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Effects of roads and roadside fencing on movements, space use, and carapace temperatures of a threatened tortoise

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ABSTRACT

Roads are widespread features of many landscapes that can negatively affect wildlife, most notably through animal-vehicle collisions. Roadside fencing has increasingly been installed to help eliminate this source of mortality. While fencing may reduce road mortality, other types of wildlife responses to this novel barrier are not well understood. Here, we examined the movement behavior, space use, and carapace temperatures of Mojave Desert Tortoises (*Gopherus agassizii*) as they interacted with a roadside fence and an unfenced road. Using GPS loggers, we tracked tortoise movements for two years at 15-min intervals. We found that carapace temperatures were greater near structures (fence or unfenced road) than away from structures; tortoises near the unfenced road had higher mean carapace temperatures, but tortoises along the fence experienced more extreme upper temperatures that approached the species' thermal limit. Movement speeds were also higher along the structures than away from them. Tortoise home range sizes decreased with proximity to the fence or road; fragmentation of home ranges and road-crossing avoidance may have contributed to smaller home ranges along the fenced and unfenced road, respectively. While tortoises crossed the road significantly less than expected by chance, they did so primarily in May and July and in areas with washes, indicating that placement of roadside fencing and animal underpasses could be optimized by targeting areas where roads intersect washes. Taken together, our results suggest that roadside fencing can affect behavior, space use, and thermal ecology of tortoises, which may require refinements to future conservation strategies involving roadside fencing.

1. Introduction

Roads have direct and pervasive effects on animal populations (Spellerberg, 1998; Trombulak and Frissell, 2000; Fahrig and Rytwinski, 2009; van der Ree et al., 2015). Populations can become fragmented when roads act as barriers to animal movement, either through mortality when animals are killed crossing roads, or because animals avoid crossing roads altogether (Anderson, 2002; Forman et al., 2003; Andrews et al., 2005; Shepard et al., 2008). Roads also contribute to habitat loss and degradation (Forman and Alexander, 1998); not only are paved areas uninhabitable for many species, but many species have reduced abundances that extend for hundreds of meters on either side of roads, resulting in road-effect zones (Forman and Deblinger, 2000; Eigenbrod et al., 2009; Shanley and Pyare, 2011; Peaden et al., 2015). These road-effect zones add to the total extent of habitat that is sometimes lost to roads. Additionally, roads often have more severe effects on species with certain ecological and life history traits, such as those with large home ranges, low reproductive rates, and otherwise high adult survival (Carr and Fahrig, 2001; Waller and Servheen, 2005). In contrast, some taxa, such as carnivores, carrion-feeding birds, and small mammals, may occasionally benefit from roads (e.g., Agha et al., 2017), which can increase access to resources, such as prey or carrion, and act as movement corridors (Whittington et al., 2011; Abrahms et al., 2016; Dickie et al., 2016). Current research on the negative effects of roads often focuses on quantifying the extent of habitat lost near roads, the numbers of animals killed on roads, and potential mitigation strategies to limit or reverse road effects (Forman and Deblinger, 2000; van Langevelde et al., 2009; Peaden et al., 2015).

Concern for the effects of roads on wildlife has led to multiple mitigation strategies (Forman et al., 2003) that have been used by transportation and natural resource agencies to reduce vehicular collisions with wildlife. Although mitigation measures may entail multiple techniques, including wildlife underpasses and land bridges, recent efforts have increasingly focused on the use of roadside fencing to prevent

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animals from entering roads. However, the long-term effectiveness of roadside fencing is not well understood (Glista et al., 2009). For example, the benefit of reduced vehicle-wildlife collisions may be offset by unintended negative consequences of fencing for some species (Hayward and Kerley, 2009; Gadd, 2012). Additionally, a spatially explicit population model showed that the effects of road fencing on population persistence can depend on frequency of traffic mortality and on individual behavior of animals in a population (e.g., road avoidance; Jaeger and Fahrig, 2004). Roadside fencing can fragment and isolate local populations (see Carr et al., 2002 for examples), which is likely to be more detrimental to population persistence than is road mortality when traffic volume is low or when behavioral avoidance of roads by the species is high (Jaeger et al., 2005).

Although roadside fencing can reduce the risk of wildlife-vehicle accidents (Boarman, 1995; Aresco, 2005; Glista et al., 2009), there is a lack of information on space use and behavioral responses to roads and roadside fencing for many species. Even with this lack of understanding, species that are highly sensitive to roads, such as those with increased local extinction probability from road mortality, have been targets for mitigation fencing (Clevenger and Waltho, 2000; Aresco, 2005; Hayward and Kerley, 2009; Peaden et al., 2015). Several studies have documented cases of mortality and altered behavior in response to fencing for several wildlife species (van Dyk and Slotow, 2003; Klar et al., 2009; Gulsby et al., 2011). However, the majority of studies on road fencing mitigation techniques and wildlife responses to date have focused on mammals (53% of studies, Taylor and Goldingay, 2010), very few of which are species of conservation concern. Among studies focused on roadside fencing, reptiles are under-represented (8% of studies, Taylor and Goldingay, 2010).

Reptiles, especially turtles and tortoises, of which > 50% are listed as critically threatened or endangered (IUCN, 2014), tend to be highly susceptible to the effects of roads (Andrews et al., 2015; Gibbs and Steen, 2005). Roads may be especially detrimental to many turtles and tortoises due to their defensive behavior of withdrawing into their shell, ultimately increasing the amount of time spent on roads. Additionally, many turtles undertake periodic movements for thermoregulation, foraging, mating, or nesting, all of which can further increase the risk of mortality (Andrews et al., 2015). For example, Aresco (2005) found that along a highway, up to 98% of turtles are killed in crossing attempts, many of which are nesting females. As a result, roadways can skew sex ratios of turtles, which could contribute to decreased population growth (Aresco, 2005). Road mortality, coupled with naturally low recruitment and high juvenile mortality of turtles and tortoises may all contribute to precipitous, unrecoverable population declines (Doak et al., 1994; Fonnesbeck and Dodd, 2003; Aresco, 2005; Nafus et al., 2013). As roadside fencing is increasingly implemented to mitigate wildlife road mortality (van der Gift et al., 2013), including mortality of turtles and tortoises, research is needed to evaluate the effectiveness and potential for negative consequences of mitigation fencing for these species.

