Biological Conservation 162 (2013) 100–106

Contents lists available at SciVerse ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Relative abundance and demographic structure of Agassiz's desert tortoise (*Gopherus agassizii*) along roads of varying size and traffic volume

Melia G. Nafus [a,*], Tracey D. Tuberville [b], Kurt A. Buhlmann [b], Brian D. Todd [a]

[a] Department of Wildlife, Fish and Conservation Biology, University of California, Davis, CA 95616, USA
[b] University of Georgia's Savannah River Ecology Lab., P.O. Drawer E, Aiken, SC 29802, USA

ARTICLE INFO

Article history:
Received 22 December 2012
Received in revised form 3 April 2013
Accepted 9 April 2013

Keywords:
Gopherus agassizii
Long-lived species
Reptile
Road
Tortoise
Traffic volume

ABSTRACT

Roads are recognized as important contributors to wildlife population declines and are thought to pose greatest risk to vagile species with large home ranges and long generation times. We examined variation in the relative abundance and demographic structure of Agassiz's desert tortoise (*Gopherus agassizii*) near roads that varied in traffic volume. We found that the abundance of tortoise sign (scat, tracks, pallets, burrows, and live and dead individuals) varied with traffic volume and distance from the road depending on traffic volume. The relative abundance of tortoise sign was greatest along roads with low traffic volume (<1 vehicle/day) compared to roads with intermediate (30–60 vehicles/day) and high (320–1100 vehicles/day) traffic volumes. Additionally, tortoise sign had lower relative abundances at least 200 m from roads with the highest traffic volumes. We found that the frequency of live tortoise encounters decreased with increasing traffic volumes. Tortoise size also correlated significantly with traffic volume, such that tortoises near the highest traffic volume road were smallest. Finally, along the highest traffic road we found greater proportions of juvenile tortoises than along either of the other traffic volume roads. Our results indicate that roads may decrease tortoise populations via several possible mechanisms, including cumulative mortality from vehicle collisions and reduced population growth rates from the loss of larger reproductive animals. Here, we provide evidence that a reptile with a slow life history is susceptible to road presence and that the effect increases with traffic volume.

1. Introduction

Roads are ubiquitous and pose a significant threat to biodiversity globally (Benitez-Lopez et al., 2010; Eigenbrod et al., 2008; Fahrig and Rytwinski, 2009; Jacobs and Houlahan, 2012). They affect wildlife through numerous mechanisms that can include mortality from vehicle collisions, and loss, fragmentation, and alteration of habitat (Marsh et al., 2008; Trombulak and Frissell, 2000). The types and magnitude of the effects may vary depending on the behaviors of the species (Andrews et al., 2005). For example, species that frequently use or cross roads are likely to be affected directly by increased mortality from vehicle collisions. Alternatively, species that avoid crossing roads may be more susceptible to indirect mechanisms, such as habitat fragmentation, as a consequence of road avoidance, and alteration of nearby physical conditions. Though roads comprise only 1% of surface area, an estimated 19% of the total land within the United States is ecologically affected by roads due to indirect effects that extend 100–800 m beyond the physical footprint of the road (Forman, 2000). The ecologically affected areas along roads, otherwise known as "road-effect zones", are those in which a change in wildlife abundance, demography, or behavior is observed. Given the extensive area affected by roads and the numerous mechanisms through which roads can affect local populations, there is a clear need to develop predictive measures for the contribution of roads to population declines and to develop effective mitigation strategies.

Currently, roads are expected to pose the greatest risk to species that are highly vagile, have large home ranges, large body mass, low reproductive rates, and long generation times (Carr and Fahrig, 2001; Gibbs and Shriver, 2002; Karraker and Gibbs, 2011; Rytwinski and Fahrig, 2011, 2012). Road effects may be particularly damaging to species with low reproductive rates and long generation times because such species have a low intrinsic ability to recover from population declines (Gibbs and Shriver, 2002; Rytwinski and Fahrig, 2012). Although the above patterns have been seen in many mammals (Rytwinski and Fahrig, 2011), there are few

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* Corresponding author. Tel.: +1 530 746 8448; fax: +1 530 752 4154.
E-mail addresses: mgnafus@ucdavis.edu (M.G. Nafus), tubervil@uga.edu (T.D. Tuberville), buhlmann@uga.edu (K.A. Buhlmann), btodd@ucdavis.edu (B.D. Todd).

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http://dx.doi.org/10.1016/j.biocon.2013.04.009

studies supporting their application to other vertebrates. In fact, studies of amphibians have found the opposite pattern, identifying small, early maturing species as those more susceptible to road mortality (Rytwinski and Fahrig, 2012). Ultimately, however, species with life history traits tied to low lifetime reproductive rates do appear to be at the greatest risk for road-related declines.

