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Delimiting road-effect zones for threatened species: implications for mitigation fencing

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Abstract

Context. Roads are a pernicious form of habitat loss for many wildlife populations because their effects often extend far beyond the roads themselves, giving rise to reduced wildlife abundance in road-effect zones. Quantifying the extent of road-effect zones more accurately portrays their impact on populations and the true extent to which habitat is lost for many species.

Aim. The purpose of the present study was to evaluate ways of determining the extent of road-effect zones for a model study species to better quantify the effect of roads on habitat loss.

Methods. We conducted road-side surveys for signs of Mojave desert tortoises (*Gopherus agassizii*) 0, 200, 400, 800 and 1600 m from county roads and interstates, two of the most common road types in critical habitat of this threatened species. Using data from these road-side surveys, we estimated the extent of road-effect zones using piecewise regression and modified von Bertalanffy models.

Key results. We found reduced abundances of tortoise sign along both county roads and interstates. Reductions extended farther from the large, high-traffic interstate than from the smaller, lower-traffic county roads (306 m versus 230 m). The increase in the abundance of tortoise signs with distance from roads approximated a negative exponential curve.

Conclusions. Interstate and county roads both contribute to habitat loss in road-side areas by making these habitats unsuitable to desert tortoises, presumably by removing animals via mortality from collisions with vehicles. Larger roads with greater traffic have more extensive effects.

Implications. Roadside mitigation fencing has been proposed as one way to reduce mortality of desert tortoises and to reclaim habitat by allowing tortoises to recolonise currently depauperate road-effect zones. Immediate mortality is more likely to be prevented by fencing county roads where tortoises occur closer to roads and are more likely to be struck by vehicles and killed. However, fencing interstate should yield more reclaimed habitat than that obtained from fencing county roads. Managers must consider balancing these goals along with other concerns when deciding where to place roadside fencing.

Additional keywords: conservation, road ecology, species recovery, turtle.

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Introduction

Habitat alteration and fragmentation are among the main drivers of global biodiversity loss (Sala *et al.* 2000; Sanderson *et al.* 2002; Fahrig 2003). Increasingly, road networks contribute to these processes, ultimately leading to species declines and extinctions (Forman and Alexander 1998; Spellerberg 1998; Fahrig 2003). Road networks have expanded in the United States to over 6 million km of paved public roads and have been estimated to affect over one-fifth of the total land area in the contiguous USA (Forman 2000). This infrastructure carries with it costs to wildlife, both directly through road mortality from vehicle collisions, and indirectly through habitat loss, increased edge effects and fragmentation (Forman and Alexander 1998; Forman *et al.* 2003). Roads effectively isolate populations when they act as barriers to animal movement, either through mortality during crossing attempts or from behavioural avoidance in some wildlife (Anderson 2002; Forman *et al.* 2003; Andrews *et al.* 2005; Shepard *et al.* 2008). Given the immense scope of road networks in the USA (National Research Council 1997), and the increasing growth of roadways in developing countries

(Fan and Chan-Kang 2005), understanding the extent to which roads affect wildlife populations and species persistence remains a primary concern for biodiversity conservation.

The distance from a road at which effects to wildlife populations is detected is termed the 'road-effect zone' (Forman and Alexander 1998). This area of impact has been identified for many species, and can range from distances as short as 100 m to over a kilometre (Keller and Largiader 2003; Bennett *et al*. 2013; Rotholz and Mandelik 2013). The extent to which roads negatively affect species can depend on the intrinsic characters of the species themselves, or may vary depending on the type of road in question. For example, surface type, width or traffic volume can all shape the response of wildlife in habitat adjacent to roads (Graham *et al*. 2010; Brehme *et al*. 2013; Nafus *et al*. 2013). Additionally, previous studies have identified that species with slow life histories, large home ranges, or those that are highly elusive, are often negatively affected by roads (Carr and Fahrig 2001; Waller and Servheen 2005; Rytwinski and Fahrig 2012).

