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Why didn't the lizard cross the road? Dunes sagebrush lizards exhibit road-avoidance behaviour

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Abstract

Context. Research has shown many negative effects of roads and traffic on wildlife and other biodiversity. The direct and indirect mechanisms through which roads and traffic harm animal populations vary across taxa, making mitigation of road effects a great challenge for conservation. As such, a large toolkit of species-specific management techniques may be needed to mitigate the negative effects of roads for wildlife and other biodiversity. The dunes sagebrush lizard, *Sceloporus arenicolus*, is a psammophilic (sand-loving) habitat specialist endemic to the Mescalero–Monahans Sandhills ecosystem of New Mexico and Texas. Within this ecosystem, roads fragment shinnery oak sand-dune landforms occupied by the species.

Aims. In the present study, we conducted behaviour trials in experimental enclosures to test whether the smallest roads restrict movements of the dunes sagebrush lizard. In addition, we also conducted trials to evaluate whether a sand-filled wildlife-crossing feature could facilitate road crossing.

Methods. We conducted behavioural trials on 24 dunes sagebrush lizards in our control enclosure and 22 lizards in our road and sand-filled wildlife-crossing enclosure. Movements were recorded for 15 min. The final locations at the end of each trial were analysed using circular statistics to determine whether movements in the road or the sand-filled wildlife-crossing enclosures were different from the control.

Key results. Our results supported the hypotheses that dunes sagebrush lizards avoid roads and do so according to a surface-avoidance mechanism. We also found that the wildlife crossing-feature design tested here had no effect on the movements or road-crossing frequency of dunes sagebrush lizard.

Conclusions. Surface-avoidance behaviour indicated that roads will persistently affect the movements of dunes sagebrush lizard, even when traffic is not present. Also, more research into an effective wildlife crossing is needed to increase connectivity of fragmented populations.

Implications. These findings help evaluate the impact of roads in creating isolated populations that experience increased demographic stochasticity and, in some instances, localised extirpation in this species. Our study can guide conservation plans for the dunes sagebrush lizard, and contribute to our understanding of road effects on biodiversity in general.

Additional keywords: direct road effects, ecopassage, indirect road effects, lizard ecology, psammophilic, road kill, road mortality, surface-avoidance behaviour, wildlife passage.

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Introduction

Roads are ubiquitous in most landscapes around the world (Forman *et al*. 2003; Andrews *et al*. 2008; van der Ree *et al*. 2015). Ecological research has shown many negative effects of roads and traffic on wildlife and other biodiversity, including the loss, fragmentation and degradation of habitat (Taylor *et al*. 1993; Forman and Alexander 1998). For terrestrial wildlife in particular, roads and traffic can create barriers to movement that result in population subdivision (Noss *et al*. 1996; Hanski 1999; Forman 2000; Clark *et al*. 2001; Lesbarrères and Fahrig

2012). For example, traffic mortality can contribute to population subdivision by reducing the flow of individuals between subpopulations (Swihart and Slade 1984; Gerlach and Musolf 2000). Habitat degradation can also contribute to population subdivision by reducing the quality of resources along roads and limiting reproduction and survival so that linear sink habitats reduce movements among subpopulations (Reijnen and Foppen 1994; Ortega and Capen 1999). At the individual level, animals can also exhibit a variety of road-avoidance behaviours that ultimately constrain their movement patterns and lead to population subdivision (Jaeger *et al*. 2005). For example, animals with noise-avoidance behaviours may stay away from areas where road noise is audible, spatially extending the road-effect zone (e.g. some birds; Reijnen *et al.* 1995, 1996, 1997).