Studies on reptiles are too scarce to develop quantitative predictions of life history traits associated with sensitivity to roads (Rytwinski and Fahrig, 2012). Behavioral traits in reptiles, such as road-side basking for thermoregulation (Sullivan, 1981), and human behavior, such as intentionally crushing reptiles encountered on roads (Ashley, 2007), may increase risk in reptiles relative to mammals. Although there are limited studies, documented effects of roads on reptiles include high mortality, altered demographic structure near roads, and increased risk of local extirpation, particularly in long-lived species (Gibbs and Shriver, 2002; Gibbs and Steen, 2005; Row et al., 2007; Taylor and Goldingay, 2010). Most turtle species have life history characteristics consistent with the predictions of high risk in mammals: late sexual maturity, low reproductive rates, and long generation times. If population-level effects apply mostly to species with "slow" life histories, turtles and tortoises are expected to be particularly vulnerable to impacts from roads. Additionally, demographic studies in turtles indicate that small increases in annual mortality of as little as 1–3% can result in population declines (Congdon et al., 1993, 1994; Doroff and Keith, 1990; Heppell, 1998). Simulated movement patterns composed of short- and longer-distance movements for terrestrial turtles indicate that roads increase annual mortality rates to over 5% (Gibbs and Shriver, 2002), a rate higher than that estimated to result in population declines. Given that turtles and tortoises are among the most threatened taxonomic groups globally (Buhlmann et al., 2009), quantifying and reducing the effects of roads on their populations represents an important contribution to biodiversity preservation.

Road effects may be especially important in structuring populations of Agassiz's desert tortoise (*Gopherus agassizii*). Agassiz's desert tortoise is a federally- and state-protected species, native primarily to the Mojave Desert, USA, and roads have been identified as a major threat to their persistence (USFWS, 2008). Desert tortoises have large home ranges (Harless et al., 2009), can require up to 20 years to reach sexual maturity (Mueller et al., 1998), and only produce an average of 4.5 eggs per clutch (Turner et al., 1986). Their slow life histories suggest that desert tortoise populations should be sensitive to the negative impacts of roads, especially increased mortality. Previous studies indicate that tortoises in the Mojave and Sonoran Deserts are negatively affected by the presence of roads and occur at lower densities near heavily traveled roads (Boarman and Sazaki, 2006; Nicholson, 1979; Von Seckendorff and Marlow, 2002). However, tortoises are also noted to be attracted to gravel roads, as demonstrated by their increased presence near these roads (Grandmaison et al., 2010). The different effects of gravel roads versus highways may be a consequence of traffic volume. Here, we examine the impact of roads and traffic volume on desert tortoises with three main objectives. Our first objective was to determine whether traffic volume correlated with the abundance of tortoise sign (scat, pallets, burrows, tracks, and live or dead individuals) along roads. Next, to determine whether the road-effect zone extends farther from roads as a result of increased traffic volume, we examined roads that varied in vehicle use. Finally, we examined the demographic structure of tortoises found near roads of differing traffic volume. Collectively, we sought to demonstrate the comparative influence of traffic volume on nearby tortoise populations.

2. Methods

2.1. Relative abundance of tortoises and tortoise sign

We conducted our study in Mojave National Preserve, a 650,000 ha protected area managed by the National Park Service and located in the eastern Mojave Desert, California, USA (34°53′N, 115°43′W). We surveyed four areas of the preserve known to have tortoises: Ivanpah Valley, Fenner Valley, Clypepper Valley, and Kelso. We grouped roads into three general categories depending on the traffic volume: paved with high traffic volume (HIGH), paved with intermediate traffic volume (MED), and paved or dirt roads with low traffic volumes (LOWs) (see Table 1 for more information).

In 2012, we surveyed nine roads across the four locations in the preserve during 5–29 June. Three roads were assigned to each of three road categories (HIGH, MED, and LOW) based on traffic volume data (Table 1). We were limited by the number of suitable roads available. We measured road-effect zones along each of the roads by surveying for tortoise sign at various distances from the road. We selected the survey distances based on previous work by Boarman and Sazaki (2006) and based on preliminary data we collected during a pilot study in 2011. The work by Boarman and Sazaki (2006) in the western Mojave Desert indicated no change in the abundance of tortoise sign between 800 and 1600 m from the road but a significant increase in sign between 0 and 400 m. Thus, we did not include a 1600 m distance and instead increased the sampling resolution of our study closer to the road. Therefore, to measure the road-effect zone, we documented tortoise sign at distances of 0, 50, 100, 200, 400, and 800 m from the road. At each distance we walked two 1600 m transects parallel to the road, separated by 20 m. We recorded all tortoise sign (scat, tracks, pallets, burrows, and live and dead tortoises) visible in a 10 m wide transect (i.e., 5 m on either side of the observer) and surveyed only one transect site per road. A 5 m sight distance from the observer is a standard used during line distance sampling for desert tortoises (Boarman and Sazaki, 2006; Zylstra et al., 2010), which maximizes detection of the animals and minimizes variation among habitat types, vegetation, or observers. Distances greater than 5 m from the observer may lead to differential detection among areas, which we sought to avoid. The total tortoise sign recorded during the two parallel transects at each survey distance was summed. We corrected for bias by treating adjacent associated signs (e.g., a tortoise inside a burrow, tracks behind a tortoise) as a single encounter, as described by Boarman and Sazaki (2006).