Turtles and tortoises have delayed sexual maturity and high adult survival, two life-history traits common in species that are sensitive to roads (Mueller *et al*. 1998). Additionally, turtles and tortoises are often of interest to resource managers because approximately half of them have been identified as threatened or vulnerable to extinction by the IUCN (van Dijk *et al*. 2014). Consequently, identifying and quantifying the impact of roads on turtles and tortoises may prove useful in developing appropriate conservation or mitigation techniques to halt declines and aid species recovery. For example, the Mojave desert tortoise (*Gopherus agassizii*) is a federally and state-protected species native to the Mojave Desert of the south-western USA. Since its listing under the *Endangered Species Act* in 1990, habitat loss and fragmentation have been identified as primary threats to desert tortoise populations (US Fish and Wildlife Service 2011). Continued human encroachment into the Mojave Desert and rapid infrastructure development have increased the loss of critical habitat (Lovich and Brainbridge 1999; Leu *et al*. 2008; Lovich and Ennen 2011). Thus, management agencies are increasingly interested in ways to reduce or mitigate threats to the Mojave desert tortoise.

One area that holds promise in reducing or mitigating road effects on desert tortoises and other long-lived vertebrates is the installation of roadway fencing to prevent animal mortality and reclaim adjacent habitat effectively lost in road-effect zones. A key premise to understanding the value of roadside fencing lies in better quantifying the distance at which road effects penetrate adjacent habitat. The purpose of the present study was to quantify the degree to which two common road types, namely, interstate and county roads, negatively affect desert tortoises. Interstate and county roads are ubiquitous across south-western deserts of the USA and, therefore, may offer considerable opportunity for reclaiming lost habitat along roads via the installation of roadway fencing. We hypothesised that interstate roads are more detrimental than are county roads because interstate roads are often three times larger, with much higher traffic volumes. Thus, we expected that the road-effect zones of interstate roads would be greater than those of county roads. Quantifying the distance at which these road-effect zones permeate adjacent habitat can allow an estimate of the potential amount of habitat that could be preserved or restored via installation of roadside fencing. These methods are likely applicable to other key species of conservation need for which road impacts are a major concern.

Materials and methods

We conducted our study in Fenner Valley and Ivanpah Valley near the Mojave National Preserve in the eastern Mojave Desert, California, USA (Fig. 1). We surveyed a total of 17 sites, including seven sites along paved interstate roads (4–6-lane divided highways) and 10 sites along paved county roads (2-lane roads; Table 1). We surveyed the county road sites in June 2012 and the interstate sites in September 2012, both being months that support similar levels of tortoise activity in this region (Ernst and Lovich 2009). All sites were chosen so that no other roads, railroads, powerline rights of way, or trails were located within 1.6 km of any transects (see below).

At each survey site, we walked two parallel transects 15 m apart for 1600 m at each of five distances parallel to the road (Fig. 1). We surveyed the first transect (i.e. 0-m transect) beginning 10 m from the road edge and conducted additional transects 200, 400, 800 and 1600 m from the road edge. Previous work from Boarman and Sazaki (2006) using survey lines 0, 400, 800 and 1600 m from the road edge found an increase in observed tortoise sign between the 0- m and 400-m transects, leading us to add transects at 200 m to better capture the possible increase in tortoise sign. Additionally, previous studies of tortoises in our region estimated mean weekly movements of 114–207 m, with maximum weekly movements ranging from 354 to 589 m (Franks *et al*. 2011). For these reasons, we expected that our sampling distances would sufficiently capture evidence of decreased tortoise abundances. We documented tortoise sign within 5 m of the centre line of each transect. Signs included tortoise burrows, pallets, scat, tracks, live tortoises and carcasses (typically old remains of shells). Burrows are deeper than they are wide, allowing them to be distinguished from pallets, which are usually shallower than they are wide. We classified tortoise burrows into one of three categories, adopted from the USFWS field manual (US Fish and Wildlife Service 2009). Class 1 burrows were those that were currently active, having either signs of recent activity or containing a visible desert tortoise. Class 2 burrows were those in good condition, but which did not appear to have been used in the past few months. Class 3 burrows were those clearly belonging to desert tortoises, but which had deteriorated and were apparently unused; Class 3 burrows were often partially collapsed.

To reduce observer error and to increase the likelihood of observing tortoises, we did not conduct surveys when shaded air temperatures exceeded 35°C at 5 cm above ground. This criterion also conforms to USFWS survey guidelines (US Fish and Wildlife Service 2009). Additionally, no observer surveyed more than eight transects in one day.