The Mojave Desert Tortoise (*Gopherus agassizii*) has experienced significant population declines from habitat fragmentation and road mortality (United States Fish and Wildlife Service, 2011). Road mortality can drastically reduce tortoise densities for the first 200–400 m from roads (Boarman and Sazaki, 2006; Nafus et al., 2013; Peaden et al., 2015), and at least one study has suggested reduced abundances may extend up to 1–4 km from a road (von Seckendorff Hoff and Marlow, 2002). In response to the threat that roads pose to desert tortoise populations, roadside fencing has been installed in many areas as a widespread mitigation measure to reduce desert tortoise mortality (US Fish and Wildlife Service, 2011). Evidence to date suggests that fences have been effective, reducing desert tortoise mortality from vehicle collisions by up to 93% in some areas (Boarman and Sazaki, 2006). A previous study reported observations that suggest potential negative effects of fencing, including tortoises observed climbing fences and pacing along fences (Boarman et al., 1997). Mitigation fencing is often installed without a full understanding of broader impacts that can occur, such as effects on animal movements, behavior, and space use. Because fences are being used throughout much of the range of the desert tortoise, it is imperative to better understand their effects on this threatened species.

Here, we evaluated the fine-scale movement behavior, space use, and carapace temperatures of desert tortoises as they interacted with a road or newly installed roadside fence (referred to collectively hereafter as “structures”) to better understand how they are affected by these structures. Specifically, we addressed the following questions: 1) To what extent does the proximity to a road or fence alter movement behavior, space use, or thermal profiles of desert tortoises? 2) To what extent does a low traffic volume road act as a barrier to tortoise movement; how frequently do tortoises cross and do they avoid crossing such roads less than expected by chance? 3) Are locations and times of road crossings non-random with respect to space or time? By answering these questions, we aim to increase our understanding of multiple, individual-level responses to fencing and unfenced roads that can contribute to more effective implementation of mitigation fencing.

2. Methods

2.1. Study area

We conducted our study at two sites in Ivanpah Valley, California, USA. One site was within the Mojave National Preserve (MNP) along an unfenced, paved 2-lane road (50 vehicles per day; Nafus et al., 2013) and the other site was 11 km north and just to the west of Interstate 15 (I-15; 50,000 vehicles per day; Peaden et al., 2015), where roadside fencing was installed just 3 months before our study began. Both locations had similar habitat with dominant vegetation of creosote (*Larrea tridentata*) and white bursage (*Ambrosia dumosa*). However, major anthropogenic features were closer to the I-15 site, with a nearby utility scale solar energy development, a California agricultural vehicle inspection station under construction just east of the study site, and a tortoise-proof fence installed parallel to the interstate to prevent tortoise ingress and mortality from heavy equipment during construction of the new inspection station (Fig. 1). Vegetation was removed for 3 m along either side of the fence and all vegetation was removed in the construction site. The fence was constructed using galvanized wire mesh and therefore was not likely to alter carapace temperatures directly; it also allowed animals a clear view of habitat beyond the fence (Fusari, 1982). Our comparison study site in the MNP was chosen for its proximity to an unfenced, low traffic volume road that runs through the site and contributes to tortoise mortality (Peaden et al., 2015). Vegetation 3 m on either side of the unfenced road is removed annually, leaving bare soil.

2.2. Data collection

In summer of 2013, we captured a total of 15 adult tortoises with midline carapace lengths > 210 mm (Berry and Christopher, 2001; MNP: 5 males and 4 females; I-15: 4 males and 2 females). All 15 animals were captured within 1 km of the unfenced road (MPN site) or the roadside fence (I-15 site). Two study animals at the I-15 site had been previously re-located from inside the newly fenced exclusion area prior to construction of the California agricultural vehicle inspection station; when we began our study, we captured those two animals outside of the fenced construction area. We individually marked each tortoise upon capture by notching unique combinations of marginal scutes (Cagle, 1939). We outfitted all animals with VHF radios (Holohil RI-2B, Holohil Systems Ltd. Ontario Canada), Global Positioning System loggers (G30L, Advanced Telemetry Systems Inc. Isanti, MN) and iButton temperature loggers (1922L, Maxim Integrated, San Jose, CA). We affixed VHF radios to the first left costal scute of female tortoises and the fifth vertebral scute of males using gel epoxy (Devcon 5 Minute Epoxy