To determine whether road category differentially affected the relative abundance of tortoise sign between categories and at the various distances, the total tortoise signs were square root transformed and analyzed using R 2.11.1 (Institute for Statistics and Mathematics, Wien, Austria) at an $\alpha = 0.10$ level. We were willing to accept higher Type I error due to our low sample sizes ($n = 3$) and with the understanding that the cost of a false negative has greater negative implications for species management than the cost of a false positive. We used analysis of covariance (ANCOVA) with tortoise sign as the dependent variable and distance from the road as the independent predictor with road name and road category included as covariates. Post hoc pairwise comparisons among means were completed using Tukey's honestly significant difference (HSD) test to compare the total relative abundance of tortoise sign and road category. We used Holm's least significant difference (LSD) test to look at the effect of each distance from the road on relative tortoise sign abundance for each road category. Because burrows represent areas where tortoises have chosen to settle, they may be more indicative of suitable habitat than other types of tortoise sign. Thus, we separated burrows from other

Table 1
Roads in Mojave National Preserve along which transects were conducted in 2011 and 2012. Category is road category based on number of vehicles per day. Type refers to whether the road was paved with asphalt or a dirt road. Lane number refers to the road width (number of lanes) present.

Road name	Location	Transect coordinates (UTM, NAD83)	Category	Vehicles per day	Type	Lane number	Posted speed limit (mph)
Goffs Rd.	Fenner Valley	0675305, 3864702	HIGH	1089[a]	Paved	2	55
Cima Rd.	Kelso	0632705, 3886389	HIGH	346[a]	Paved	2	55
Morning Star Mine Rd.	Ivanpah Valley	0643597, 3913717	HIGH	325[a]	Paved	2	55
Essex Rd	Clypepper Valley	0646939, 3858103	MED	59[a]	Paved	2	55
Ivanpah Rd.	Ivanpah Valley	0650922, 3915068	MED	47[a]	Paved	2	55
Lanfair Rd.	Fenner Valley	0675683, 3867932	MED	35[a]	Paved	2	55
None	Kelso	0618555, 3861175	LOW	<1[b]	Dirt	2	Not posted
None	Ivanpah Valley	0645971, 3911505	LOW	<1[b]	Paved	1	Not posted
None	Fenner Valley	0672552, 3869031	LOW	<1[b]	Dirt	1	Not posted

[a] Data source: <http://www.sbcounty.gov/dpw/trafficadt/>, (accessed 10.03.12).
[b] Estimated from personal observations during data collection.

tortoise signs and repeated the analyses used for total tortoise sign to test for the effects of road category and distance on the relative abundance of burrows.

We compared the number of live to dead tortoises encountered during all road transects among road categories throughout Mojave National Preserve. In order to do so we used a Chi-square test of independence to test for departures from random between road category and the number of live and dead tortoises.

From 14–24 October 2011, we measured the distance (m) from the road to the first burrow located for three roads, one in each road category (HIGH, MED, and LOW), in Ivanpah Valley. We selected five haphazard points along each of the three roads and walked perpendicularly away from the road until we located a burrow. We analyzed the effect of road category on square root transformed distance to first observed burrow using a one-way analysis of variance with $\alpha = 0.10$.

2.2. Habitat

In Ivanpah Valley from 01 April – 20 July 2011, we collected habitat data on three roads, each of which was categorized into the HIGH, MED, and LOW road category. We collected habitat data at distances of 0, 200, 400, 600, 800, 1000, 1200, 1400, and 1600 m at five randomly selected points along each road. At each sampling point we measured perennial shrub volume (height and width [cm]), distance to nearest three shrubs (m), and number of small mammal burrows (important refugia for juvenile tortoises) under the nearest three shrubs. We used ANCOVAs to examine the effect of distance with road category included as a covariate on the dependent factors perennial shrub volume (cm^3), distance to the nearest three shrubs (m), or the number of small mammal burrows with $\alpha = 0.10$. Perennial shrub volume was log transformed prior to analyses.