Typically, the magnitude of this road effect depends on traffic volume rather than road size (Jaeger *et al*. 2005). Car-avoidance behaviours can also limit animal movements in proportion to traffic volume, but the extent of the road effect is limited to the road itself (Jaeger *et al*. 2005). A third type of road-avoidance behaviour of particular importance to animals that exhibit strong habitat preferences or specialisations is avoidance of the actual road itself, where individuals avoid the surface and edge of roads because of perceived inhospitable conditions (e.g. no shelter, different microclimate, lack of vegetation, substrate differences; Merriam *et al*. 1989; McGregor 2004). Road effects on the movements of species exhibiting surface-avoiding behaviours are continuous, even when traffic is not present (Jaeger *et al*. 2005).

By reducing or preventing movements, roads decrease landscape connectivity for animal populations (Taylor *et al.* 1993). Efforts to mitigate road effects typically involve the design and installation of wildlife-crossing structures, sometimes called wildlife passages or ecopassages, to increase landscape connectivity (van der Ree *et al*. 2007). Although many wildlife-crossing structures have been installed, a recent review has concluded that some studies contain little useful information for evaluating the efficacy of crossings for mitigating the effects of roads on wildlife population connectivity (van der Ree *et al.* 2007; Gilbert-Norton *et al*. 2010). The reasons for these research failures are complex; however, in many cases, the failure occurs because wildlife researchers are not involved in the pre-construction, wildlife-crossing study design (e.g. Eberhardt *et al*. 2013). As a result, these studies often suffer from a lack of scientific rigor related to poor experimental design and absence of data before and after wildlife-crossing construction. Alternatively, research shows that the most successful wildlife-crossing studies and mitigation projects are those aimed at minimising the barrier effects of roads for individual species rather than more generic designs targeting effects on all wildlife (Lesbarrères and Fahrig 2012).

Here, we investigate the effect of roads on movements of the dunes sagebrush lizard (*Sceloporus arenicolus*) and the potential behavioural mechanisms responsible for any observed effect. We also evaluate the effectiveness of a proposed wildlife-crossing feature designed to increase road-crossing frequency for this species. The dunes sagebrush lizard is a psammophilic habitat specialist endemic to the Mescalero–Monahans Sandhills ecosystem of south-eastern New Mexico and adjacent western Texas (Degenhardt *et al*. 1996). Within this ecosystem, the dunes sagebrush lizard resides only in shinnery oak (*Quercus havardii*) sand-dune landforms, which consist of parabolic dunes and depressions called blowouts that are created from an interaction among wind, sand and the dune-stabilising shinnery oaks (Fitzgerald and Painter 2009; Laurencio and Fitzgerald 2010; Ryberg *et al*. 2015). Within this landform, this species prefers large blowouts with steep slopes (Fitzgerald and Painter 2009; Ryberg *et al*. 2012; Hibbitts *et al*. 2013; Ryberg and Fitzgerald 2015*a*). Population persistence in this species depends on dispersal throughout interconnected habitat patches (Ryberg *et al*. 2013).

Roads made of caliche (a mineral used for road and oil and gas well pad construction) fragment shinnery oak sand-dune landforms and have been shown to restrict movements of dunes sagebrush lizard (M. E. Young, W. A. Ryberg, L. A. Fitzgerald and T. J. Hibbitts, unpubl. data)), creating isolated populations that experience increased demographic stochasticity, greatly reduced abundance and potentially localised extirpation (Leavitt and Fitzgerald 2013). Direct mortality from vehicular traffic has been documented only once for the dunes sagebrush lizard (A. L. Fitzgerald, pers. comm.). These observations suggest that movements of dunes sagebrush lizard are most likely restricted by road surface-avoidance, car-avoidance, or noise-avoidance behaviours.

In the present paper, we report results from an experiment designed to test the hypotheses that caliche roads affect the movements of dunes sagebrush lizards and that the effects transpire through road surface-avoidance mechanisms. Caliche roads are made of compacted calcium carbonate rock, which provides a hard surface for vehicular traffic but is still permeable compared with asphalt or other paved roads. We also evaluated a proposed mitigation technique designed to minimise the effects of roads on movements of dunes sagebrush lizards, by creating sand-filled wildlife-crossing features across caliche roads.