Statistical analysis

We summed total counts of tortoise signs along the transect pair at each of the five distances from the road. Counts of burrows, pallets, carcasses and scat were not normally distributed and could not be normalised using transformations. Additionally, in

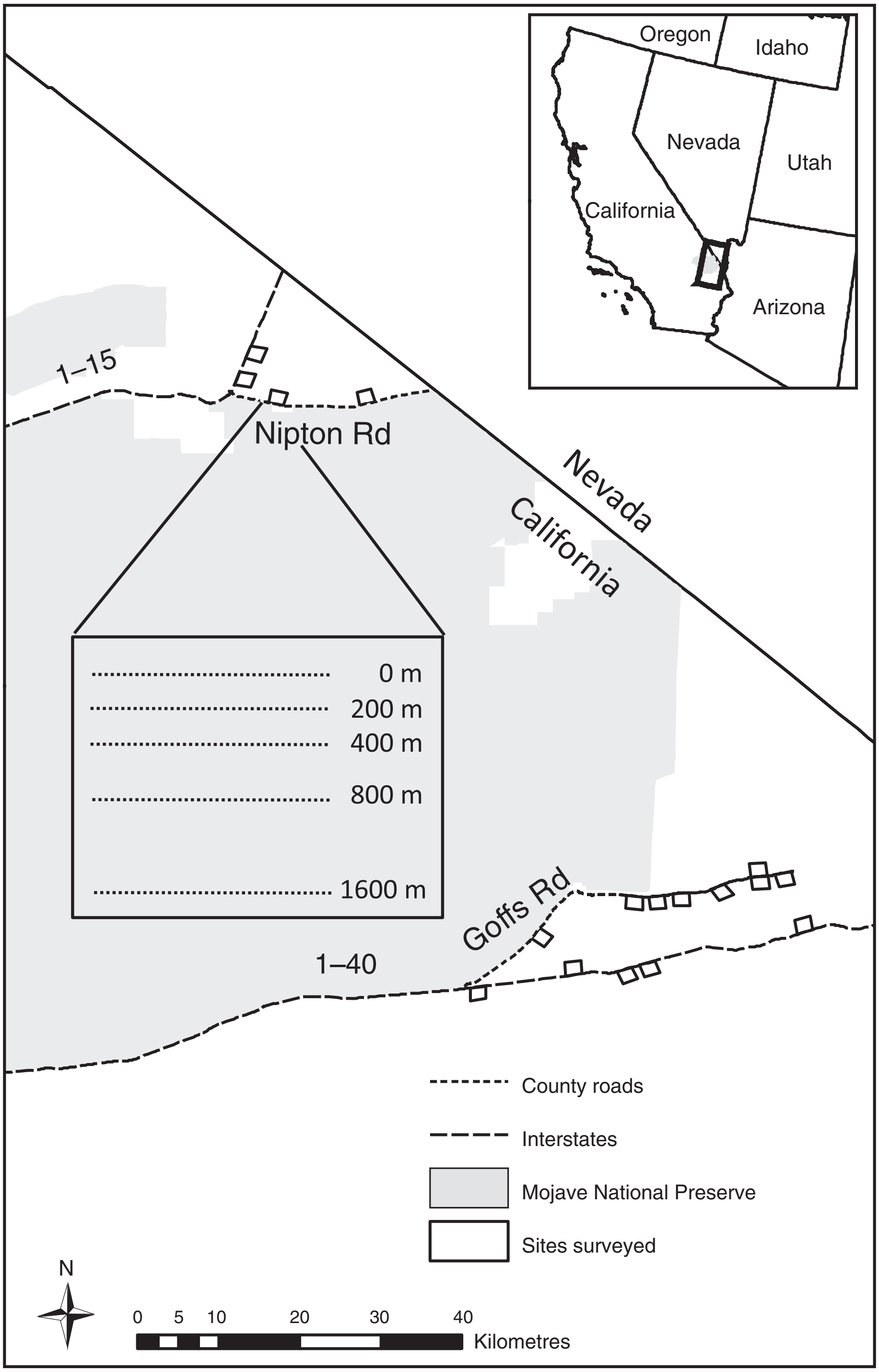

Fig. 1. A map showing the study region, study roads and location of plots where data were collected in the Mojave Desert of the south-western United States. Inset shows distances at which transects were conducted. Dotted lines illustrate transect distances from roads at each plot.

