. In many locations, the rugose dune landscape consists of interconnected dune blowouts with vegetated arms creating U-shaped dunes. In other areas, open sandy areas are more eroded and shinnery oak grows in hummocks of variable size. Blowouts and open sandy areas vary in size, depth, shape of the perimeter, and steepness of the slopes. The dunes may be supply limited, implying that long-term re-activation may not occur (Muhs and Holliday, 2001).

Perceptions of the shinnery oak dunes as a dynamic system is a question of timescale and the extent of sandy areas. Dunes in the Mescalero-Monahans Sandhills are active due to the constantly moving sand and presence of active Barchan dunes like the large dunes at Monahans Sandhills State Park, Texas. Yet, the characteristic blowout landforms are surprisingly persistent over relatively long timescales. Individual blowouts can be very old. It is not rare to find Chupadero black-on-white pottery and other artifacts from Ancestral Pueblo peoples in dune blowouts. Prehistoric artifacts such as plain brown or gray pottery shards, lithic scatter, arrowheads and scrapers are common. The Ancestral Pueblo people inhabited the region and were making Chupadero-style pottery between 1000 CE and 1500 CE People have been visiting and using the Mescalero-Monahans Sandhills for thousands of years.

Because the dune blowout landform depends on the interactions between wind, sand, and the stabilizing shinnery oak vegetation, loss of any of these components results in loss of the dune-blowout landform. Dunes that have been flattened will not rise up again. Removal of shinnery oak through herbicide spraying, for example, results in irreversible loss of dune blowouts. Analyses based on remote sensing also showed that dune areas that were small tended to shrink over time while large expanses of dunes were more stable. An implication of that study was that fragmentation of dune areas may enhance their erosion and loss (Dzialak et al., 2013). Without the stabilizing vegetation, wind erodes the dunes into a flatter landscape with different vegetation associations. Similarly, landscape fragmentation appears to disrupt the geomorphological processes that allow the dune blowout landform to sustain itself. Shinnery oak dunes that were disturbed over 30 years ago have not recovered and there are no areas where new dunes are being formed (Ryberg and Fitzgerald, 2016) (Fig. 3).

Inland dune formations like the Mescalero-Monahans Sandhills, often called parabolic dunes, occur throughout the world. Because they are old, relatively stable, and have patchy unique landforms, parabolic dune formations often contain endemic and ecologically specialized plants and animals. The Mescalero-Monahans Sandhills is not only home to the endemic Dunes Sagebrush Lizard, but also at least 16 endemic insects (Leavitt, 2012). The Mescalero sands Jerusalem cricket (*Stenopelmatus mescaleroensis*), the Monahans Sandhills Jerusalem cricket (*Stenopelmatus monahansensis*), the Mescalero shield-back katydid (*Plagiostira mescaleroensis*), the Mescalero camel cricket (*Ammobaenetes mescalero*), and the Mescalero thread-legged katydid (*Arethaea mescalero*), are endemic to the ecosystem as well as at least 10 endemic beetles (Henderson, 2006, Leavitt, 2012, Longing pers. comm. 2021; https://texasnongameprogram.wordpress.com/2014/04/04/first-ever-comprehensive-survey-of-monahans-sandhills-endemic-insects/; accessed 1 Oct 2021).

Habitat requirements

The habitat requirements of the Dunes Sagebrush Lizard have been studied in detail at several spatial scales ranging from microhabitat use (Fitzgerald et al., 1997; Hibbitts et al., 2013), to landscape-scale patterns of habitat configuration (Ryberg et al., 2013; Walkup et al., 2019). The Dunes Sagebrush Lizard is known to occur in shinnery oak dunes with blowouts, and in areas with shinnery oak hummocks and patches of open sand where the topography is dune-like and rugose. Habitat selection studies demonstrated the Dunes Sagebrush Lizard is a habitat and microhabitat specialist, occurring exclusively within and among interconnected blowouts and open sand patches in shinnery oak dune habitat (Fitzgerald et al., 1997, Hibbitts et al., 2013).

Areas of shinnery oak dunes within and immediately adjacent to the known geographic range of the species can be classified as suitable habitat. The Dunes Sagebrush Lizard may not occur in all areas of suitable habitat due to chance, and the dynamic nature of extinction and colonization of suitable habitat through time. Suitable habitat may be identified in areas that have not been surveyed and where presence is not confirmed. However, it is sensible to assume the species occupies the entirety of contiguous, interconnected, expanses of shinnery oak dunes where the species has been found, as indicated on the distribution map in Fig. 2. The Dunes Sagebrush Lizard is not found at sites lacking shinnery oak dune habitat.

Dispersal habitat and so-called "corridors" for dispersal also consist of shinnery oak dunes with open sandy patches. Dispersal habitat is thus contiguous areas of shinnery oak dunes. No life stage of the species uses any other habitat than shinnery oak dunes. Inter-dune dispersal studies and extensive mark-recapture studies show Dunes Sagebrush Lizards do not traverse scrublands and grasslands that separate shinnery oak dunelands (Leavitt and Fitzgerald, 2013). There are no observations of back-and-forth dispersal between shinnery oak dune areas. Intensive studies of settlement and vacancy of micro-habitat areas within occupied shinnery oak dunes revealed shifting patterns of use of more heavily vegetated micro-sites and expansion and contraction to or from the periphery of a dune system (Walkup et al., 2019). Dunes Sagebrush Lizards disperse as neonates and young-of-year among open sandy patches and dune blowouts, which vary in size, shape, rugosity, and dispersion. Adult males are territorial, and females have clearly definable home ranges (Hill and Fitzgerald, 2007; Young et al., 2018). Mesquite grasslands, roadways, right-of-ways, and other vegetation types are not dispersal habitat. Even at shinnery dune sites where the lizard does occur, it is not found in adjacent