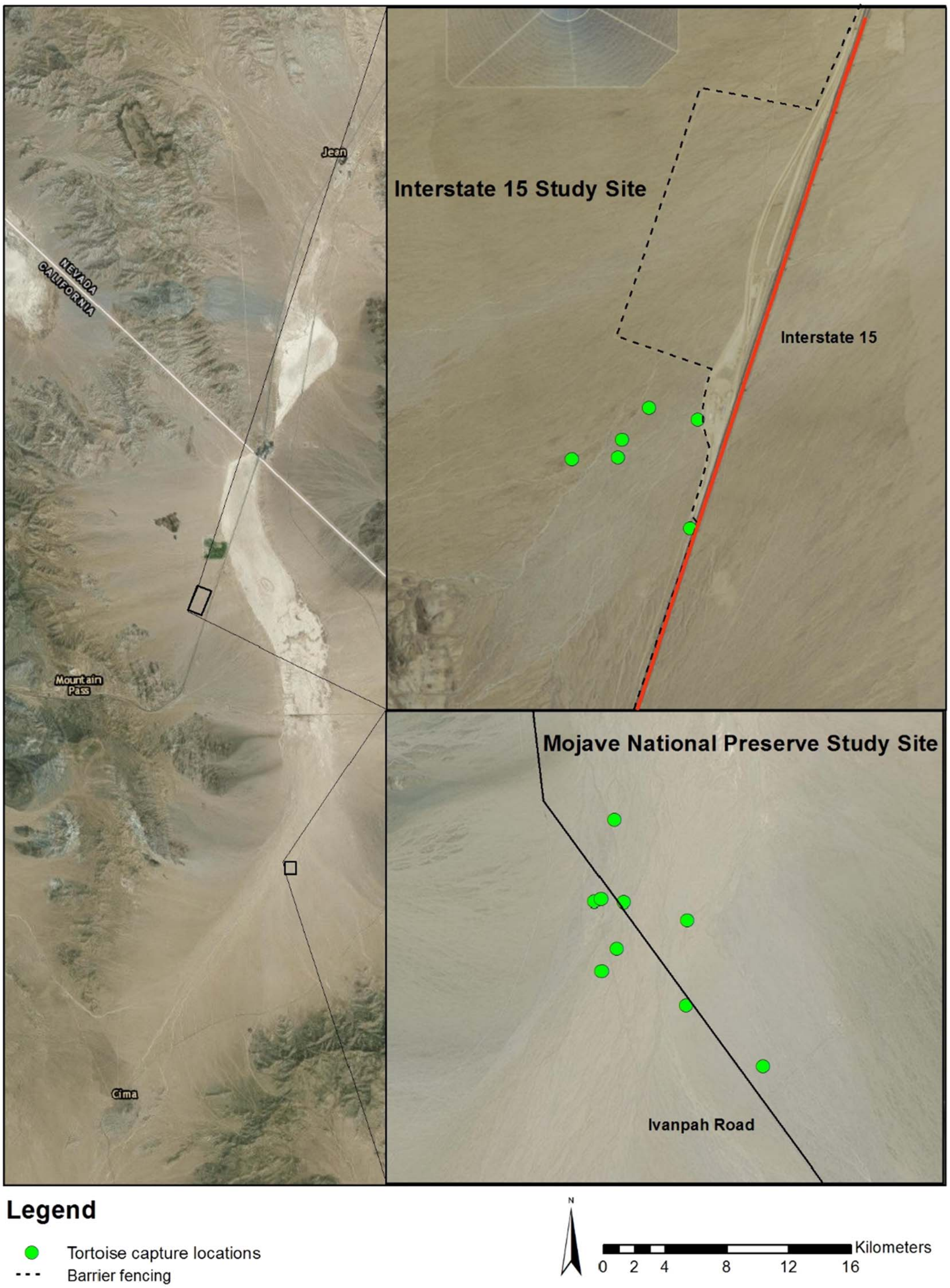

Fig. 1. Map of the study site in California, USA near the border with Nevada. Insets show the two study locations along I-15 (top right) and in the Mojave National Preserve (bottom right). Green dots show the initial site of capture of study tortoises that were outfitted with GPS-telemetry units. Note that Ivanpah Road bisects the Mojave National Preserve study site, selected to evaluate the effect of roads on space use and behavior of nearby tortoises. The I-15 site was chosen to investigate the effects of recently installed fencing (3 months prior to study start) on space use and behavior of resident tortoises. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Gel). We affixed GPS loggers with custom brackets on the second costal scute of all tortoises. These brackets allowed for quick removal and replacement of GPS loggers with fully charged batteries in under 1 min to minimize disturbing animals in the field. The mean location error of the GPS loggers was 8.6 m (range 3–38 m) as determined by previous field trials. With desert ectotherms, behavioral thermoregulation within physiological limits is critical for movement, water balance, foraging efficiency, reproduction, and overall survival (Brand et al., 2016; Zimmerman et al., 1994; Nagy and Medica, 1986). Previously, carapace temperatures have been used as a proxy for internal body temperatures for the desert tortoise (Zimmerman et al., 1994; Brand et al., 2016). To understand the thermal ecology of desert tortoises near and away from structures, we affixed iButton temperature loggers to the first right or first left costal scute of each study animal with epoxy putty (J-B Weld SteelStik). The GPS logger units and attachment methods were designed and approved in consultation with the USGS and USFWS, and we only outfitted large, mature tortoises with GPS loggers. This allowed the maximum total weight of all affixed equipment to comprise < 6% of the body mass of each tortoise. After attaching GPS loggers, we checked animals daily for at least the first 3 days to ensure that devices did not hinder movement or limit access to burrows. During the course of our study, we observed typical behavior among the study animals, including foraging, mating, ability to right during male combat, and use of burrows at various depths and positions. No study animals showed signs of stress, unusual behavior, or inability to use burrows due to attached equipment. We removed all GPS loggers when we ended the study in June 2015.

We programmed GPS loggers to balance the amount of location data obtained with the need to conserve battery life. This resulted in an optimal fix schedule of 15–30 min intervals. Temperature data loggers were programmed to record carapace temperatures every 15 min. We recaptured tortoises over the course of the study to download GPS and thermal data and to redeploy GPS units with charged batteries. All handling, processing, and equipment attachment methods were approved by United States Fish and Wildlife Service (TE-17838A), California Department of Fish and Game (SC-0011221), University of California, Davis International Animal Care and Use Committee (18141), and Mojave National Preserve (MOJA-2011-SCI-0056).

2.3. Home range analyses

We calculated multiple movement and space use metrics to evaluate tortoise responses to structures (the road or fencing). First, we calculated four metrics of home range for each study animal: Minimum Convex Polygon (100% MCP), 50% Fixed Kernel density home range (KDR), 90% KDR, and 95% KDR. MCP was used to provide a total area that study animals could have used throughout the study, in addition to provide comparable results to other studies. We calculated 100% MCPs using all GPS locations in the Geospatial Modeling Environment (GME, Beyer, 2015. Version 0.7.4.0) with command ‘genMCP’, followed by the ‘addarea’ command to calculate the total area encompassed for each animal. We calculated KDRs in GME using least-square cross-validation smoothing factors (Seamen and Powell, 1996). We calculated the 50% KDR to identify core use areas, with 90% and 95% KDRs representing home ranges without including the exploratory movements included in 100% MCPs. We used *t*-tests to compare all home range sizes between male and female study animals and between MNP and I-15 animals. We used linear models to determine whether home range size changed with proximity to the road or fencing. Because home range size can differ between sexes, we standardized 95% KDR and 100% MCP estimates by sex and calculated the mean distance to structures across all locations for each animal, providing a measure of distance from the center of the home range for each animal for this analysis.