many cases, there were no counts of some types of sign along transects. Thus, we analysed these data using generalised linear mixed models (GLMM) with a Poisson distribution in R package 'lme4' (Bates *et al*. 2015). We then constructed and compared the fit of four different models for each dataset (burrows, pallets, carcasses or scat). Each of these four models included a random effect of site. However, the models differed in which fixed effects they included; one model included a fixed effect of road type, one model included a fixed effect of distance from road, one model included both of these fixed effects, and the

Table 1. Roads in the eastern Mojave Desert, USA, along which transects were conducted in 2012

Road name	Road type and site	Transect coordinates (UTM, NAD83)	Vehicles per day
Nipton Rd	County road site 1	0645501, 3926103 11S	995[A]
Nipton Rd	County road site 2	0654223, 3926256 11S	826[A]
Fenner Rd	County road site 3	0673370, 3860060 11S	1089[A]
Goffs Rd	County road site 4	0682597, 3864585 11S	1089[A]
Goffs Rd	County road site 5	0684989, 3864623 11S	1089[A]
Goffs Rd	County road site 6	0687356, 3865067 11S	1089[A]
Goffs Rd	County road site 7	0691470, 3866036 11S	1089[A]
Goffs Rd	County road site 8	0695103, 3868939 11S	1089[A]
Goffs Rd	County road site 9	0695310, 3867235 11S	1089[A]
Goffs Rd	County road site 10	0697826, 3867720 11S	1089[A]
Interstate 15	Interstate site 1	0643143, 3931312 11S	50 000[B]
Interstate 15	Interstate site 2	0642194, 3928172 11S	50 000[B]
Interstate 40	Interstate site 3	0666956, 3853080 11S	12 300[B]
Interstate 40	Interstate site 4	0676531, 3856417 11S	12 300[B]
Interstate 40	Interstate site 5	0682000, 3855596 11S	12 300[B]
Interstate 40	Interstate site 6	0684370, 3856455 11S	12 300[B]
Interstate 40	Interstate site 7	0699781, 3862186 11S	12 300[B]

[A]Data source: http://www.sbcounty.gov/dpw/trafficadt/ (accessed 16 March 2015).
[B]Data source: http://traffic-counts.dot.ca.gov (accessed 16 March 2015).

fourth and final model included both fixed effects and their interaction. Models were evaluated using an information-theoretic approach with Akaike's information criterion corrected for a small sample size (AIC_c) as the metric for comparison (Burnham and Anderson 2002).

Following the methods of Boarman and Sazaki (2006), we adjusted counts of tortoise signs so that closely associated signs within 3 m of each other were counted only once (total corrected sign; TCS). For example, if scat was found at a burrow entrance or if a tortoise was found next to a burrow, these counts were treated as a single count and not as two. We square-root transformed TCS to normalise the data, and variances among groups were homogeneous. We used a two-way ANOVA in SPSS version 20.0 (IBM Corp., Armonk, New York) to determine whether TCS differed by road type, distance from road or with the interaction of distance-by-road, treating each site as a random block. We used Tukey's honestly significant difference *post hoc* tests for pair-wise comparisons.

Counts of TCS as a function of distance from road approximated a negative exponential function. By modifying the von Bertalanffy growth equation (von Bertalanffy 1938), it is possible to estimate the maximum expected TCS and the shape of the negative exponential curve for each of the two road types, county road or interstate road. This, in turn, allows the calculation of the distance from a road edge (i.e. the road-effect zone) at which a given proportion of the maximum estimated TCS would be expected to occur. The modified equation takes the form of

$$C_{t2} = a - (a - C_{t1}) \times \mathrm{e}^{-\mathrm{k}d},$$

where C_{t1} is the count of TCS at the first distance, C_{t2} is the count of TCS at the second distance, d is the interval difference between the two distances, e is the mathematical constant for the base of the natural logarithm, a is the estimated asymptotic count of TCS, and k is the estimated characteristic constant that defines the shape of the curve. The values of C_{t2}, C_{t1} and d are provided by each possible pair of distance interval for transects at a site (10 possible combinations from the five distances), and the values of a and k are calculated using non-linear curve fitting based on maximum-likelihood estimation (Kirkwood 1983). We constructed a modified von Bertalanffy model using all combinations of transect data at each site for county roads ($n = 100$) and separately for interstate roads ($n = 70$) using PROC NLIN in SAS version 9.3 (SAS Institute Inc., Cary, North Carolina, USA). We then solved these equations to calculate the distances at which one would expect to find 50%, 75%, 90% and 95% of the total estimated asymptotic counts of tortoise sign away from roads.