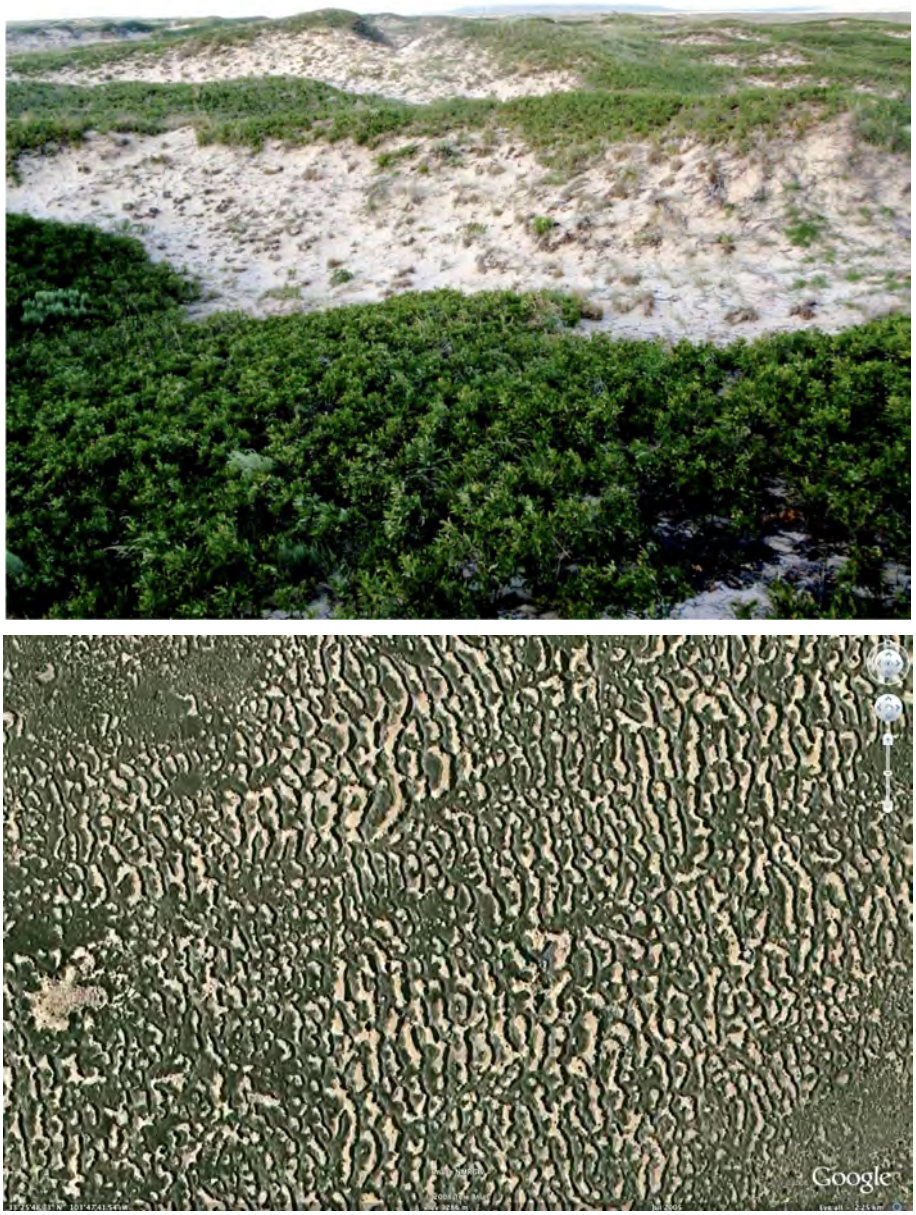

Fig. 3 Views of shinnery oak sand dunes in the Mescalero-Monahans Sandhills Ecosystem. The top image from ground-view shows the dune blowouts stabilized by shinnery oak (*Quercus havardii*). The aerial view of the same area shows a landscape of dune blowouts of varying size and shape in a matrix of shinnery oak. Shinnery oak sand dunes with blowouts and open patches of sand are the only habitat used by the Dunes Sagebrush Lizard. The patchy dune blowout landform is an emergent property of the interaction between wind, sand, and the shinnery oak (*Quercus havardii*) that stabilizes the dunes. Blowouts are bowl-shaped depressions created by wind with vegetated perimeter and trailing arms of vegetation. In some areas the dune formations are more eroded and contain hummocks of shinnery oak among open patches of sand.

grasslands or scrublands more than 50 m from dune topography. The Dunes Sagebrush Lizard is never found on roads that are not bordered by shinnery oak dunes. There are anecdotal reports of Dunes Sagebrush Lizards on sandy ranch roads traversing suitable habitat. A radio-tracking study revealed road avoidance, with one individual crossing a road only where it was covered with wind-blown sand (Young et al., 2018). A set of controlled behavior trials showed that Dunes Sagebrush Lizards avoid even very small caliche (compacted calcium carbonate) tracks (Hibbitts et al., 2017).

Hierarchy of habitat selection

The Dunes Sagebrush Lizard exhibits a remarkable hierarchy of habitat selection. At the smallest, most ephemeral scale, Dunes Sagebrush Lizards actively select their resting sites based on temperature of the air and substrate, distance to cover, the size of the dune blowout, and the slope and aspect. Results of micro-habitat selection studies showed that lizards selected relatively cool places