2.4. Analyses of movement, space use, and thermal condition in response to roads and fencing

We used T-LoCoH – an R package that accounts for time of location – to calculate movement and space use metrics in relation to local convex hulls constructed around each point (Lyons et al., 2013; R Core Team 2014). T-LoCoH estimates a utilization distribution by a nonparametric kernel function to create hulls and then ranks these hulls according to density. These hulls allow estimating the amount of time an animal spent in each hull before leaving to another area of its established home range, known as duration of visit to each hull. Hulls were created based on the 125 nearest neighbor points to a parent point; nearest neighbor distance was based on the separation among points in both time and space (i.e., *k* method). This method requires defining a parameter, s, which determines the influence of time on the calculation of nearest neighbor distances. Although there may be other points closer in space to the parent point, they may have been months apart and are therefore omitted from that hull. When $s = 0$, time has no influence in creating hulls, and when $s = 1$, hulls are created based on the order of points collected. We determined s for a subset of animals by plotting a distribution of *s* values for daily movements (see Lyons et al., 2013). We chose a value for s of 0.03 because this value equalized both space and time for hull construction. We defined parameter *k* by visually inspecting the complete hull sets for multiple *k* values, in addition to plotting isopleth area curves. A *k* value of 125 was visually determined to best balance Type I and Type II errors of isopleth maps, a method detailed by Lyons et al. (2013). We calculated metrics for 24 h time periods (as opposed to summarizing the data to weekly or monthly time periods) because we were most interested in fine-scale space use and behavior represented by daily patterns of movement (i.e., pacing and similar behaviors would have been missed in longer periods).

We calculated the additional movement metrics of step length and bearing between consecutive telemetry points using the GME ‘movement.pathmetrics’ function. For each location, we also calculated the nearest distance to road (MNP animals only) and distance to fence (I-15 animals only) using the ‘Near’ analysis tool within ArcGIS® (Environmental Systems Resource Institute. 2014. ArcMap 10.2. ESRI, Redlands, California). For each location, we defined the season such that points recorded from 01 March – 30 June were classified as ‘Spring, Early Summer’ season, those from 01 July – 15 November were classified as ‘Monsoon, Fall’ season, and those from 16 November – 28 February were classified as ‘Winter’ season. Because we were interested in comparing movement behavior at and away from the road or fence, we defined a binary variable “structure”, which differentiated locations that were within 20 m from the road or fence and locations that were not. We chose this 20 m distance to account for GPS error and the width of the road.

We used linear mixed effects models to analyze the responses of step length, carapace temperature, duration of visit, bearing, and velocity. We log-transformed response variables that were not normally distributed prior to analyses (step length, duration of visit, bearing, and velocity). We fit season, sex, site, and structure as fixed effects. Very few winter points were recorded ($N = 319$, $< 0.5\%$ of locations) because animals overwintered in burrows and did not move; we therefore excluded these points from analysis. We included tortoise identities as random intercepts. Because data were serially autocorrelated, we fit models with an ARMA 1 temporal autocorrelation error structure (Zuur et al., 2009). For computational efficiency, we analyzed a subset of the total locations by including only locations that were > 5 h apart. Because we were primarily interested in road and fencing effects on movement and behavior, only tortoises that interacted with structures (the road or fencing) were included in this analysis ($n = 11$, Supplementary Table 1). We examined effect sizes and significance of estimates for site (i.e., I-15 vs MNP) and structure (animal locations were near or away from the fence or road) terms after controlling for sex and season; all models were fit with sex and season as covariates. For each response variable, we fit models with additive effects of site and structure and separately with the interaction between site and structure. Interactions between site and structure were assessed to determine whether the responses differed with proximity to the different types of structure (road versus fence), which would be indicated by a significant interaction between site and structure.

2.5. Analyses of road crossings

We determined whether tortoises were more or less likely to cross the road than expected at random by comparing observed and simulated tortoise paths for all animals that crossed the road. Animals at the fenced I-15 site were not included in this analysis. We generated observed movement paths for each study animal in GME using the ‘convert.pointstolines’ function, which joins consecutive location data points. To determine the observed road crossings, we used the intersect tool within ArcGIS® with two layers: the animal line movement path and a digitized shapefile of the road at the MNP study site. A buffer of 10 m was included on both sides of the road to account for GPS error and the width of the road. Road crossings were only counted if the path

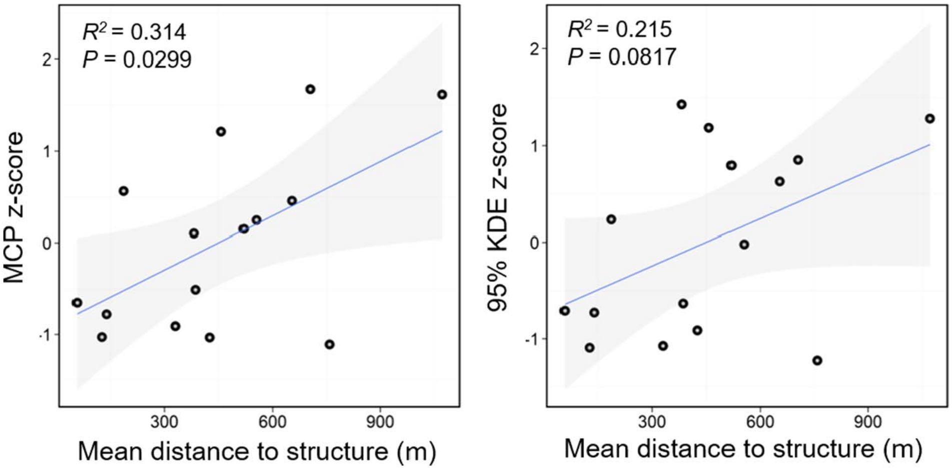

Fig. 2. Relationship between distance to structure (road or roadside fencing) and home range size for desert tortoises estimated by Minimum Convex Polygon (MCP) in left panel and 95% Kernel Density Estimate (KDE) in right panel.

segment completely crossed the road and buffer. On occasion, an animal would approach the road then turn back, not completing the crossing. In these instances, a road crossing was not counted. We calculated the mean time of the two points on either side of the road during a crossing to estimate the time and date of crossing.

Using GME, we simulated 100 movement paths using correlated random walks (CRW) for each of the six tortoises that crossed the road during the study. Each of the simulated random paths had identical start locations as the observed path of the animal. Furthermore, the simulated paths were constrained by each animal's observed 100% MCP, had identical total step lengths to the observed data, and had the same number of locations as the observed data. These simulated random movement paths were based on the empirical distribution of step length and turn angles. We then compared the number of actual road crossings from those expected in random walks for each tortoise. Road crossing avoidance was calculated by z-score, or standard deviation from the mean (Whitlock and Schluter, 2009). *Z*-score was calculated by subtracting the mean expected road crossing count from observed crossings and dividing by the standard deviation of expected road crossings. The resulting score describes the degree to which an animal crossed the road more or less often than random. We considered the observed number of road crossings significantly different from that expected at random if these values were outside the 95% confidence (i.e., *Z*-scores > 1.96) intervals around the mean number of crossings from simulated paths.