2.3. Tortoise demography

To determine whether tortoises varied in size among road categories, we measured all tortoises that we encountered in Ivanpah Valley from 01 April – 25 October 2011. Our 2011 Ivanpah Valley road transects overlapped spatially with areas where we conducted additional field research. Thus, all tortoises encountered in Ivanpah Valley during road transects and any other ongoing field work in 2011 were included in demographic comparisons. We located tortoises visually and handled them when shaded air temperatures were below 35 °C. For each animal encountered, we recorded location (UTM, NAD83) using a Global Positioning Unit (Garmin eTrex Venture HC [±3 m]), mid-line carapace length (MCL; distance from the nuchal scute to the pygal scute [mm]), mass (g), and sex when possible based on external secondary sexual characteristics. Desert tortoises begin showing secondary sexual characteristics around 180–190 mm MCL (Turner et al., 1987). Individuals below 180 mm MCL were recorded as sexually immature juveniles. We permanently marked each individual by notching unique combinations of marginal scutes with a triangular file (Cagle, 1939). We released all tortoises at the point of capture immediately following handling, which was limited to 30 min. We also measured MCL and recorded sex for all intact shells of dead animals that were encountered. We marked each shell with a permanent marker to ensure they were not double counted. We followed procedures approved by the Institutional Animal Care and Use Committee through the University of California, Davis (IACUC # 15997) and the University of Georgia (A2010 04-059-Y3-A0) during our handling of all animals. Our study was done in accordance with permits provided by US Fish and Wildlife Service (Permit # TE-17838A), California Department of Fish and Game (Permit # SC-11072), and Mojave National Preserve (Permit # MOJA-2011-SCI-0023).

We assigned live and dead tortoises encountered during all field activities in Ivanpah Valley during 2011 to a road category using the location selection tool in ArcEditor 9.31.1 (ESRI, California, USA). We assigned individuals within a 500 m buffer of the HIGH road to HIGH; individuals within a 500 m buffer of the MED road to MED, excepting those already assigned to HIGH; and individuals within a 500 m buffer of the LOW road to LOW, excepting any previously assigned to either HIGH or MED. Individuals that were not encompassed by HIGH, MED, or LOW buffers were assigned to a new category of NONE. For tortoises that were encountered multiple times, we used only the first encounter for analysis. After category assignment, we tested MCL data for normality and found the assumptions of normality and homogeneity of variance were violated. Thus, we used the non-parametric Kruskal–Wallis rank sum test to examine the relationship between road category and tortoise MCL. To reduce potential bias from sex- or stage-specific (e.g. adult or juvenile) mortalities near a given road, we included sex and stage as covariates, as both can affect MCL. We completed a post hoc comparison test on the results from the Kruskal–Wallis rank sum test using the "pgirmess" package in R with $\alpha = 0.10$.

We summed all tortoise encounters in Ivanpah Valley in 2011 by road category (i.e., HIGH, MED, LOW, or NONE) and used Chi-square tests to examine the ratio of adult to juvenile tortoises and male to female tortoises among the various road categories.

3. Results

3.1. Relative abundance of tortoises and tortoise sign

The average abundance of the total tortoise sign recorded for all six transect distances in 2012 was 253.7 ± 98.2 (mean ± 1 SE, $n = 3$) for LOW roads, 195.3 ± 80.8 ($n = 3$) for MED roads, and 149.0 ± 23.6 ($n = 3$) for HIGH roads. We found a significant effect of road

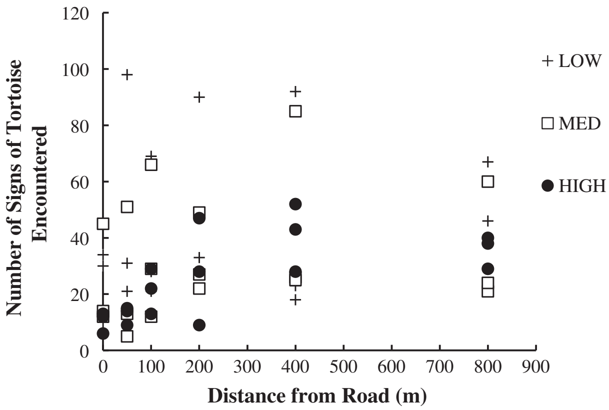

Fig. 1. Abundance of tortoise sign at each of distance sampled for the high traffic volume (HIGH), intermediate traffic volume (MED), and low traffic volume (LOW) road categories in Mojave National Preserve.

category on relative abundance of tortoise sign (road category effect: $F_{2,36} = 8.7$, $p < 0.001$) and of distance on the relative abundance of tortoise sign (distance effect: $F_{1,36} = 9.8$, $p = 0.003$; Fig. 1). We did not find any significant interaction between road category and distance (interaction effect: $F_{2,36} = 2.3$, $p = 0.11$). Tukey's HSD revealed LOW roads had significantly greater abundances of total tortoise sign than either MED ($p = 0.07$) or HIGH ($p < 0.001$) road categories. Holm's LSD tests showed no significant differences between relative abundance of tortoise sign at any of the distances for the LOW and MED roads. However, relative abundance of tortoise sign along HIGH roads increased significantly at 400 m ($p = 0.04$) and at 800 m ($p = 0.08$) compared with 0 m.