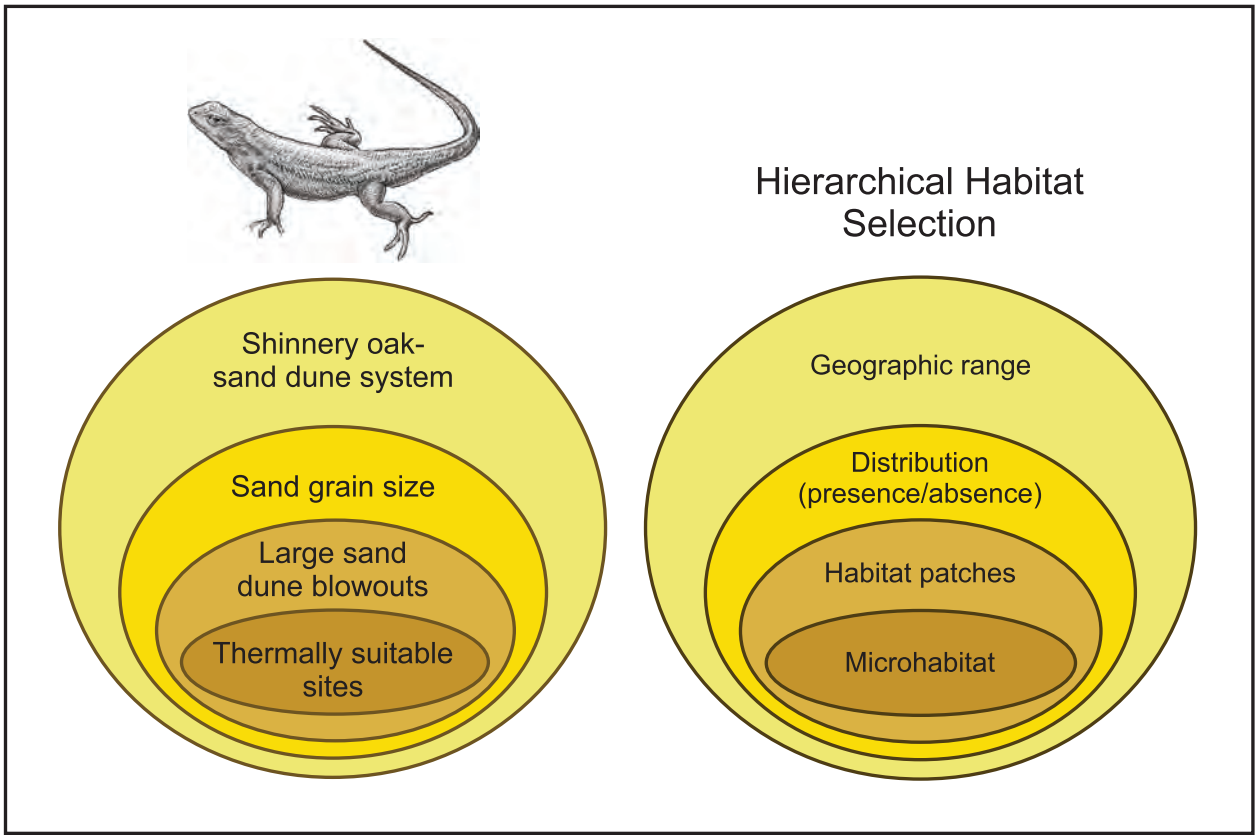

Fig. 4 The nested hierarchy of habitat selection by the Dunes Sagebrush Lizard. At the smallest scale, individuals choose sites based on factors related to opportunities for thermoregulation. Within their habitat, these lizards select relatively large sand dune blowouts with steep slopes. At the landscape scale, Dunes Sagebrush Lizards only occur where the sand is relatively coarse. At the highest level, the species is endemic to the shinnery oak sand dunes in the Mescalero-Monahans Sandhills Ecosystem. From Fitzgerald LA, Painter CW, Sias DA and Snell HL (1997) The range, distribution, and habitat of Sceloporus arenicolus in New Mexico. Final report to New Mexico Department of Game and Fish: Santa Fe, NM; Fitzgerald LA and Painter CW (2009) Dunes sagebrush lizard (Sceloporus arenicolus). In Jones LC and Lovich RE (eds.) Lizards of the American Southwest: A Photographic Field Guide, pp. 198–120. Tucson, AZ: Rio Nuevo Publishers.

favorable to thermoregulation, and preferred relatively large dune blowouts (Fitzgerald et al., 1997). Dunes Sagebrush Lizards selected microhabitat sites with steeper slopes (Leavitt, 2012) and more open sand than expected by chance (Hibbitts et al., 2013). Bigger blowouts increase the availability of sites for territories and for thermoregulation. Small blowouts and flat sand patches in contiguous shinnery oak dunes are used, but much less so than large blowouts, which are used significantly more than expected based on their availability (Fitzgerald et al., 1997). Across the species' range, Fitzgerald et al. (1997) found significant differences in the composition of sand between sites that were occupied and unoccupied with occupied sites having slightly coarser sand than unoccupied sites. Finally, the entire geographic distribution of the species is limited to the Mescalero-Monahans Sandhills Ecosystem. Thus, the nested hierarchy of habitat selection from smallest scale to largest begins with Dunes Sagebrush Lizards selecting thermally suitable sites with steep slopes found within large dune blowouts comprised of coarse sand grain composition distributed throughout the Mescalero-Monahans Sandhills Ecosystem (Fig. 4).

Population ecology

Population dynamics

Previous studies in New Mexico have examined how population dynamics of Dunes Sagebrush Lizards are linked to the shinnery oak sand dune landscape. Population estimates of Dunes Sagebrush Lizard population estimates carried out at multiple sites in New Mexico during two field seasons by Smolensky and Fitzgerald (2010) used both distance sampling and total removal plots. Distance sampling and other visual encounter survey methods underestimate numbers of lizards because many individuals are not available for detection (e.g., in burrows) or not seen by observers (e.g., detection bias). Dunes Sagebrush Lizard densities ranged from 4.6/ha using distance sampling methods to 30/ha using total removal plots.

A five-year mark-recapture study in practically undisturbed habitat in New Mexico yielded much information on population dynamics of the Dunes Sagebrush Lizard (Ryberg et al., 2013; Ryberg and Fitzgerald, 2016). The research showed that among six independent trapping grids in contiguous shinnery dune habitat, the lizard population could be conceived as groups of individuals

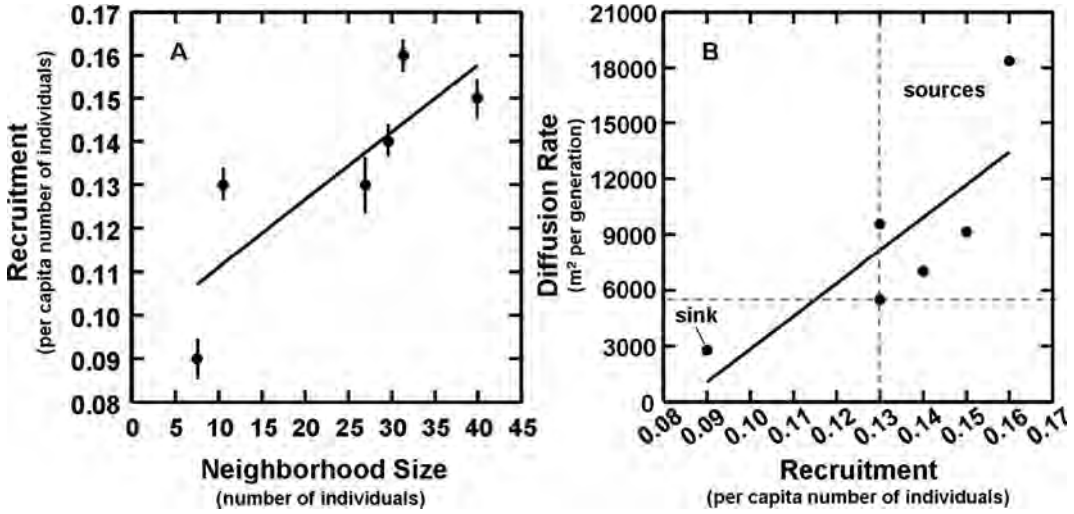

Fig. 5 Across landscapes of contiguous shinnery oak dunes with blowouts, the Dunes Sagebrush Lizard population can be understood in the context of neighborhoods of interacting individuals. Neighborhood size is calculated from population density and movements of individuals in the habitat. Graph A shows the strong correlation between neighborhood size and recruitment of neonates into the population ($R^2 = 0.82$, $df = 4$, $P = .05$; bars = ±SE). Graph B on the right shows that diffusion dispersal of neonates across the landscape is correlated to recruitment ($R^2 = 0.80$, $df = 4$, $P = .05$). The dashed lines estimate the level of recruitment and dispersal necessary maintain a stable local population growth rate. Three of the neighborhoods produced excess recruits, two were stable, and one neighborhood was a local sink where recruitment was too low to sustain that neighborhood. Persistence of the sink neighborhood was dependent on immigration of dispersing recruits from source neighborhoods.

living in neighborhoods that were isolated from other neighborhoods by distance (Wright, 1946). We used this approach to quantify the size and vitality of lizard neighborhoods. The number of lizards in a neighborhood was a function of the local population density and the movement histories of lizards in a mark-recapture trapping grid. Larger neighborhoods produced more hatchlings and recruits into the local neighborhood because there were more males and females interacting and breeding. Because hatchling Dunes Sagebrush Lizards disperse by diffusion through the interconnected shinnery oak dunes, the rate of diffusion dispersal was also a direct consequence of the size of the lizard neighborhood.