To identify the temporal variation in road crossing frequency, we fit mixture models to observed road crossings (e.g., Owen-Smith et al., 2012; Agha et al., 2015). These models allowed us to parse out periods of increased road crossing activity during the primary active season for desert tortoises. These models adequately represent multi-model frequency distributions that cannot be modeled in a regression context. We fit normal mixture models with 1–3 mixture components using the R package ‘Mixtools’ (Young et al., 2009) and selected the top model using Akaike Information Criterion (AIC). Parameters within the mixture models reflect different factors: π, representing the percent of road crossing taking place within each period, μ, indicating the mean day of year for crossing period, and Σ, identifying the temporal duration of the crossing periods. We then used parametric bootstrapping to produce 95% confidence intervals for the parameters of the top models (B = 500). In order to visualize if crossing periods could be due to precipitation events, we acquired mean daily precipitation across the two years of study at MNP (Prism Climate Group, 2017).

Because tortoises can use washes as travel corridors (Jennings, 1997; Riedle et al., 2008; Todd et al., 2016) and washes frequently intersect roads, we analyzed locations where tortoises were observed crossing roads to determine whether those locations were non-random with respect to the density of washes along the road. To do this, we first digitized washes from satellite imagery (United States Department of Agriculture, taken 26 May 2014, 1-m resolution). We then generated random points along the road equal in number to that of actual road crossings for each tortoise. The location of random points was constrained by the width of the MCP polygon of each tortoise where the polygon intersected the road. We then generated 50-m buffers around all road crossing points and random points and measured the length of wash within each buffer. Buffer size approximates the mean step length of three consecutive locations (representing a 45 min time interval), a scale at which we expect tortoises are making decisions when moving across the landscape, given the data. We used generalized linear models with binomially distributed errors to analyze the effect of length of wash on the probability that a point was an observed tortoise road crossing point versus a random point.

3. Results

3.1. Home ranges

The final dataset included 91,302 total tortoise locations, with a mean of 6086 locations per tortoise (range 1854–9237). We obtained GPS locations for a mean time of 512 days across all study animals (range 100–734 days). Minimum convex polygon (MCP) home ranges for desert tortoises ranged in size from 23.6–181.0 ha with a mean of 86.6 ha (SE 13.6 ha, Supplementary Table 1). Mean 95% KDR home range was 31.8 ha (SE 5.2 ha) and mean core use area (50% KDR) was 3.5 ha (SE 0.8 ha) across all study animals. We found no significant differences in home range sizes between sexes or sites ($P > 0.05$). Mean MCP increased significantly with distance from a structure ($R^2 = 0.314$, $P = 0.029$, Fig. 2). The 95% KDR followed a similar trend ($R^2 = 0.215$, $P = 0.081$).

3.2. Movement, space use, and thermal condition in response to roads and fencing

In our analysis of movement metrics, we investigated the influence of site and structure, while controlling for sex and season, on the responses of step length, carapace temperature, duration of visit, bearing, and velocity for animals that encountered the road or fencing. Where there was a significant interaction between site and structure, we focus interpretation on the interactive model; otherwise, we report the results from the model without interactions. For step length, there was no statistically significant effect of site or structure. For carapace temperatures, there was a significant interaction between site and structure (site*structure, + 2.1 °C, $P = 0.013$, Table 1). Mean tortoise carapace temperatures were greater (+ 1.1 °C, $P = 0.04$) within 20 m of a structure (29.8 °C, ± 0.1) than farther away (27.2 °C, ± 0.1, Table 1),

Table 1
Results of linear mixed effects models predicting tortoise responses to variables of interest. The left side of the table shows results of a model that only included additive effects of site (Mojave National Preserve and I-15) and barrier (near road or fence). The right side of table shows results of a model that includes an interaction between site (Mojave National Preserve and I-15) and structure (near road or fence). Numeric values are P values. Bold denotes responses that were significant at $\alpha = 0.05$ level.

Response	Site	Structure	Sex	Season	Site	Structure	Sex	Season	Site * Structure
Velocity	0.919	**0.029**	**0.016**	**0.000**	0.918	0.091	**0.016**	**0.000**	0.892
Carapace temperature	0.837	**0.000**	0.418	**0.000**	0.979	**0.045**	0.455	**0.000**	**0.013**
Step length	0.192	0.344	0.291	**0.001**	0.212	0.414	0.300	**0.001**	0.836
Duration of Visit	0.009	**0.032**	0.262	**0.007**	**0.009**	0.282	0.260	**0.008**	0.446
Bearing	0.503	0.562	0.760	0.555	0.885	**0.027**	**0.012**	0.696	0.117

and this increase in mean carapace temperature was greater along the road (+ 3.2 °C) than along the fence (+ 1.1 °C; Fig. 3). However, we observed a greater frequency of extremely high carapace temperatures along the fence (Fig. 3) than along the road. For example, a female study animal was observed pacing along the fencing at the I-15 site. During this observation, the tortoise recorded carapace temperatures > 46 °C, with a mean of 44.5 °C sustained for > 1 h. We provided shade for this animal and then moved the animal to a previously known burrow. Ultimately, however, she was found dead a day later along the fencing once again. Duration of visit, or how long an animal spent within a hull before exiting to another part of its home range, was significantly greater when animals were near structures (Fig. 4; + 1.2 mean number of locations per visit, $P = 0.03$). For bearing, there was no significant effect of site or structure. Finally, with tortoise velocity as the response, there was a significant effect of structure such that animals near the road or fence moved 0.29 m per h faster.