As an alternative method to the modified von Bertalanffy model to quantify the road-effect zones, we created a linear piecewise regression model for the county-road data and separately for the interstate-road data to estimate threshold distances in changes of counts of tortoise sign as a function of distance from roads. We fitted these piecewise regression models to the square-root transformed TCS data using the package 'segmented' in R (Muggeo 2015). We estimated a single breakpoint for each of the two road types (i.e. threshold distance; Toms and Lesperance 2003), and we generated 95% confidence intervals for the estimated breakpoints and used Davies' test to compare the slopes of the regression lines before and after each breakpoint (Muggeo 2015).

So as to estimate the potential habitat recovered by the installation of roadside fencing, we used the distances at which given percentages of the total tortoise sign (TCS) were recovered on the basis of the modified von Bertalanffy models described above. For our calculations, we made the assumption that a 1-km section of fencing was installed on one side of the road, although most roads would need fencing along both sides and would stand to gain habitat on both sides if so. To provide an additional estimate for comparison, we also used the threshold distances from the piecewise regression models to calculate the area recovered on one side of the road from a 1-km section of fencing on that side of the road.

Results

Burrows were the most common sign observed (68%), with pallets (13%), carcasses (11%) and scat (5%) constituting most of the remaining signs encountered on transects. The majority of burrows were Class 3 burrows (54%), followed by Class 2 burrows (38%) and Class 1 burrows (8%). Tortoise tracks were not commonly found (6 total in 272 km). Overall, we found on average 2.4 burrows, 0.45 pallets, 0.18 scats, 0.09 live tortoises and 0.37 carcasses per kilometre.

We found significantly more TCS along county-road transects than along interstate-road transects (4.0 versus 2.6 km^{-1}; $F_{1,60} = 35.9$, $P < 0.001$; Fig. 2*a*). TCS also increased significantly as distance from roads increased ($F_{4,60} = 56.9$, $P < 0.001$; Fig. 2*a*). TCS was lowest immediately adjacent to roads compared with all other distances ($P < 0.001$; Fig. 2*a*). TCS was also significantly reduced along the 200-m-long transects compared with 800-m-long transects ($P < 0.001$; Fig. 2*a*). There was a trend ($P = 0.07$)