Materials and methods

Study area

Our study area was in the Mescalero–Monahans Sandhills ecosystem of south-western Andrews County, Texas, USA. Shinnery oak sand-dune landforms throughout this ecosystem are dissected by roads of various sizes, ranging from unpaved jeep tracks to caliche roads to paved county, state and federal highways. For the present study, we selected a site situated within a large shinnery oak sand-dune landform known to be occupied by the dunes sagebrush lizard that was also partially bisected by a small caliche road. This particular road represents the smallest type of caliche road found within the ecosystem, a relatively narrow (5 m) flat track of caliche, lacking roadside ditches, that lead to an abandoned oil well pad used less than once per day. Because the effect of roads on wildlife and habitat should increase with the size of the road (Montgomery *et al*. 2013), this choice of a small caliche road allowed us to develop a null hypothesis, that the road would not affect movements of dunes sagebrush lizard, which was difficult to reject. If the null hypothesis were rejected in the present study, conducting trials with the smallest type of caliche road, then it stands to reason that much larger and more developed roads ranging up to asphalt-paved highways with roadside ditches should pose an even greater barrier to lizard movements. In addition, we were given permission to block traffic during the entire experiment so as to isolate a mechanism (i.e. road avoidance vs car or noise avoidance) for any observed changes in lizard movement. Although this opportunity to block traffic afforded us the ability to design a tightly controlled experiment, it also limited the number of sites and roads available for the experiment.

Study design

At the study site, we constructed two circular enclosures 15 m in diameter that were separated by 250 m (Fig. 1). We used circular enclosures for two important reasons. Circular enclosures in these behavioural trials avoid bias created by corners in a rectangular structure. Pilot studies indicated that lizards tended to move towards the closest wall in a square enclosure. Circular enclosures also ensured that the entire enclosure wall was equidistant from the central starting point. We used opaque plastic to form the 0.5-m-high walls of the enclosure. Enclosure walls were also buried in sand to prevent lizards from escaping underneath the plastic. Vegetation was cleared from the enclosures, and we placed a small clump of live shinnery oak at each of the cardinal directions 1 m away from the wall of the enclosure. At the centre, we placed a 50 × 50 cm plywood board, which was covered with a thin layer of sand. This was the lizard release point for our trials.

The control enclosure was located in undisturbed occupied habitat where sand was the only substrate. The experimental enclosure also contained sand, but was divided by the 5-m-wide caliche road running alongside the release point (Fig. 1*a*). No traffic was allowed on this road during the experiment. To construct the enclosure for the second experiment, which tested the hypothesis that the dunes sagebrush lizard will use a sand-filled, wildlife-crossing feature, we dug a 1-m-wide, 20-cm-deep trench across the caliche road, directly in front of the lizard release point, and filled it with sand from the occupied habitat (Fig. 1*b*).

Behaviour trials

All trials were conducted on clear days in full sun from 6 to 10 August 2014. To minimise the effects of time and weather, we conducted all trials during the peak activity period of the lizards (from 0830 hours to 1200 hours) at air temperatures between 25°C and 35°C. Lizard subjects were captured from the surrounding habitat by pitfall trapping, noosing and hand-capture. Subjects were temporarily marked with permanent ink pens for individual identification and held in 20-L buckets containing 15 cm of sand between trials. After the end of the each trial, the lizard was removed from the enclosure and returned to the holding bucket and was later released at their point of capture after completion of the study, in accordance with approved institutional animal care and use committee standards

Trials began by placing the subject on the centre board under an opaque plastic container. One observer sat outside the enclosure 15 m from the release point, and used a string-and-pulley system to lift the container and start the trial. Most lizards stayed at the starting point for some time and appeared to make decisions about the direction they moved. Some lizards moved multiple times before the end of the trial, whereas others reached the edge of the enclosure in one movement. In cases where the lizard was startled by the lifting of the container, the trial was started again after 5 min. The observer, with the aid of binoculars, recorded the distance, direction and time of each movement made by the lizard for 15 min. Trials were completed after 15 min or if the subject reached the enclosure wall. At the end of each trial, we recorded the subject's location in the enclosure. The same 22 subjects were used in all enclosures, with two additional lizards used in the control enclosure. We randomly selected half of the subjects to start in the control enclosure and the other half in the road enclosure. All trials in the experimental