3.3. Road crossings

Only animals in the MNP had the potential to cross an unfenced road. Of the nine MNP study animals, six crossed the road at least once during the study period. When comparing the observed movement paths of tortoises that crossed the road to the simulated random walk models, all tortoises crossed the road less than expected at random

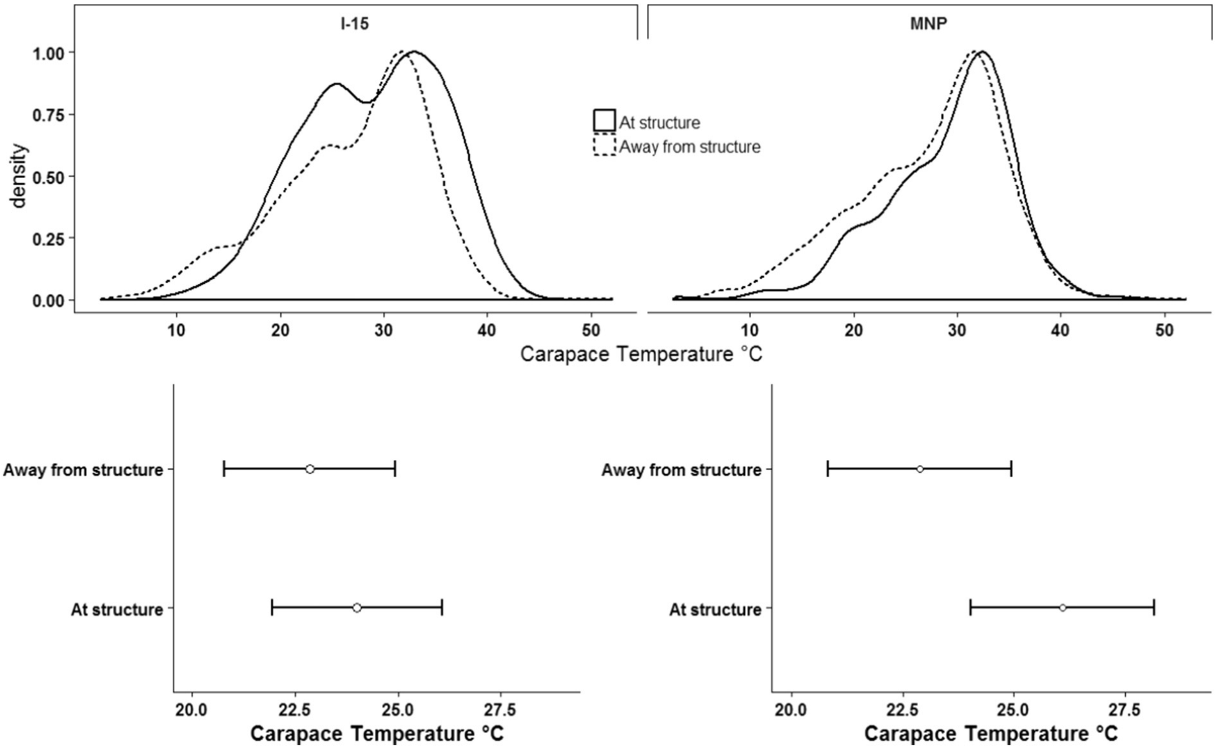

Fig. 3. Desert tortoise carapace temperature near I-15 (fenced highway) and Mojave National Preserve (bisected by road). Solid lines represent when animals were within 20 m of structure (road or roadside fencing). Dashed lines represent when animals were farther than 20 m from structure. The top panel shows the scaled density of recorded carapace temperatures as a function of whether tortoises were at structures (solid line) or away from structures (dashed line) for the I-15 site (left side) or Mojave National Preserve (right side). The bottom panel shows mean carapace temperatures with 95% confidence intervals for I-15 (left side) or Mojave National Preserve (right side). Note the greater frequency of high temperatures at the barrier at the I-15 site compared to the MNP site.

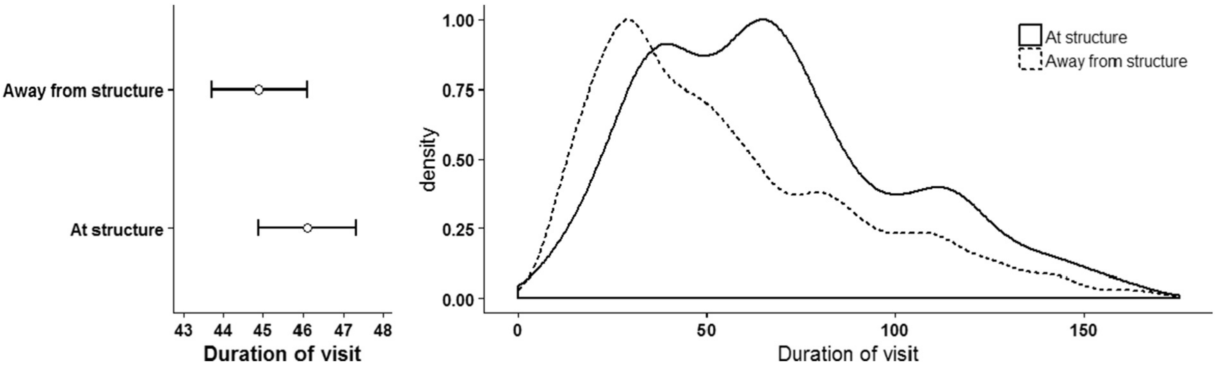

Fig. 4. Duration of visit (mean number of locations per hull visit) by desert tortoises near or away from a structure (road or roadside fencing). The left panel shows mean duration with 95% confidence intervals for animals near or away from structures. The right panel shows scaled density of visit durations for animals near or away from structures. Solid lines represent when animals were within 20 m of structures. Dashed lines represent when animals were further than 20 m from structures.