Analyses of mortality and natality across the shinnery oak dune landscape showed that population growth varied among the lizard neighborhoods. Annual survival at the sites varied from 0.46 to 0.74 annually and recruitment ranged from 0.09 to 0.16 per neighborhood. But the realized rate of population growth was stable (indistinguishable from 1.0) across the entire landscape of occupied habitat (Ryberg et al., 2013). However, some neighborhoods were thriving and providing excess juvenile recruits that were dispersing across the contiguous area of shinnery oak dunes. Other neighborhoods were stable, and one neighborhood out of the six that were studied had a negative population trend where mortality was greater than natality (Fig. 5). The reason a small, precarious, neighborhood could persist was because the local neighborhoods, together, created a localized source-sink dynamic. Dispersal originating from thriving neighborhoods kept the overall population stable at the landscape scale. A declining neighborhood in isolation would be on a path to local extinction because it could not be rescued by immigrant recruits dispersing from afar.

We also found direct linkages between aspects of the shinnery oak dune blowouts and the lizard neighborhoods. The size of neighborhoods was significantly correlated with the area of blowouts, soil compaction (indicating coarse loose sand), the contiguity of the dune blowout features, and the slope and aspect of the terrain where the neighborhoods were located. In fact, the one neighborhood that was a population sink was in an area that had been disturbed by herbicide spraying that killed off much of the shinnery oak, affecting the integrity of the dune blowout landform at that site (Ryberg et al., 2013).

With the same mark-recapture study, Ryberg and Fitzgerald (2016) also examined the linkages between configuration of the blowout areas and survivorship of adults and juveniles, and fecundity of females (population vital rates). The configuration of the dune-blowout landscape and complexity of the blowout landform was directly linked to the population growth rate (λ), which was sensitive to proportional changes in fecundity and juvenile survival in irregular blowouts with more edge. In more regularly shaped blowouts with less edge, the population growth rate was more sensitive to proportional changes to adult survival (Ryberg and Fitzgerald, 2016). These studies linking population dynamics and dispersal to the condition of the shinnery oak dunes are important, because they showed very precisely how population growth was directly related to the condition of a species' habitat. For the Dunes Sagebrush Lizard, a healthy landscape translates directly to a healthy population.

Population genetics

Detailed studies of genetic variation within and among populations of the Dunes Sagebrush Lizard (Chan et al., 2009, 2020) detected significant genetic differentiation across the range (Fig. 2). Early studies found support for three genetic clusters corresponding to north, central, and southern regions of the species' entire range across southeastern New Mexico and West Texas (Chan

et al., 2009). The study also showed limited gene flow between two sites in the northern and central populations, as well as from the southern population to the western central population. Migration estimates between the genetic populations were low, although there is a suggestion of asymmetric migration from the north to the central region. Later studies focusing on phylogeographic differentiation across the range described even greater genetic structure (Chan et al., 2020). The most pronounced genetic divergences were between the northern Mescalero Sands and southern Mescalero Sands and among three regions in the Monahans Sandhills portion of the range in Texas. Chan et al. (2020) additionally recovered unique mtDNA haplotypes corresponding to a minimum of three regions in the northern Mescalero Sands and two regions in the southern Mescalero Sands. Nuclear data supported these patterns and it is clear that gene flow is restricted among Dunes Sagebrush Lizard populations, particularly across areas of unsuitable habitat. This more recent study also corroborated earlier findings by Chan et al. (2009) suggesting colonization of the southern Mescalero Sands and Monahans Sands from northern Mescalero populations.

Effects of fragmentation

Construction of networks of caliche well pads and roads for oil and gas development within the shinnery oak sand dune landscape results in the loss and fragmentation of shinnery oak sand dune habitat (Fig. 6). Research has identified potential correlates between oil and gas development and abundance of Dunes Sagebrush Lizards. Using data from visual transect surveys and measurements of oil pad density Sias and Snell (1998) found a significant, negative correlation between lizard abundance and density of oil pads. Additionally, Smolensky and Fitzgerald (2011) identified a positive association between the amount or extent of blowouts within the surrounding habitat. That is, the amount of dune blowout habitat was positively correlated with the average size of dune blowouts. This is important considering the species' demonstrated preference for relatively large dune blowouts. There was not a linear relationship between abundance of Dunes Sagebrush Lizards and total area of caliche well pads and roads because the habitat is highly variable from place to place. To more fully investigate the effects of fragmentation on populations of the Dunes Sagebrush Lizard, a replicated mark-recapture study was undertaken near Loco Hills, NM (Leavitt, 2012). Despite their known presence at all the study sites in recent history, populations in fragmented habitat had very low abundance compared to populations in unfragmented habitat and skewed demographic structure (Fig. 6). Over 5 years of intensive mark-recapture studies at 27 independent trapping grids (18 unfragmented habitat, 9 fragmented habitat) a total of 1421 Dunes Sagebrush Lizards were captured in unfragmented sites and only 30 in the fragmented sites. On fragmented grids, the yearly capture rate started at 0.0019 captures/trap-day in 2009 and 2010 and decreased every year until, in 2013, zero Dunes Sagebrush Lizards were captured on fragmented grids (Walkup et al., 2017). The Dunes Sagebrush Lizard completely disappeared from some fragmented sites where they were historically documented. Among the 27 independent trapping grids, the rate of local extinction was 0.42 ± 0.15. Extinction probability was only 0.04 ± 0.03 at the unfragmented sites (Leavitt et al. personal communication).