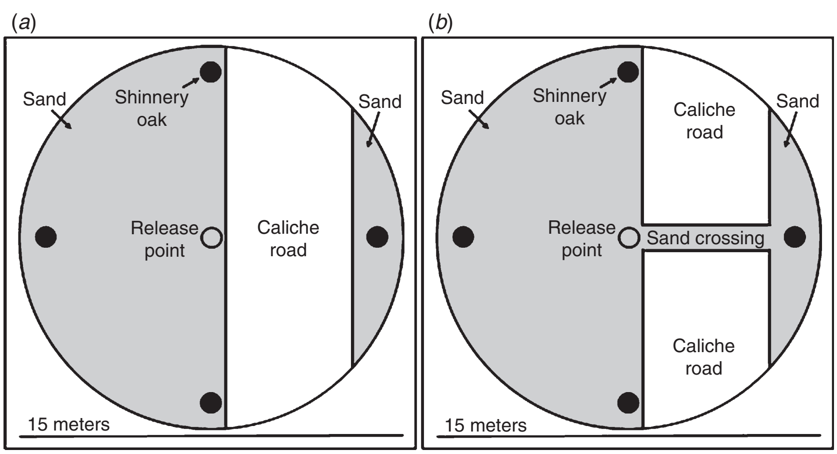

Fig. 1. Diagram of (*a*) road enclosure and (*b*) road enclosure with sand-filled, wildlife-crossing feature. The control enclosure (not pictured) was identically constructed, but lacked the caliche road. All enclosures were operational 6–10 August 2014 during dunes sagebrush lizard (*Sceloporus arenicolus*) behavioural trials and were located within the Mescalero–Monahans Sandhills ecosystem of south-western Andrews County, Texas, USA.

wildlife-crossing enclosure were conducted last. We conducted 22 trials in the road and experimental wildlife-crossing enclosures, and 24 trials in the control enclosure.

Statistical analyses

We tested for uniformity of movements in each enclosure by using circular statistics (Fisher 1993). Failure to reject the null hypothesis in tests of uniformity would indicate that movements of dunes sagebrush lizard were uniformly distributed or equally likely around the circular enclosure. Alternatively, rejection of the null hypothesis would indicate that the distribution of the movements of dunes sagebrush lizard was significantly different from uniform.

For each enclosure (control, road, wildlife crossing), we ran three tests of uniformity by grouping or binning the final lizard locations in three different ways, corresponding to halves, thirds and quarters of the enclosures. By using multiple grouping arrangements, we can be certain that our results were not affected by the number and position of bins chosen for analysis. For each grouping arrangement, we totalled the number of times each trial ended in each bin of the enclosure. We then compared that observed distribution of the movements of dunes sagebrush lizard with the expected uniform distribution of movements for each grouping arrangement by using a chi-square test (χ^2) and $\alpha = 0.05$ significance threshold.

Results

We used 13 female and 11 male dunes sagebrush lizards in these trials. Mean snout–vent-length was 57.91 mm (s.d. = 4.01 mm), mean tail length was 72.36 mm (s.d. = 21.11 mm) and mean mass was 5.44 g (s.d. = 1.30 g).