In 2012 we encountered a total of 56.0 ± 9.0 burrows on LOW traffic roads, 36.0 ± 5.5 on MED, and 32.3 ± 7.6 on HIGH roads. We found a significant effect of road category (road category effect: $F_{2,36} = 5.1$, $p = 0.01$), distance (distance effect: $F_{1,36} = 23.8$, $p < 0.001$), and an interaction of distance and road category (interaction effect: $F_{2,36} = 2.6$, $p = 0.09$) on the relative abundance of burrows (Fig. 2). Tukey's HSD revealed LOW roads had significantly greater abundances of burrows than either MED ($p = 0.06$) or HIGH ($p = 0.01$) road categories. Holm's LSD tests showed no significant differences between relative abundance of burrows at any of the distances for the LOW and MED roads. Relative abundance of burrows along HIGH roads increased significantly at 400 ($p = 0.01$) and 800 m ($p = 0.01$) compared with 0 m. Distance to the first burrow also correlated positively with traffic volume, such that the first burrow encountered was farthest from HIGH roads and closest to LOW roads ($F_{2,12} = 6.7$, $p = 0.01$; Fig. 3).

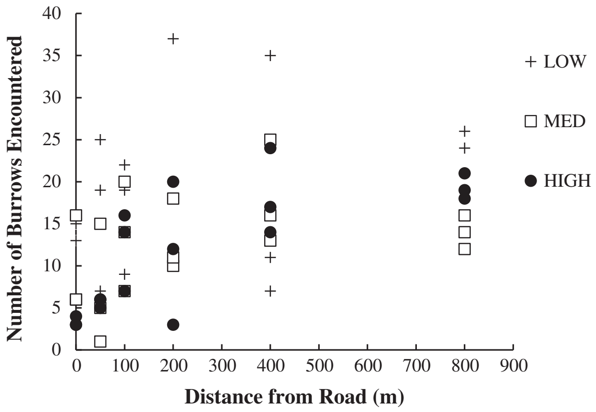

Fig. 2. Abundance of burrows at each distance sampled for the high traffic volume (HIGH), intermediate traffic volume (MED), and low traffic volume (LOW) road categories in Mojave National Preserve.

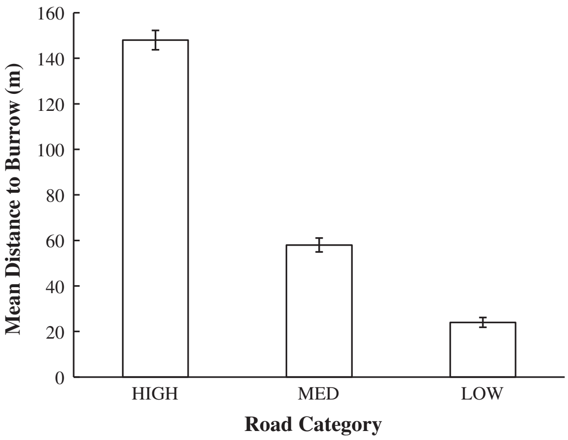

Fig. 3. Mean (±1 SE) distance to the first burrow encountered along high traffic volume (HIGH), intermediate traffic volume (MED), and low traffic volume (LOW) road categories. Road category had a significant effect on distance to the first burrow observed.

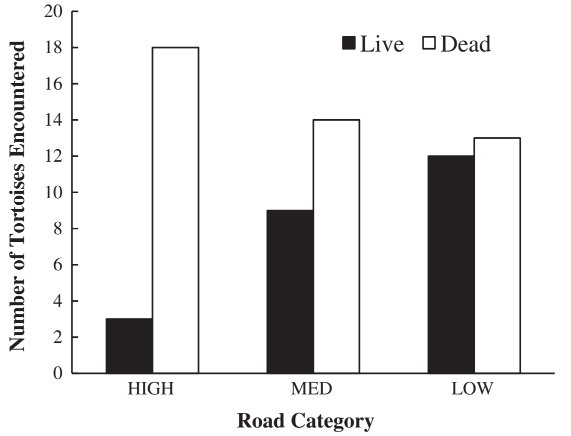

Fig. 4. Number of live and dead tortoises encountered during road transects in Mojave National Preserve. The distribution of observations differed significantly from random.

The number of live and dead tortoises encountered among the different road categories was nonrandomly distributed ($\chi^2 = 6.01$, $df = 2$, $n = 69$, $p = 0.05$; Fig. 4). The number of dead tortoises encountered increased with increasing traffic volume, whereas the number of live tortoises decreased.

3.2. Habitat

We found no effect of distance from road ($F_{1,122} = 1.2$, $p = 0.28$), road category ($F_{2,122} = 1.8$, $p = 0.17$), or their interaction ($F_{2,122} = 0.35$, $p = 0.70$) on perennial shrub volume. Similarly, we found no effect of distance from road ($F_{2,122} = 0.16$, $p = 0.69$), road category ($F_{2,122} = 1.1$, $p = 0.32$), or an interaction ($F_{2,122} = 1.6$, $p = 0.20$) on distance to the nearest three shrubs. Finally, we found no effect of distance from road ($F_{1,122} = 0.01$, $p = 0.93$), road category ($F_{2,122} = 2.1$, $p = 0.13$), or an interaction ($F_{2,122} = 0.13$, $p = 0.88$) on the number of small mammal burrows.