A community of 11 species of lizards share the landscape and habitat of the Dunes Sagebrush Lizard (Leavitt and Fitzgerald, 2013). The disappearance of the Dunes Sagebrush Lizard from fragmented areas also accounts for the disassembly of the local lizard community in fragmented habitat. The predictable pattern of community structure across the Mescalero Sands (Leavitt and Fitzgerald, 2013; Ryberg and Fitzgerald, 2016) was essentially randomized. This likely occurred due to changes in the configuration of the dune landscape in fragmented sites which had fewer large dune blowouts than unfragmented sites (Leavitt and Fitzgerald,

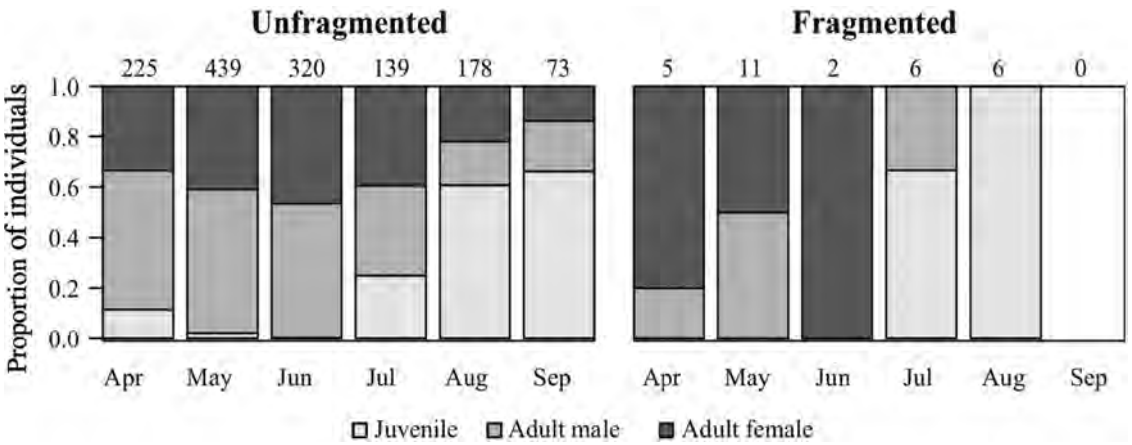

Fig. 6 Effects of landscape fragmentation on the population structure of the dunes sagebrush lizard (from Walkup DK, Leavitt DJ and Fitzgerald LA (2017) Effects of habitat fragmentation on population structure of dune-dwelling lizards. *Ecosphere* 8: e01729. doi: 10.1002/ecs2.1729.). The percent of adult male (dark gray), adult female (gray), and juvenile (light gray) dunes sagebrush lizards varied during the activity season (April-September) during a 5-year mark-recapture study. In 18 unfragmented sites 1374 individuals were sampled and the population structure reflected the annual cycle of recruitment of juveniles. In fragmented areas during the same 5-year period only 30 dunes sagebrush lizards were captured. Moreover, the population structure was severely disrupted, with only a few males, females, or juveniles appearing at these sites.

2013). Because the Dunes Sagebrush Lizard has the narrowest niche breadths of the lizard in this community it was often the first to disappear (Leavitt, 2012). Fragmentation by roads both degraded the dune-blowout habitat and prevented effective dispersal throughout the habitat because the lizards avoid roads (Hibbitts et al., 2013, 2017; Young et al., 2018).

The research on population dynamics and effects of fragmentation, together, led to the conclusion landscape fragmentation causes local populations to decline. It has been shown that Dunes Sagebrush Lizards avoid roads (Hibbitts et al., 2017, Young et al., 2018). Roads create complex challenges for the Dune Sagebrush Lizard. Roads cause habitat loss and degradation. Roads seem to provide avenues for lizard predators and invasion of the dunes by mesquite (*Prosopis* spp.) and other plants. Associated infrastructure like power lines often accompany road construction. Fragmentation is clearly associated with degradation of the shinnery oak dune blowout formations and as explained above, we know that extent of the dune blowout habitat and quality of the habitat are correlated. In turn, condition of the landscape directly affects survivorship and fecundity of local lizard neighborhoods. In relatively short time scales, populations decline, their population structure is disrupted and because rescue from dispersing lizards is not possible, local extinction occurs and has been demonstrated (Leavitt and Fitzgerald, 2013; Walkup et al., 2017).

Translocation research

Because of its narrow habitat requirements and inability to disperse through any areas that are not shinnery oak dunes with blowouts, sustaining the range-wide pattern of occupancy throughout the distribution of the Dunes Sagebrush Lizard is likely to require proactive conservation interventions. In fragmented landscapes, actively translocating individuals to rescue populations or to re-establish populations that have been extirpated may be a valuable conservation strategy. Conservation translocations are purposeful translocations intended to benefit biodiversity. To date, there has been only one attempt at restoring a Dunes Sagebrush Lizard population through a conservation translocation (Parker et al., 2019). Prior to this 4-year study, the Dunes Sagebrush Lizard was known from one locality in Crane County, TX in 1970, but had not been found there since despite repeated surveys. Intensive surveys conducted in the 5 years prior to the translocation attempt did not detect any Dunes Sagebrush Lizards, though highly suitable habitat conditions are present at and around the historical locality.

Translocated Dunes Sagebrush Lizards were sourced from robust donor populations during the breeding season to increase the likelihood that translocated females were already gravid or had at least already mated. Translocated individuals were placed into temporary enclosures at the release site, where their behaviors were closely monitored by observers with binoculars. Once females had nested and hatchlings were detected, the enclosures were removed, releasing the lizards into the broader landscape of the release site. The incipient population was monitored using a landscape-scale pitfall trapping grid of 597 traps covering 14.7 ha and visual encounter surveys (Fig. 7). Lizards were translocated during the first 2 years of the project. Efforts in the final 2 years of the project were focused solely on intensive monitoring. A total of 76 Dunes Sagebrush Lizards were translocated. In the first 3 years of the study, 28 individual Dunes Sagebrush Lizards that hatched at the site were detected. Repeated captures of the same hatchlings in pitfall traps showed that lizards hatched at the site were growing and not dispersing away from the release site. Despite these early successes the population did not persist by the final year of the study. However, this study revealed important lessons that are immediately applicable to future conservation translocations not only for the Dunes Sagebrush Lizard, but also for similarly imperiled habitat specialists and micro-endemics worldwide.

Perhaps the over-arching lesson from the translocation experience is that multiple attempts may be needed for a population to become established. This means that long-term institutional commitment and funding are required and the willingness to endure repeated translocation attempts before long-term population establishment is achieved. A second lesson was the translocation approach was reasonable and feasible. The translocation approach was designed to jump start population growth at the release site. A combination of translocating Dunes Sagebrush Lizards during the breeding season and using a female-biased propagule allowed reproduction to occur at the release site in the first year. Reproduction in the first year was an important milestone, as it eliminated concerns that lizards would not reproduce at the site, due to the stress of translocation or unsuitable nesting sites. The delayed release approach of acclimating lizards to the release site facilitated close monitoring of translocated individuals. Behavioral observations indicated that translocated lizards were performing essential behaviors such as foraging and thermoregulating. A third critical lesson was the importance and magnitude of post-translocation monitoring that is necessary to assess the incipient population. The pitfall trapping grid used to monitor the incipient population was much larger than any documented movements of Dunes Sagebrush Lizards in previous studies (Ryberg and Fitzgerald, 2016; Young et al., 2018; Walkup et al., 2019), and trapping effort was intensive, amounting to 112,451 trap-days over 4 years and 415 h of visual searches. Without such a large trapping effort and high density of traps (597 traps covering 14.7 ha), individuals persisting at the release site as the translocated population dwindled may have been missed.