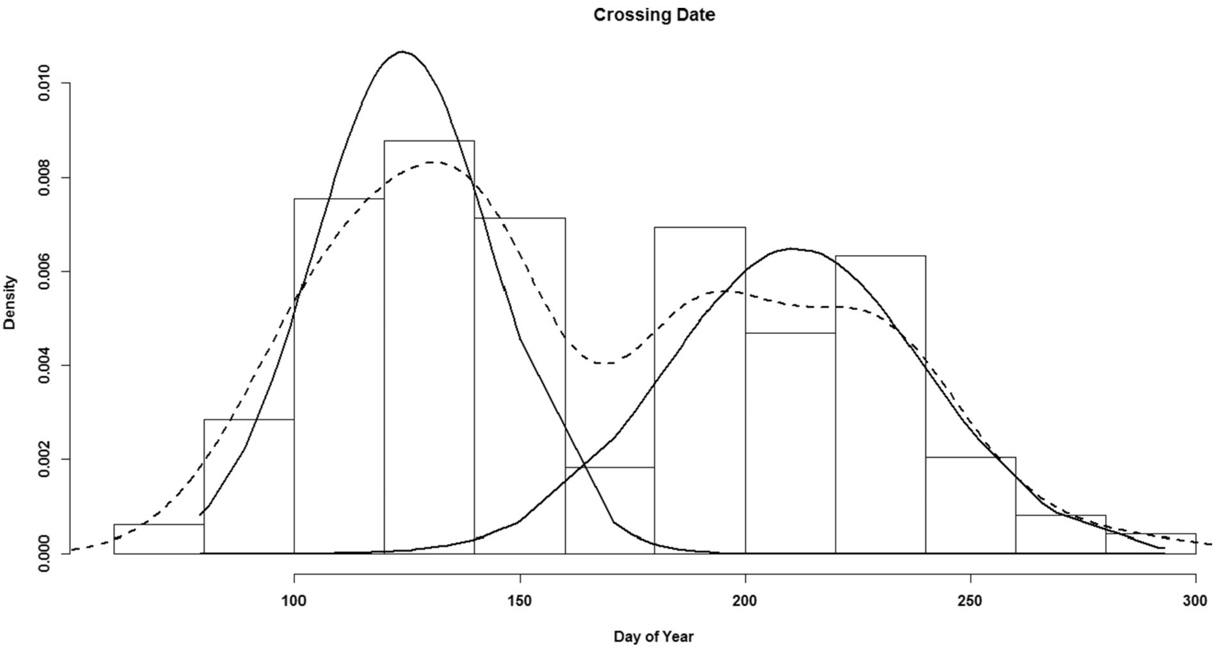

Fig. 5. Temporal distribution of road crossing activity by desert tortoises in the study in Mojave National Preserve. Histogram bars show density of road crossing activity. Solid lines show the density and peak crossing periods predicted from a bimodal mixture model. The dashed line shows the nonparametric density estimate from the mixture distribution.

(34.1–49.2% less), with two animals crossing significantly less (*Z*-score range -0.23–(-2.06), $\mu = -0.9$).

The bimodal mixture model distribution with two distinct road crossing dates was best supported compared to trimodal and unimodal mixture models which were second and third, respectively. Within our bimodal model, peak road crossing occurred at day of year 124 and 211, corresponding to 04 May and 30 July, respectively, in non-leap years (Fig. 5). The variance of the first peak in road crossing ($\Sigma = 19.86$), was less than the second peak in crossings ($\Sigma = 28.85$), meaning that road crossings occurred during a shorter window earlier in the year. Our trimodal distribution was also somewhat supported (ΔAIC 1.704), and should be considered. Within our trimodal mixture model, peak road crossing occurred at day of year 125, 189, and 221, corresponding to 05 May, 08 July, and 09 August, respectively, in non-leap years. The variance of the crossings was greater later in the year (09 August, $\Sigma = 25.69$), followed by 05 May ($\Sigma = 20.96$) and 08 July ($\Sigma = 2.18$). Tortoises crossed the road in areas with significantly more washes around them compared to road crossing points randomly generated within the home ranges of the tortoises ($P < 0.01$, slope = 0.407, Supplementary Fig. 1.).

4. Discussion

A common way wildlife managers mitigate the negative impacts of roads is by installing roadside fencing. Roadside fencing is intended primarily to reduce wildlife mortality associated with crossing roads, yet the full ecological impacts of this practice on animal behavior remain poorly understood. Here, we examined the effects of both recently-installed fencing and an unfenced road on the space use and movement behavior of the Mojave Desert Tortoise. Several aspects of tortoise behavior and movement differed closer to the structures of a road or fencing. Notably, proximity to either fencing or the unfenced road affected carapace temperatures and tortoise movement velocity, compared to tortoises farther away from either structure. Carapace temperatures were greater when animals were within 20 m of either structure compared to when animals were farther away. Vegetation immediately surrounding both the road or fencing was similar, with vegetation removed 3 m from both sides of the road and the fencing. Although carapace temperatures were greater on average for animals along the road than for those near the fencing, animals along fencing had greater variation in carapace temperatures that included more extreme high temperatures (> 40 °C). If one ignores these potentially lethal temperatures and only considers the mean temperatures that were recorded, fencing would appear to be an acceptable form of mitigation because temperatures on average were not elevated for animals along the fence compared to those encountering the road. However, the extremely high temperatures of animals near fencing paints a different picture. In this desert landscape, tortoises rely on shelter sites, large creosote bushes, or burrows to escape lethal temperatures. Tortoises at the MNP site may tolerate high temperatures by using burrows known to them. When new fencing is installed, however, as was the case at the I-15 site just before we began the present study, animals can lose access to previously used burrows and have their home ranges reduced in size by new fencing, leading to exposure to high temperatures that raise carapace temperatures to lethal levels.

We also found that tortoise movement velocity was greater when animals were near the fence or road than away from them. These results, along with data on carapace temperatures, reveal that when tortoises encountered fencing they moved faster and had higher carapace temperatures, on average, than when away from fencing, which could result in increased energy expenditure and risk of thermal stress. For reptiles, increases in body temperatures within optimal performance ranges are directly linked to increased velocity (Crowley, 1985), however this increase in movement rate is quickly diminished as reptiles near critical thermal levels (Irschick and Higham, 2016; Kaufmann and Bennett, 1989), such as tortoise near fence. Along fencing, pacing activity of desert tortoises has been observed in previous studies, with animals pacing up to 6.5 km (Fusari, 1982; Ruby et al., 1994; Boarman et al., 1997; Wilson and Topham, 2009). Pacing behavior was also observed frequently in the present study. As animals paced along a fence, carapace temperatures would, in some instances, exceed 43 °C. For example, one female tortoise was found pacing the fence on 28 August in the late afternoon, a time when desert tortoises are typically at rest in the shade of their burrows (Zimmerman et al., 1994). When the same tortoise was observed the following day, it was found along the fence dead. After downloading temperature data from her logger, we found carapace temperatures > 46 °C before death, with a mean of 44.5 °C sustained for > 1 h. While the mean body temperature of desert tortoises found above surface was found to be 34.6 °C in one study (Zimmerman et al., 1994), critical thermal maximum body temperatures of desert tortoises are believed to range from 38.6–45.1 °C (Hutchison et al., 1966; Naegle, 1976). To date, there is no known published literature of how long desert tortoises can endure these extreme temperatures without suffering lethal consequences. Although our temperature loggers were placed on the carapace, Zimmerman et al. (1994) found that internal body temperatures differ from external body temperatures by < 1 °C when animals were not immediately entering or exiting burrows. It is thus likely that this animal reached temperatures above thermal limits, resulting in acute thermal stress and subsequent death. Additionally, we observed another tortoise pacing the fence during the study. The prevalence of pacing behavior and its population-level implications should be evaluated further, as roadside fencing is becoming a commonly implemented mitigation strategy for desert tortoises and other species.