3.3. Tortoise demography

In 2011, we encountered 94 live tortoises (32 female, 47 male, 15 juvenile) and an additional 38 intact shells of dead animals (13 female, 13 male, 12 juvenile) in Ivanpah Valley during all field work. Search times in the different areas were not documented so we cannot compare abundance of individuals by road category with this dataset. The mean MCLs for tortoises in each road category were 213 ± 7 mm for NONE, 235 ± 9 mm for LOW, 230 ± 10 mm for MED, and 146 ± 21 mm for HIGH. Mean MCL of tortoises differed significantly among road categories ($H = 22.2$, $df = 3$, $n = 132$, $p < 0.001$). Tortoises in the vicinity of HIGH roads were significantly smaller than tortoises near the LOW, MED, and NONE road categories, whereas tortoises near the LOW road were significantly larger than tortoises that were not associated with any road (Fig. 5).

The distribution of adults to juveniles differed significantly from random among road categories ($\chi^2 = 8.64$, $df = 3$, $n = 132$, $p = 0.05$). The proportion of juvenile tortoises found within 500 m from the HIGH road was greater than the proportion found near MED, LOW, or NONE road categories (Fig. 6). Males and females were encountered with similar frequency among all road categories ($\chi^2 = 0.37$, $df = 3$, $n = 105$, $p > 0.1$; Fig. 6).

4. Discussion

The results of our study demonstrate that roads of varying traffic volumes differentially affect the relative abundance of tortoise sign, the width of the road-effect zone, and the demography of desert tortoises in Mojave National Preserve. The relative abundance of tortoise sign and burrows were significantly greater along "low" traffic volume roads (<1 vehicle per day) than either "intermediate" (30–60 vehicles per day) or "high" (320–1100 vehicles per day) traffic volume roads. We also found significantly lower relative abundances of total tortoise sign and burrows at the 400 and 800 m distances for high traffic volume roads. The lack of significant differences in measured habitat characteristics with distance from the road or between road categories suggests that changes in the relative abundance of tortoise sign were related to direct effects of traffic volume, via mortality or avoidance by the animals, and not to indirect effects such as changes in habitat resulting from road presence. However, we did not measure annual vegetation abundance near roads, though roads may have a greater effect on annual vegetation than perennial vegetation. A previous study found that the abundance of tortoise sign was lower at least 400 m from the roadside along a single heavily used highway, although traffic data are not available for that site (Boarman and Sazaki, 2006). Thus, our observations are consistent with previous findings that the relative abundance of tortoise sign is lower near roads, but provide new information about the interaction between traffic volume, demography, and relative abundance.

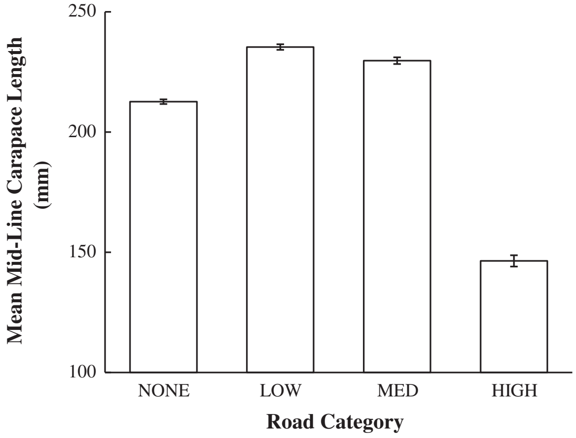

Fig. 5. Mean (±1 SE) mid-line carapace length (MCL) of tortoises encountered within 500 m of HIGH, MED, LOW, or NONE road categories for all tortoises encountered in Ivanpah Valley. Traffic volume correlated significantly with tortoise MCL.

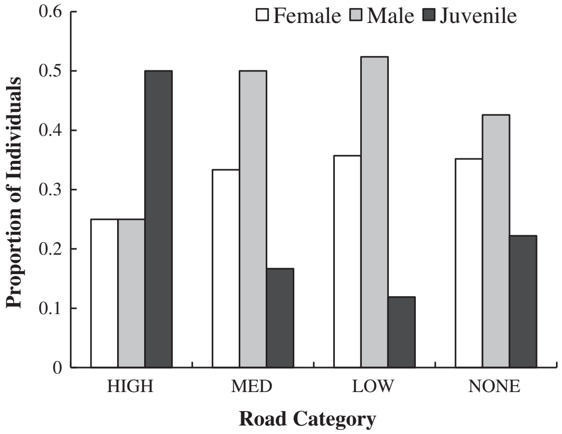

Fig. 6. Proportion of male, female, and juvenile tortoises ($n = 132$) found within 500 m of roads in the high traffic volume (HIGH, $n = 12$), intermediate traffic volume (MED, $n = 24$), low traffic volume (LOW, $n = 42$), and no road (NONE, $n = 54$) categories. Within a traffic volume category, proportions sum to 1. The proportion of adult to juvenile tortoises was significantly non-random across road observations, with the greatest proportion of juveniles observed near the HIGH category.