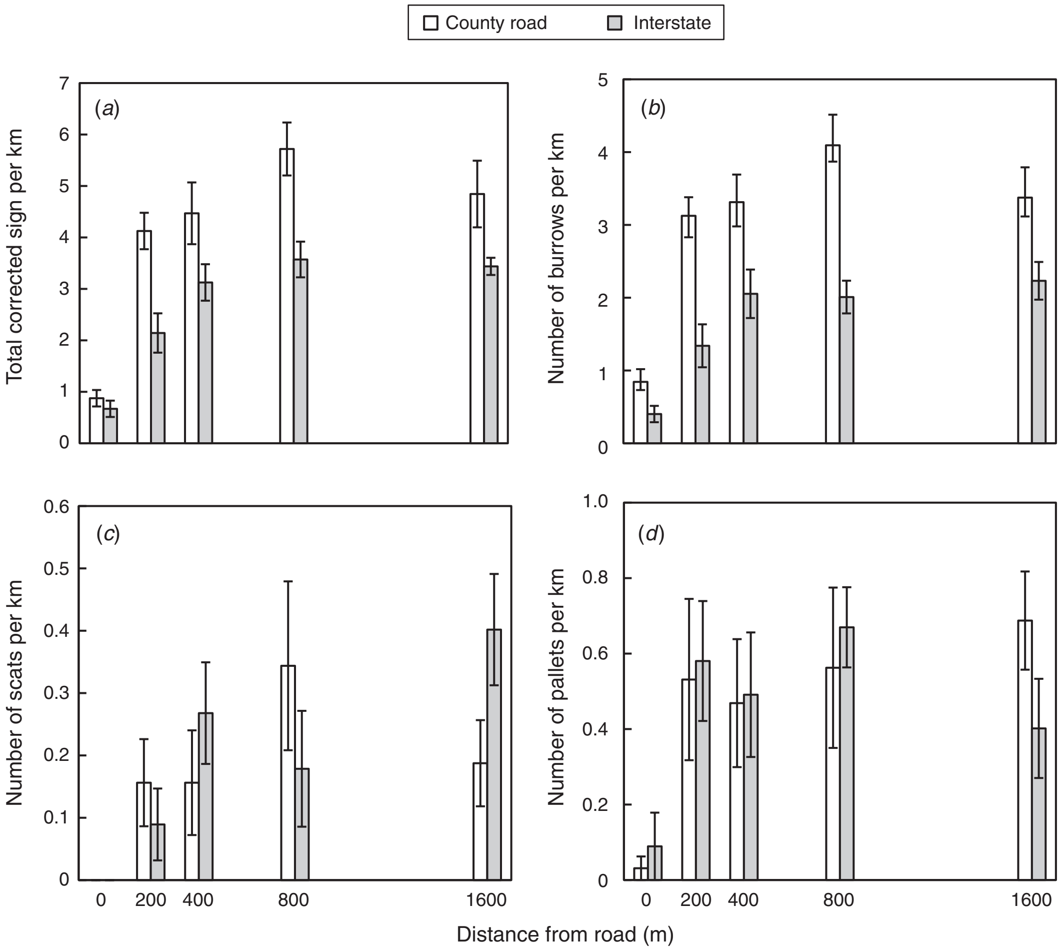

Fig. 2. Mean (± 1 s.e.) tortoise sign on road-side transects collected at varying distances from either county roads (open columns) or interstate roads (shaded columns). (*a*) Total corrected sign per kilometre, (*b*) number of burrows per kilometre, (*c*) number of scats per kilometre and (*d*) number of pallets per kilometre. Note that scales of *y*-axes may differ among graphs.

towards lower TCS along 200-m transects compared with 1600-m transects, but TCS did not differ significantly among transects at any other distances ($P \geq 0.12$; Fig. 2*a*). TCS also varied among sites along county roads and interstate roads ($F_{15,60} = 3.5$; $P < 0.001$), but there was no evidence of an interaction between the road type and distance from the road ($F_{4,60} = 1.9$; $P = 0.13$).

The results of the GLMMs for burrow distribution were qualitatively similar to the results of the parametric ANOVA on TCS, indicating support for both distance and road-type effects, likely because burrows comprised the majority of tortoise signs observed. The other three models, including the model with an interaction effect, performed significantly poorer (Table 2). There were more burrows observed on county-road transects than on interstate-road transects, and burrow abundance was greater farther from roads (Fig. 2*b*). For pallets, carcasses and scat, the model including only the fixed effect of distance was identified as the best model (Table 2). All other models had less support ($\Delta AIC_c > 2$), although the model including both distance and road type as fixed effects performed second best and carried some weight of evidence (Table 2). Scat was more abundant farther from roads (Fig. 2*c*, Table 2), as were pallets (Fig. 2*d*, Table 2). Carcasses were similarly more abundant farther from roads (Fig. 3*a*, Table 2). Too few live tortoises were encountered along transects to be analysed. However, live tortoises were found along 200-m transects on county roads but not on interstate roads (Fig. 3*b*).

The slopes of the modified von Bertalanffy models fitting TCS as a function of distance from road are depicted in Fig. 4, with dashed or dotted lines overlaid to highlight where one would expect to observe 50% and 95% of the estimated maximum observed sign. TCS fit the von Bertalanffy models well for both the county roads ($R^2 = 0.93$) and interstate roads ($R^2 = 0.96$). The estimated theoretical maximum TCS was 4.52 signs km^{-1} ± 0.14 (mean ± 1 s.e.) along county-road transects and 3.6 signs km^{-1} ± 0.12 (mean ± 1 s.e.) along interstate-road transects. TCS initially increased with distance more rapidly along county roads, before tapering off (0.01 ± 0.004, mean ± 1 s.e.), whereas TCS increased with distance more gradually along interstate roads, before tapering off (0.004 ± 0.0008, mean ± 1 s.e.). Consequently, the distances at which different proportions of the expected maximum TCS would be reached were much smaller for county roads than for interstate roads (Table 3). The estimated amounts of habitat that could be

Table 2. Comparisons of four generalised linear mixed models fitting tortoise sign data and including either distance or road type as a fixed effect, and their interaction

In all models, each 1.6 km × 1.6 km plot where data were collected was modelled as a random effect. Too few live tortoises were observed to include in analysis