We found that desert tortoises remained for longer periods of time in areas near the road or fence than they did when moving in areas away from these structures. We suggest several possible explanations for this observation. First, the increased duration of visit near the unfenced road may be explained by increased opportunities for obtaining resources near roads. When it rains in the desert, paved roads may provide runoff from rainfall and pools of water from which tortoises can drink (Johnson et al., 1975). Additionally, roadside edges in desert systems can provide increased annual plant productivity and forage opportunities (Johnson et al., 1975; Vasek et al., 1975; Lightfoot and Whitford, 1991). Within the MNP, roadside edges are mechanically graded annually. With this grading schedule, little to no perennial vegetation is able to grow, whereas annual vegetation still germinates and grows, particularly with increased rainfall runoff. An increase in annual vegetation along roads could provide greater foraging opportunities for tortoises, thereby attracting them to roadside areas. Second, and similarly, desert tortoises may perceive roadside edges as similar to naturally-occurring desert washes. Washes have been suggested to be important foraging sites for the desert tortoise, due to increased annual vegetation (Jennings, 1997; Jennings and Berry, 2015; Todd et al., 2016). Third, and alternatively, the increased duration of visit near the unfenced road may result from a general reluctance of desert tortoises to cross roads, therefore increasing time spent in habitat immediately around the road. Road-crossing avoidance could eventually lead to genetic differentiation and reduced gene flow such as that seen in a population at Fort Irwin, California (Latch et al., 2011). Fourth, animals within our I-15 study site also exhibited increased duration of visits near the fence. Desert tortoises are known to be habitual in their repeated use of the same burrows over time (Lovich and Daniels, 2000; Lovich et al., 2014). A novel obstruction, such as a fence, could impede access to previously used burrows. In response, some animals may pace the fence, increasing time spent in areas around fences.

We found that tortoise home range sizes decreased with proximity to structures. Smaller home ranges may result from multiple processes, including road-avoidance behavior, greater resource density along roads that requires less movement by resident animals, or selection on tortoises whose home ranges include roads such that only the more sedentary animals with smaller home ranges remain. Effects of traffic noise or vibrations could lead to behavioral avoidance, restricting movements of tortoises with established home ranges near roads (Forman and Alexander, 1998). Alternatively, roads may increase the density of available forage (Vasek et al., 1975; Lightfoot and Whitford, 1991), as discussed above. Increased resources, such as water runoff or forbs, would therefore reduce the need for tortoises to range widely to find resources.

Desert tortoises crossed roads significantly less often than expected by chance. Several other studies have documented similar avoidance of road crossings in several turtle and tortoise species (Forman and Alexander, 1998; Bowne et al., 2006; Shepard et al., 2008). However, environmental and life history variation can create notable exceptions. For example, during periods of drought, an increased number of semi-aquatic turtles in Florida were found attempting to cross roadways in search of more suitable habitat (Aresco, 2005). Road edges also provide open, sunlit nesting areas that can be limiting for many semi-aquatic turtles (Wood and Herlands, 1997). In contrast, desert tortoises typically nest at their burrows, and so, are less likely to cross roads while searching for nest sites like semi-aquatic turtles sometimes do. Instead, they appear to avoid roads, although the proximate cause of road avoidance remains unknown. While the road at the MNP site was a semi-permeable barrier to our study animals that crossed infrequently, roads of greater width or traffic volume could represent greater barriers to movement. Greater avoidance could further isolate populations and restrict gene flow, elevating the probability of local extinction from both demographic and genetic effects (Andrews et al., 2015).

Desert tortoise road crossings did not occur at random, spatially or temporally. Our analyses showed that desert tortoises tended to cross the road near washes. Their preference for crossing near washes may stem from their use of washes as travel corridors (Jennings, 1997; Riedle et al., 2008; Todd et al., 2016), which suggests that efforts to mitigate road effects could be enhanced by focusing on areas where roads intersect washes. The majority of road crossings also occurred at two distinct times, during spring and late summer-early fall. During spring, germination and flowering of annual vegetation is high, especially in washes where tortoises are known to forage (Jennings, 1997). The first peak in road crossing also corresponded to the beginning of nesting season (Lovich et al., 2014). The second peak in road crossing activity corresponded with monsoon events near our study site (Supplementary Fig. 2) and in the eastern Mojave (Beatley, 1974; Kurc and Benton, 2010; Nafus et al., 2017). At this time, between day of year

175–215, rainfall accumulates on roads and nearby from runoff. Although tortoises tended to generally avoid crossing the road, our results identified seasonal increases in road crossings and a likely associated risk of road mortality.

Here, we provide new insights into the effects of roads and roadside fencing on the movement behavior and space use of desert tortoises. Our study shows that carapace temperature and movement speeds increase when tortoises are along roads and roadside fencing compared with away from these structures, indicating potential unintended effects of fencing on behavior and thermal condition of tortoises. We found that desert tortoises crossed roads less than expected by chance, and we posit that road avoidance behavior may have contributed to smaller home ranges of individuals near roads. In addition, we found that road crossings frequently occurred near washes.

Our results should be useful for land managers responsible for maintaining viable populations and mitigating road effects on sensitive species. At a local scale, decisions should focus on the benefits and costs of fencing to focal populations, as it may not be a panacea for population recovery. Roadside fencing can reduce the number of wildlife-vehicle mortalities; however, it may also have unintended consequences in the short term. Our study suggests a need to further evaluate and refine mitigation strategies that include roadside fencing. For example, the use of shade structures should be considered when installing mitigation fencing, which could allow tortoises to cool themselves during times when they may initially pace fences after recent installation. As an alternative, leaving shrubs near roads and mitigation fencing could also allow tortoises to seek nearby thermal refugia. Additionally, our finding that tortoises tend to cross roads near washes suggests that placement of roadside fencing and road underpasses could be refined by targeting areas where roads intersect washes, which may lead to reduced wildlife vehicle collisions (Boarman et al., 1997). Overall, our study suggests that mitigation fencing could be a valuable tool for conservation managers; however, fencing should be thoroughly evaluated for optimal placement and construction before widespread adoption of this mitigation strategy in habitat management and species recovery plans.

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Appendix A. Supplementary data

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