Abundance or density of tortoise sign may generally reflect the abundance of individuals or their relative use of habitats (McCoy and Mushinsky, 2007; Mushinsky et al., 1994). Density or abundance of individuals is thus often considered a reflective measure of habitat quality (Andersen et al., 2000; Van Horne, 1983). Our methods did not allow us to determine whether the lower relative abundance of tortoise sign was a result of increased mortality, behavioral avoidance of roadways, or both. However, both increased mortality in an area and behavioral avoidance of that area can result in reduced use by a population. Consequently, we suggest that lower relative abundances of tortoise sign and burrows near roads with traffic volumes as low as 300 vehicles per day result in decreased quality or loss of adjacent habitat for desert tortoises.

Demography of populations near roads may also be differentially affected depending on vehicle use (Taylor and Goldingay, 2010). In Ivanpah Valley, using additional data that we had available, we found that the demographic structure of tortoises along the high traffic road differed from those found along the low, intermediate, and no road categories. Although male desert tortoises, being more vagile and having larger home ranges (Franks et al., 2011; Harless et al., 2009), might be more susceptible to roads than females, we did not find that sex ratios differed among the road categories. However, we encountered only three male and three female tortoises near our high traffic volume road, so we caution against forming strong inferences on effects on the sexes from this dataset. Larger sample sizes may yield more information about the relative effects of traffic volume on male versus female tortoises. We did find that tortoises located near the high traffic road were at least 30% smaller on average than tortoises associated with lower traffic volumes or no roads. These results are similar to a study of road impacts on freshwater turtles, which found that areas with lower densities of roads had turtles of larger sizes (Patrick and Gibbs, 2010). In our study, the mean size of tortoises associated with the highest traffic volume road was below the typical size of sexual maturity in either sex.

A reduction in the average size of individuals along the high traffic road may result in lower population growth rates, even if individuals do reach sizes great enough for sexual maturity. Body size in many reptiles, including the desert tortoise, correlates strongly with fecundity (Congdon et al., 1987; Ford and Seigel, 1989; Mueller et al., 1998; Winck and Rocha, 2012). Though tortoises in different populations or geographic regions may exhibit responses that vary from those we observed, our results are similar to previous predictions for terrestrial turtles. Gibbs and Shriver (2002) found that traffic volumes of >100 vehicles per lane per day would be sufficient to result in population declines of terrestrial turtle species. In this paper, we provide evidence that traffic volumes of 300 vehicles per day may be sufficient to decrease the abundance of individuals through direct mortality and indirectly by removing larger reproductive animals that contribute more to population growth (Doak et al., 1994).

In addition to the smaller sizes of adult tortoises, there were also a greater proportion of juvenile tortoises near the high traffic volume road than along any of the other road categories. There are several potential explanations as to why we observed more juveniles in this area. One likely explanation is that juveniles are less susceptible to road mortality due to smaller home ranges and lower rates of movement than adults (Harless et al., 2009; Hazard and Morafka, 2002; O'Connor et al., 1994). Thus, juveniles may less frequently encounter and be killed on roads. Alternatively, areas near high traffic volume roads may be attractive to dispersing juveniles due to lower densities of tortoises and associated reductions in intraspecific resource competition. Additionally, tortoises near the high traffic volume road may have shorter lives from greater mortality. The lower number of live animal encounters and the greater number of observed mortalities near our highest traffic road category provides supporting evidence. The longer an individual lives near a road or the greater the frequency of passing vehicles, the more likely an individual is over time to encounter a vehicle with potentially fatal consequences, thus leading to the loss of older animals. The presence of greater relative proportions of juveniles in habitat near high traffic volume roads may ultimately indicate that habitat near roads used by as few as 300 vehicles per day represents sink habitat for desert tortoises.