Release site selection is a vital component of any conservation translocation, but it is even more critical when the target species is an extreme habitat specialist that relies on unique geological formations, such as the Dunes Sagebrush Lizard. Availability of suitable, yet unoccupied habitat, is a limiting factor, which is further complicated by land use and tenure and stakeholder support of translocation efforts. However, the Dune Sagebrush Lizard translocation study demonstrated how suitable release sites can be selected, despite limited options. Because of the past work on the species highlighting the link between population dynamics of the species and landscape configuration, landscape metrics were used to choose a suitable release site for the translocation study. This approach can be applied to translocations of other specialist species that rely on increasingly rare landforms. Another lesson from the Dunes Sagebrush Lizard translocation is that habitat suitability is only one component of selecting a release site. In the final year

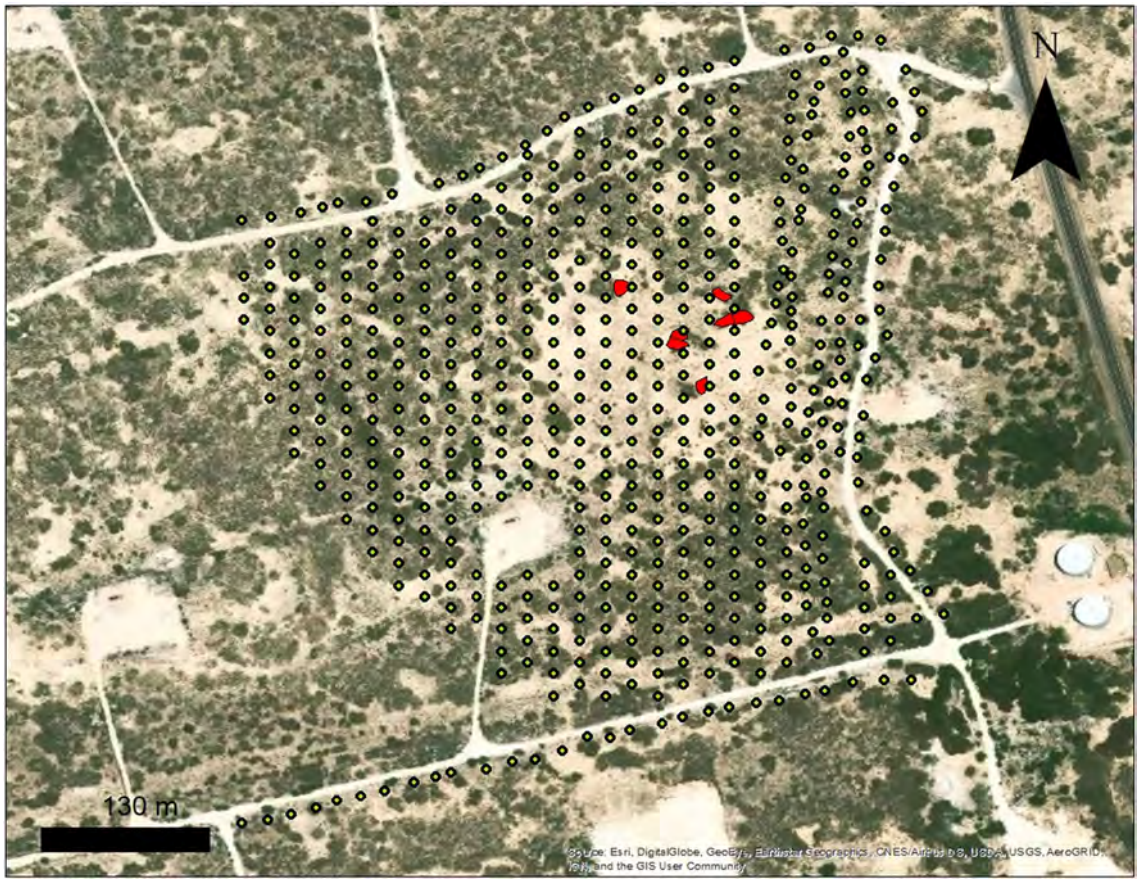

Fig. 7 Aerial view of the translocation site for dunes sagebrush lizards in Crane County, Texas, United States. The delayed-release enclosures are denoted by the small polygons. Individual pitfall traps are shown as dots. The extent of the trapping grid for post-translocation monitoring was 14.7 ha and consisted of 597 traps spaced 15 m apart.

of the study, the property on which lizards were translocated was sold, with both new owners and researchers unaware of each other and the translocation effort. After completion of this study, there was no interest in allowing future studies on the property. This underscores the importance of land security when choosing a release site for a conservation translocation.

Implications for conservation

The Dunes Sagebrush Lizard is imperiled by the land-use activities that disturb the shinnery oak dunes in the Mescalero-Monahans Sandhills. Because of the direct linkages between the lizard populations and condition and extent of the shinnery oak dunes with blowouts, damage to the habitat has severe consequences for the local population of Dunes Sagebrush Lizard. Removal of shinnery oak by herbicide spraying and development of oil and gas fields with networks of interconnecting roads, and most recently mining of the sand to use in hydraulic fracturing (fracking) are the principal threats to the shinnery oak dunes. There is no evidence we are aware of that livestock grazing or recreational use of areas in the region cause habitat degradation at any appreciable scale. Thus, conservation of the Dunes Sagebrush Lizard is entirely dependent on areas of relatively intact shinnery oak dunes. This same recommendation, to preserve the shinnery oak dunes with blowouts, has been repeated since 1997 with increasing precision in every publication (Fitzgerald et al., 1997, Ryberg et al., 2015, others cited herein).

The irreplaceable dune-blowout landform

Once disturbed, the dune-blowout landform is irreplaceable. Because the dune blowout landform depends on the interactions between wind, sand, and the stabilizing shinnery oak vegetation, loss of any of these components results in loss of the landform. The breakdown of the complex feedbacks that create the dune-blowout landform causes the emergence of new stable states across the landscape. Removal of shinnery oak through herbicide spraying, for example, results in irreversible loss of dunes (Fig. 8). Without the stabilizing shinnery oak vegetation, wind erodes the dunes into a flatter landscape with different vegetation associations. Landscape fragmentation also appears to disrupt the geomorphological processes that allow the dune blowout landform to

Fig. 8 Flat grasslands emerged after herbicide application to a shinnery oak sand-dune landform in 1993. A fence line marking sprayed and intact landscape bisects the images. In 1996, dead shinnery oak was still present, but by 2005, dead oaks had decomposed and the landform had eroded and was replaced with a flat grassland. By 2011, the dune blowout landform was still absent from the sprayed site. The view from this sprayed area looking east (far right) was of a flat landscape with remains of sand-dune blowouts surrounded by sunflowers (shinnery oak is absent). Intact shinnery oak sand-dune landforms with blowouts are in the background.

sustain itself. Shinnery oak dunes that were disturbed over 30 years ago have not recovered and there are no areas where new dunes are being formed (Ryberg and Fitzgerald, 2016).