Model	Number of parameters	AICc	ΔAIC	AICc Weight
Effect on burrows				
Distance and road type	7	101.9	0.0	0.96
Distance, road type, and interaction	11	108.4	6.5	0.04
Distance	6	115.7	13.8	0.00
Road type	3	212.1	110.2	0.00
Effect on pallets				
Distance	6	123.3	0.0	0.76
Distance and road type	7	125.7	4.4	0.23
Distance, road type, and interaction	11	132.8	19.1	0.01
Road type	3	152.4	22.5	0.00
Effect on carcasses				
Distance	67	106.7	0.0	0.68
Distance and road type	7	109.1	2.4	0.21
Distance, road type, and interaction	11	110.2	3.5	0.12
Road type	3	146.3	39.6	0.00
Effect on scat				
Distance	6	84.5	0.0	0.74
Distance and road type	7	86.7	2.2	0.25
Distance, road type, and interaction	11	92.2	7.7	0.02
Road type	3	102.9	18.4	0.00

reclaimed along one side of the road from roadside fencing and recolonisation were greater for interstate than for county roads (Table 4).

The piecewise regression models were a good fit for the square-root-transformed TCS data for both county roads ($R_{adj}{}^2 = 0.62$) and interstate roads ($R_{adj}{}^2 = 0.68$). For county roads, the estimated breakpoint was 229.6 ± 34.0 m (95% CIs: 163.0–296.2), and the slopes of the two regression lines differed significantly ($P < 0.001$; Fig. 5*a*). For interstate roads, the estimated breakpoint was 305.7 ± 60.7 m (95% CIs: 186.7–424.8), and the slopes of the two regression lines differed significantly ($P < 0.001$; Fig. 5*b*). Although the breakpoint was farther from the road edge for interstate than for county roads, the 95% confidence intervals overlapped between the two road types. On the basis of the estimated breakpoints, for each kilometre of fencing installed along one side of the road, 23.0 ha of habitat would be reclaimed along that side of a county road and 30.6 ha would be reclaimed along that side of an interstate road by reducing tortoise mortality and allowing recolonisation of areas along roads.

Discussion

Previous studies of the effects of roads on desert tortoises have generally found a negative association with paved roads. For example, a study on a single state highway with traffic volumes intermediate to the county roads and interstate roads in our study found significantly reduced tortoise sign up to 400 m from the road edge (Boarman and Sazaki 2006). Additionally, even paved roads with traffic volumes of fewer than 60 vehicles per day have been found to have reduced abundances of tortoise sign for at least 200 m (Nafus *et al*. 2013). However, no studies have explicitly included in surveys paved roads that vary in traffic volume up to an order of magnitude in the same region, and none has examined interstate roads that support high traffic volumes. Additionally, by collecting data more intensively at closer intervals to the roads, we were able to more precisely estimate the distance at which road-effect zones extend. Additional transects at distances even closer to the road and at a finer sampling grain may allow even more precise estimates of road-effect zones. This may be especially true for smaller roads where transects closer to the road have been used to identify smaller road-effect zones (e.g., Nafus *et al*. 2013). The interstate and county roads we examined represent two of the most common road types across the Mojave Desert region, with the 4–6-lane divided interstate roads representing the most extreme case of road impacts expected on this species, given their high traffic volume and size.

Studies of other taxa have also frequently found that roads negatively affect wildlife species or have altered biological communities alongside them (Fahrig and Rytwinski 2009). For example, in open habitat, northern lapwings (*Vanellus vanellus*), black-tailed godwits (*Limosa limosa*) and common redshanks (*Tringa tonanus*) were all found in reduced numbers up to 600 m along rural roads, and up to 1800 m along larger highways (van der Zande *et al*. 1980). Larger animals, such as golden jackals (*Canis aureus*), African elephants (*Loxodonta africana*) and blue wildebeests (*Connochaetes taurinus*), are also adversely affected by roads, exhibiting road-effect zones up to 600 m from highways in Mikumi National Park (Newmark *et al*. 1996). Road-effect zones are present even for smaller, less mobile taxa such as amphibians, with negative effects extending up to 1500 m for some ranid frogs (Carr and Fahrig 2001).