Use of space and movements within the control enclosure could not be differentiated from random (i.e. uniform), whether the enclosure was divided into halves, thirds or quarters (Table 1). In both the road enclosure and the wildlife-crossing enclosure, the null hypothesis in the test of uniformity of movements was rejected under all three data-grouping arrangements. Rejection of the null hypothesis indicated that the distribution of the movements of dunes sagebrush lizard was significantly different from uniform in the road and wildlife-crossing enclosures. In 44 trials (22 in the road enclosure and 22 in the wildlife-crossing enclosure), eight subjects crossed the road. In the road enclosure, three subjects either ran onto the road or crossed the road. In the wildlife-crossing enclosure, with the 1-m sand-filled trench, 0 of 22 subjects used the trench, and five subjects ran onto the road or crossed it. In all the other 36 trials, the lizards avoided the road and the sandy area across the road from the starting point. The sand-filled, wildlife-crossing feature had no detectable effect on use of space or movements of dunes sagebrush lizard.

Table 1. Statistical results of chi-square test (χ^2) using a threshold of $\alpha = 0.05$ for significance (*) comparing observed distribution of movements of dunes sagebrush lizard (*Sceloporus arenicolus*) with the expected uniform distribution of movements for each enclosure and data grouping

All enclosures were operational from 6 to 10 August 2014 and were located within the Mescalero–Monahans Sandhills ecosystem of south-west Andrews County, Texas, USA. Degrees of freedom (d.f.), sample size (*N*), and *P*-values are reported

Enclosure	d.f.	*N*	χ^2	*P*
Control halves	1	24	0.17	0.700
Control thirds	2	24	3.25	0.200
Control quarters	3	24	7.00	0.100
Road halves	1	22	8.91	0.010*
Road thirds	2	22	23.38	<0.001*
Road quarters	3	22	38.73	<0.001*
Wildlife-crossing halves	1	22	14.73	<0.001*
Wildlife-crossing thirds	2	22	32.97	<0.001*
Wildlife-crossing quarters	3	22	38.00	<0.001*

Discussion

The present experiment demonstrated that a small caliche road bisecting occupied habitat affected movements of the dunes sagebrush lizard. In the control enclosure, movements of dunes sagebrush lizard were uniformly distributed or equally likely throughout the circular enclosure, whereas in the road enclosure, the distribution of the movements of dunes sagebrush lizard was significantly different from uniform. In 82% of trials, the dunes sagebrush lizard completely avoided the road and sand-filled, wildlife-crossing feature. This road effect on the movements of dunes sagebrush lizard was not influenced by vehicle traffic and noise because we excluded these factors during the experiment. It is important to also note that the road selected for the study was nearly abandoned, having been used far less than once per day for some time. With these other road-avoidance mechanisms excluded, we conclude that deviation from uniformity in movements of dunes sagebrush lizard is driven by behavioural avoidance of hard road surfaces such as caliche. Sand is the exclusive substrate that is used by dunes sagebrush lizards. No evidence exists that they will cross other substrate types; in fact, they prefer the steepest sandy slopes within their habitat (Hibbitts *et al*. 2013) and are not known to cross large expanses of flat sand. This preference for steep slopes within the Mescalero–Monahans Sandhills ecosystem may also affect their willingness to cross a flat open road with a caliche (rocky) substrate.

Evidence of surface avoidance limiting the movements of dunes sagebrush lizard leads to several meaningful implications for conservation of this species, as well as other species exhibiting similar road-avoidance behaviours. First, the effects of roads on dunes sagebrush lizard populations must be considered long term and persistent. This means that even if roads were simply closed and abandoned, the effects on populations will persist as long as caliche is present. Second, because we controlled for noise and traffic in the present experiment, it is unclear how the dunes sagebrush lizard might respond to these factors. Noise and traffic may also have a negative effect on the movements of dunes sagebrush lizard, which may make roads even greater barriers to movement than has already been observed.

Third, we expect that larger caliche and paved roads, which make up the extensive checker-board network of roads in the Mescalero–Monahans Sandhills ecosystem, represent a much stronger effect on movements of the dunes sagebrush lizard. Because we rejected the null hypotheses that this small caliche road would not affect lizard movements, we are confident in the prediction that wider and more developed roads ranging up to asphalt-paved highways pose a greater barrier to movements in this species. Larger roads are usually elevated above-grade and have roadside ditches. The larger the road, the more pronounced the effect of ditches and the roadway, which represent a rather broad swath of inhospitable habitat to the dunes sagebrush lizard. The trend of decreased crossing rate in association with increasing road width has been shown in several other species that are not specialised on a particular habitat (Brehme *et al*. 2013).