Ryberg et al. (2015) considered, "failure to recognize the irreplaceability of self-organized landforms on which biodiversity depends may lead to uninformed or ineffective habitat management practices with correspondingly poor outcomes for threatened or endangered species." Because disruption of shinnery oak dunes results in emergence of alternative stable states, reliance on ecological succession is not a viable conservation strategy. Research has shown repeatedly that populations of Dunes Sagebrush Lizards need contiguous expanses of shinnery oak dunes with blowouts covering hundreds of hectares (Leavitt and Fitzgerald, 2013; Ryberg et al., 2013; Walkup et al., 2017). Thus, it is also implausible to consider artificial construction of dunes or restoration of shinnery dune-blowouts at any scale of importance to conservation. Using heavy machinery to create dunes and then establish shinnery oak is unlikely to work to re-create 100 s of hectares of lost dune-blowout areas and would be an expensive and Herculean task in the conservation world. One must also consider the scale at which restoration efforts would change the outlook for conservation of the Dunes Sagebrush Lizard as a species.

In the Mescalero-Monahans Sandhills, endemic biodiversity including the Dunes Sagebrush Lizard evolved in concert with the emergent dune-blowout landform. As such, conservation of this specialized biodiversity is a dual challenge of conserving existing populations of specialized species and preserving the irreplaceable landforms on which they depend (Ryberg et al., 2015).

The double whammy of fragmentation

The neighborhood dynamics described above are critical for maintaining stable populations of the Dunes Sagebrush Lizard. Moreover, these neighborhood dynamics are directly linked to the condition and configuration of the irreplaceable dune-blowout landform, the condition of which determines survival and fecundity rates of the lizards at local scales. Landscape fragmentation lands a double whammy, or twofold blow, to both the populations of the lizards and the irreplaceable landform on which it depends. In fragmented areas, local neighborhoods of lizards are isolated because diffusion dispersal that would normally occur across contiguous areas of habitat is impeded. This leads to local population disruption and in some cases local extinctions. At the same time, fragmentation disrupts the geomorphological feedbacks that sustain the dune-blowout landform. In increasingly fragmented areas the quality of habitat declines, become less topographically complex and invaded with more grasses and woody vegetation like mesquite (*Prosopis* spp.).

All these research findings converge on the conclusion that to conserve populations of the Dunes Sagebrush Lizard it is paramount to preserve contiguous expanses of the shinnery oak dunes with interconnected dune blowouts.

Confronting landscape fragmentation is a vexing problem because of long-established protocols for oil and gas extraction, landowner rights, and the way that leases for oil and gas development are allocated. At the most local scales, well-intentioned conservation actions such as avoiding disturbance of a dune may not thwart the larger-scale problem of fragmentation. For example, moving oil wells one-by-one may not avoid the problem of bisecting and isolating contiguous areas of shinnery oak dunes at a larger scale (Figs. 6 and 9, respectively). Undoing the damage caused by fragmentation is an impractical request because the dune-blowout landform will not restore itself through ecological succession. In some fragmented areas abandoned well pads and caliche roads are being removed, which is a positive land stewardship practice that may help sustain integrity of nearby shinnery oak dunes. It should remain the highest priority to de-incentivize fragmentation of shinnery oak dunes.

Conservation history and policy mismatches

Conservation history

The Dunes Sagebrush Lizard and the unique inland dune ecosystem that it occupies has been of great concern to conservationists, natural resource agencies, landowners, the oil and gas industry and other stakeholders since the mid-1980s. Indeed, Sherwin (2014)

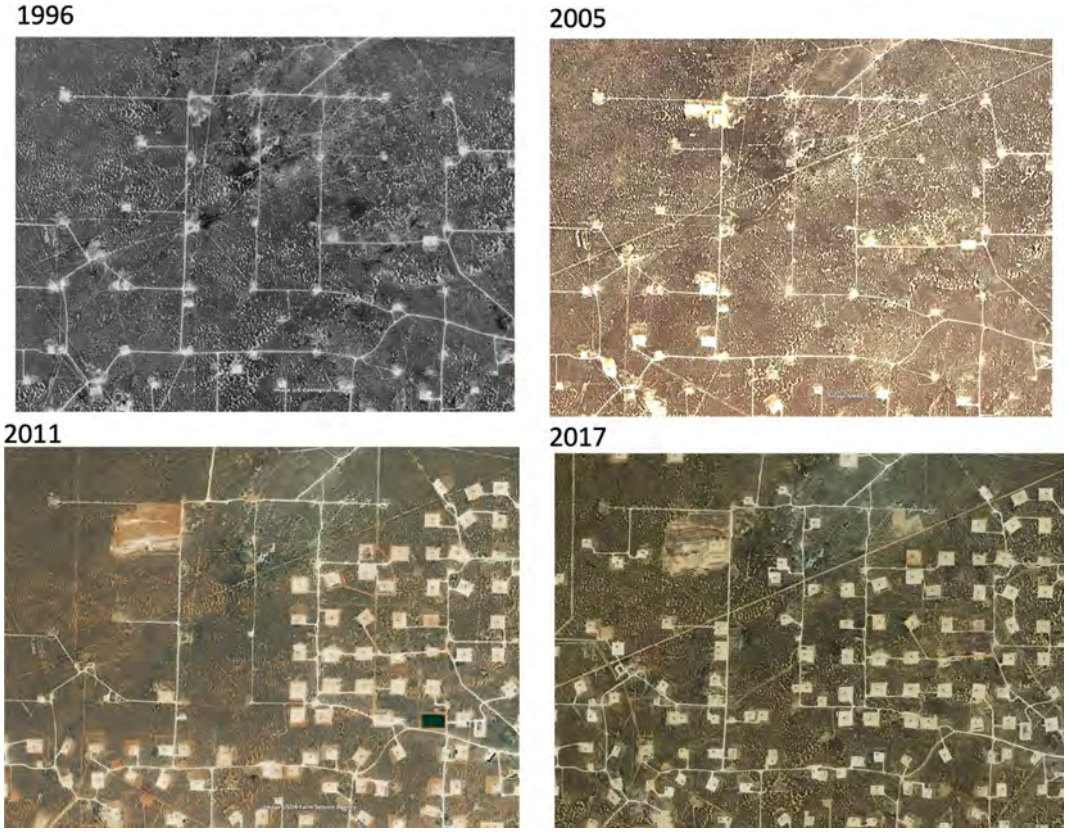

Fig. 9 Images showing continuing fragmentation of shinnery oak sand dunes in the Mescalero-Monahans Sandhills ecosystem. The images of the same area show increasing fragmentation of the habitat due to addition of caliche well pads and interconnecting caliche roads. The dunes sagebrush lizard is known from this area.