We found no significant negative effects on tortoises near low and intermediate traffic volume roads as measured by road-effect zone, tortoise size, or demographic composition. However, we did observe that intermediate traffic volume roads had lower over-all relative abundance of tortoise sign compared to low traffic volume roads. We further observed that our intermediate traffic volume roads had mean values that were frequently between the low and high traffic volume roads, suggesting that even our intermediate traffic roads may affect nearby tortoises. Availability of roads within the preserve limited our sample size, which may have limited our ability to statistically detect the more subtle effects of intermediate traffic volume roads. Interestingly, tortoises encountered along the low traffic volume road were larger on average than were tortoises found >500 m from any road. One possible explanation is that roads may physically alter habitat in a way that can be beneficial when mortality is not also increased from tortoise-vehicle collisions. For example, roads increase water runoff, a factor that may increase drinking opportunities in water-limited deserts and which may also increase biomass of road-side annual vegetation. Increased water and forage availability can increase growth rates and survival of the desert tortoise (Nagy and Medica, 1986; Peterson, 1996). However, even if roads have the potential to positively alter habitat characteristics, the increased disturbance or mortality that occurs with as few as 300 vehicles per day likely negates such changes. Furthermore, the interaction between low traffic roads and local habitat quality is likely species-specific. For instance, previous studies have indicated that black bears avoid gravel roads (Reynolds-Hogland and Mitchell, 2007). Although none of the metrics we measured had statistically observable negative associations between our lowest traffic road and desert tortoises, other metrics, tortoise populations, or species may demonstrate negative responses.

Our results should be considered a conservative estimate of road-effect zones for desert tortoises. The traffic volumes studied in this paper, even for our "high" traffic volume roads, were relatively low (Grilo et al., 2009). Our highest traffic volume roads were lower than volumes on highways and interstates, which are frequently targeted or recommended for wildlife mitigation measures (Bissonette and Rosa, 2012; Ford et al., 2011; Gonzalez-Gallina et al., 2013). Within Mojave National Preserve, a designated wilderness area, the traffic volumes are lower than those in much of the desert tortoise's range due to the absence of commercial traffic, highways, and interstates. Thus, our results likely under-represent road-effect zones that tortoises experience in many other parts of their distribution, as well as emphasize the importance of studying the effects of even relatively low traffic roads. The noticeable effects of the relatively low traffic volumes studied here highlight the need to estimate the species' capacity to absorb additive mortality associated with a variety of traffic volumes and the contribution of these differing roads to population declines.

Though the installation of barrier fencing is a prescribed mitigation tool for reducing road mortality and road impacts on many species including the desert tortoise (USFWS, 2008), the use of fencing is not without controversy. Fences can transform a semipermeable barrier into an impermeable one. As a result, fencing may fragment populations, prevent recolonization of depauperate but otherwise suitable habitat, and subsequently increase extinction risk. Given the prospect of changing climate in coming decades, fencing as a mitigation tool may drastically reduce likelihood of species persistence by limiting the ability of populations to follow shifts in the location of suitable habitat. Consequently, fences are predicted to have greater negative effects on population persistence than roads when road mortality is sufficiently low (Jaeger and Fahrig, 2004). The development of predictive measures to estimate traffic threat to nearby populations, population responses to fencing, fencing effectiveness, and willingness of individuals to use culverts are thus important future topics. Our results suggest that additional preventative measures (such as fencing) against road mortality along roads with as few as 300 vehicles per day may be beneficial at least in preventing initial population declines.

Our findings provide additional evidence that a vagile reptile species with a large home range and long generation time (Franks et al., 2011; Mueller et al., 1998) is susceptible to road presence, and that increasing traffic volume exacerbates associated effects. For many species, particularly those already experiencing declines, the impact of roads is of growing concern. Protected areas, such as national parks, can represent important buffers against extinction. Often, protected areas are treated as secure from anthropogenic impacts and human encroachment. However, even in otherwise protected areas, roads can present important threats to wildlife populations (Roger et al., 2012). Furthermore, over half of surveyed US national parks have expressed concern for the adverse effects of roads on endangered species within their borders, but most parks have little data documenting road effects on wildlife (Ament et al., 2008). In spite of this, many agencies responsible for managing wildlife populations may lack the resources necessary to acquire these data for the majority of species encompassed. Thus, knowledge of life history characteristics or patterns that correlate with sensitivity to road presence is an increasingly valuable conservation tool. Such a tool would allow wildlife or land managers to easily identify species or habitat zones that require road mitigation efforts to prevent declines in local abundances of target species, even in protected areas where they are often presumed secure.

Acknowledgements

We thank E.A. Eskew and two anonymous reviewers for their invaluable contributions and recommendations of improvement to this manuscript. We thank D. Hughson, the Mojave National

Preserve, and the Piedmont South Atlantic Coast Cooperative Ecosystem Studies Unit for assistance with this project. This material is based upon work supported by the National Science Foundation Graduate Research Fellowship Program under Grant No. DGE-1148897. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation. We also thank the Community Foundation Desert Legacy Grant for funding support. This report was also prepared as a result of work sponsored in part by the California Energy Commission under agreement 500-10-020 to UC Davis. It does not necessarily represent the views of the Energy Commission, its employees, or the State of California. The Energy Commission, the State of California, its employees, contractors, and subcontractors make no warranty, express or implied, and assume no legal liability for the information in this report; nor does any party represent that the use of this information will not infringe upon privately owned rights. Manuscript preparation by T.D. Tuberville and K.A. Buhlmann was partially supported by the Department of Energy under Award Number DE-FC09-07SR22506 to the University of Georgia Research Foundation.

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