The effects of roads on wildlife exhibiting road-avoidance behaviours are poorly described for many species, because these animals seldom enter the roadway and, therefore, are rarely detected (Andrews *et al*. 2015). As a result, species-specific differences in such behaviours are less understood than is variation in species-specific mortality rates on roads. Rates of mortality on roads, including those of reptiles, vary by species and also by type of road, season, weather, individual age- or stage-class, sex, and many other factors (Fahrig *et al*. 1995; Andrews *et al*. 2008; van der Ree *et al*. 2015). Variation in direct and indirect effects of roads and the mechanisms (e.g. surface, car, noise avoidance) driving road-avoidance behaviours within and among taxa might be explained by many of the same factors. Although broad generalisations for reptiles in particular are not possible at this time, road-avoidance tendencies have been noted for tortoises, lizards and snakes, and most of those studies identified inhospitable surfaces, substrates or other features as the most likely cause of avoidance (Andrews *et al*. 2008 and references therein). This behavioural avoidance mechanism appears logical, given that reptiles are well known for having adaptations (e.g. fringed toes) and performance capabilities (e.g. running on sand, climbing on rocks and trees) closely tied to different surfaces and substrates within habitats (Garland and Losos 1994 and references therein).

Similar logic was applied in the present study to design a simple and inexpensive wildlife-crossing feature with a sandy surface that could facilitate road crossings by dunes sagebrush lizard. In natural settings, the dunes sagebrush lizard has been observed using linear sandy features, such as pipelines constructed across shinnery dune complexes. In a radio-tracking study, a single dunes sagebrush lizard individual crossed a sand-covered section of a caliche road bisecting continuous shinnery oak dunes where the lizard's territory abutted the road (M. E. Young, W. A. Ryberg, L. A. Fitzgerald and T. J. Hibbitts, unpubl. data). Despite our crossing design being informed by these observations, the sand-filled wildlife crossing tested in the present study did not significantly affect movement patterns or increase the rate of road crossings in the dunes sagebrush lizard. No dunes sagebrush lizard subjects used the wildlife-crossing feature. We believe that lizards may not have been able to quickly perceive this feature during our trials and, after a longer time in the enclosure, may have found and used the wildlife-crossing feature; however, the feature also may have been too narrow or could have needed some sort of fencing directing lizards to the crossing for it to be more effective. Whereas more research is needed to explore alternative wildlife-crossing designs that are capable of facilitating movements of dunes sagebrush lizards across roads in occupied habitat, roads that fragment shinnery dune landscapes will remain a challenge to maintenance of population and landscape connectivity in the Mescalero–Monahans Sandhills ecosystem.

Conclusions

Persistence of dunes sagebrush lizard depends on the quality and connectivity of large contiguous areas of suitable habitat across the Mescalero–Monahans Sandhills (Fitzgerald and Painter 2009; Laurencio and Fitzgerald 2010; Hibbitts *et al*. 2013; Ryberg *et al*. 2013, 2015; Ryberg and Fitzgerald 2015*b*), and recent research has indicated that roads are the main source of fragmentation in this ecosystem (Smolensky and Fitzgerald 2011; Leavitt and Fitzgerald 2013). The best strategy to maintain the quality and connectivity of large contiguous areas of suitable habitat is avoidance of shinnery oak sand-dune landforms when constructing new roads. When areas of occupied habitat are fragmented by existing roads, connectivity of habitat patches might be restored through road removal. Candidates for road removal can be selected in sites with high road redundancy (multiple access roads to the same location) or in areas where roads are no longer in use. Additional research into effective wildlife-crossing features for the dunes sagebrush lizard should continue, with the goal of increasing connectivity at sites where road removal or road avoidance is not possible.

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