pointed out that the Dunes Sagebrush Lizard "has arguably been one of the most controversial species involved in the recent battles over listing species under the Endangered Species Act (ESA)". The entire range of the species overlies the Permian Basin, which is among the most important regions for oil and gas production for the United States. There has been strong opposition to listing the species under the ESA based on fears there could be restrictions on land use and negative economic impacts that would arise from protecting the lizard's habitat. The history of conservation of the Dunes Sagebrush Lizard has been fraught with mismatches between ecological knowledge and conservation policies. In short, conservation actions have not taken place at the scale necessary to achieve permanent legal protection of contiguous areas on shinnery oak dunes.

The U.S. Fish and Wildlife Service (USFWS) classified the Dunes Sagebrush Lizard as potentially appropriate for listing under the Endangered Species Act (ESA) in 1982. The species received protected status from the New Mexico Department of Game and Fish in 1975 and is currently listed as Endangered by that agency. The species is considered critically imperiled by the Texas Parks and Wildlife Department's action plan (Texas Parks and Wildlife Department, 2012). At the federal level, the species has been categorized as a "species of concern" or "candidate" for protection under the ESA since 1982. Petitions or proposed rules to list the Dunes Sagebrush Lizard as Endangered under the ESA have been filed several times, most recently in 2010 and 2018.

Conservation agreements

To avoid perceived regulatory burden with federal listing of the species as threatened or endangered with or without critical habitat, voluntary conservation agreements have been put into place in New Mexico and separately in Texas. These agreements are established by partnerships of either Federal and State agencies called "Candidate Conservation Agreements" (CCA) or with partnerships with private entities, generally called "Candidate Conservation Agreements with Assurances" (CCAA). These CCAs and CCAAs are legal agreements between the USFWS and a designated permit holder who administers them. The agreements are designed to incentivize protection of the shinnery oak dunes and include various stipulations related to conservation of the Dunes Sagebrush Lizard and its habitat. Participation in the CCAAs is voluntary and participants agree to a fee structure that generates funds to cover costs of administering the agreement and the conservation interventions. The assurances in these CCAAs are the incentive for participation. They guarantee to participants that activities allowed under the CCAA can continue in perpetuity even if the species is listed under the ESA. However, there are no legal statutes that carry penalties for non-participation or for unauthorized take of Dunes Sagebrush Lizards or habitat destruction.

The Dunes Sagebrush Lizard was proposed for federal listing as endangered by the USFWS in December 2010 (U.S. Fish and Wildlife Service, 2010). In June 2012, the proposed rule was withdrawn, based on the USFWS assessment that the threats were being addressed by the implementation in 2008 of the New Mexico CCA and CCAA, the Texas CCAA ("Texas Conservation Plan" [TCP]), and the Bureau of Land Management's (BLM) Resource Management Plan Amendment (U.S. Fish and Wildlife Service, 2012). In New Mexico the CCAA has been viewed as largely successful. More than 600 oil wells have been re-located from their proposed location to avoid dunes and blowouts. The CCAA in New Mexico addresses conservation concerns for the Lesser Prairie Chicken and the Dunes Sagebrush Lizard. This duality has fostered broad participation by landowners and resulted in essentially all of the habitat for these species to be covered by the CCAA. In Texas, the TCP never achieved coverage of more than about half of the habitat for the Dunes Sagebrush Lizard. The TCP was rescinded in 2018. One major contributing factor to its withdrawal was the start of sand mining in the Permian Basin in 2017, since the TCP could not address impacts on the shinnery oak dunes by the sand mining industry.

In mid-2018, the Dunes Sagebrush Lizard was again petitioned for listing by the Center for Biological Diversity and Defenders of Wildlife; the USFWS determined that listing may be warranted based on changes in habitat or range due to oil and gas developments and operations and sand mining, potential impacts from climate change, and an inadequacy of existing regulation (U.S. Fish and Wildlife Service, 2020). The Texas Comptroller for Public Accounts submitted a new version of the TCP to the USFWS in 2019. That TCP and the associated take permit was transferred to the American Conservation Foundation (ACF; https://www.ac-foundation.com/) in 2020. Also, in 2020, an additional CCAA for Texas was created to include both private landowners as well as stakeholders in the oil and gas and sand mining industries (Canyon Environmental LLC, 2020). To inform the listing process, a Species Status Assessment of the Dunes Sagebrush Lizard is due to be finished in late 2021.

Future of the Dunes Sagebrush Lizard

After more than two decades of conservation attention, the future of the Dunes Sagebrush Lizard is still uncertain. The only certainty for the Dunes Sagebrush Lizard, given its very restricted and naturally disjunct distribution and the land use practices that have caused fragmentation and loss of habitat, is that the conservation policies being developed today will determine its fate. Ideally those policies reflect knowledge gained from the integrated research findings described above, such that under the best-case scenario, the Dunes Sagebrush Lizard persists as a conservation reliant species requiring regular conservation interventions in areas where fragmentation and disturbance have degraded suitable habitat.

Population monitoring at representative sites is ongoing as a result of the conservation agreements. The conservation agreements and other entities also fund research on the conservation biology of the Dunes Sagebrush Lizard. The conservation agreement in New Mexico is promoting land stewardship practices and continually striving to improve practices aimed at minimizing disturbance of shinnery oak dunes. However, it is too early to tell if the conservation agreements in Texas will be effective.

There is a clear need to protect areas of relatively undisturbed shinnery oak dunes that are as extensive as possible. Unfortunately, there is only one formally protected area within the Mescalero-Monahans Sandhills Ecosystem, Monahans Sandhills State Park, Texas. This park is privately owned and leased to the Texas Parks and Wildlife Department. It is surrounded by active oil fields and sand mines are operating in the large Monahans Dune formation. Dunes Sagebrush Lizards occur there, but they are not as abundant as in areas in the Mescalero Sands of New Mexico. There are no other protected areas of shinnery oak dunes in Texas. In New Mexico, the U.S. Bureau of Land Management maintains two Areas of Critical Environmental Concern for Conservation with habitat for the Dunes Sagebrush Lizard, but the designation of these public lands can be changed by decree within the U.S. Department of the Interior.

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