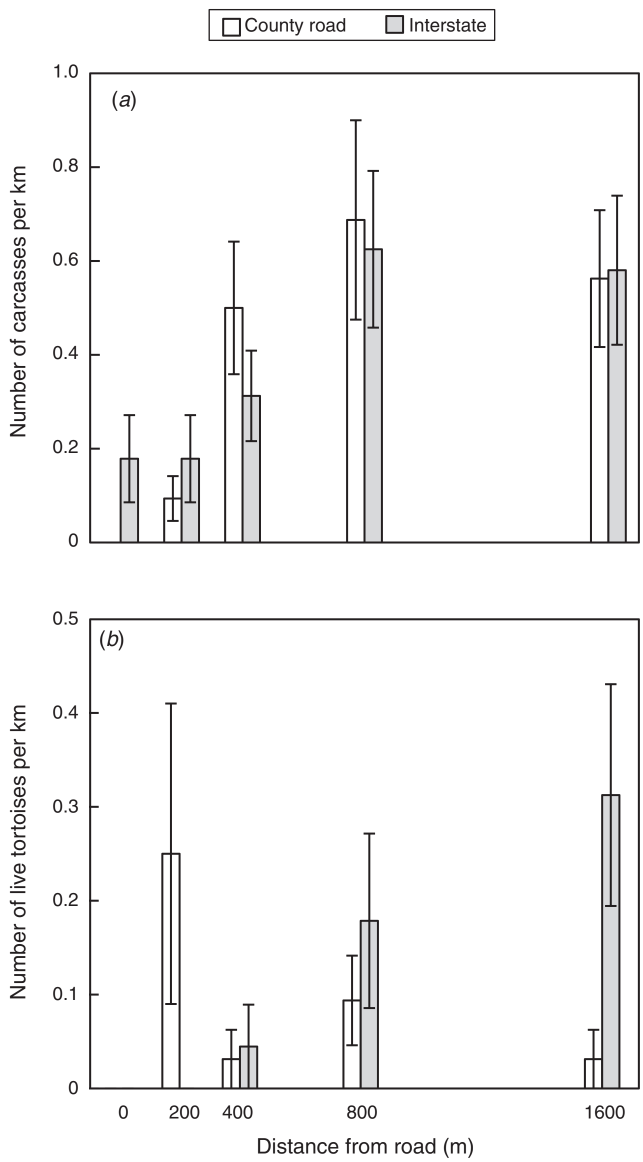

Fig. 3. Mean (± 1 s.e.) tortoise sign on road-side transects collected at varying distances from either county roads (open columns) or interstate roads (shaded columns). (*a*) The number of carcasses per kilometre and (*b*) the number of live tortoises per kilometre. Note that scales of *y*-axes may differ among graphs.

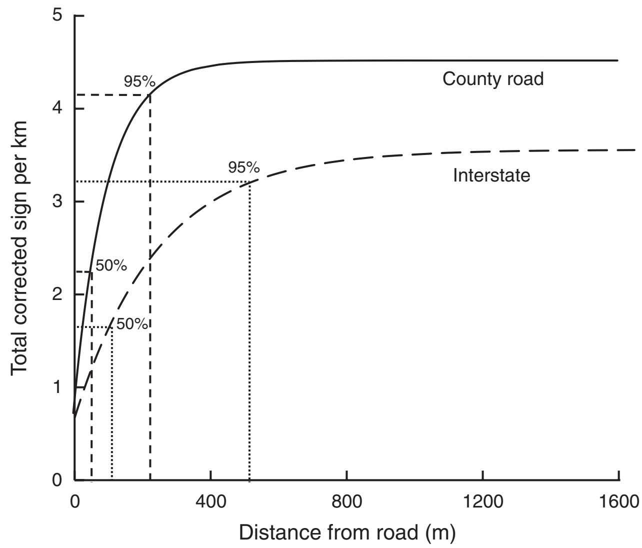

Fig. 4. Slopes of modified von Bertalanffy models showing an increase in total corrected sign of desert tortoises per kilometre as distance from road increases. Counts are shown for county roads on the solid line and interstate roads on the dashed line. Dotted lines show intercepts at 50% or 95% of the estimated asymptote for total corrected sign along the roads.

Table 3. Estimated distance at which counts of total corrected sign (TCS) reach a given percentage of the estimated maximum TCS calculated from a modified von Bertalanffy equation

Road type	Estimated distance (m)			
	50%	75%	90%	95%
County road	46.0	112.6	200.7	267.4
Interstate	119.1	289.4	514.5	684.8

Table 4. Estimated amount of habitat that would be recovered for each 1 km of roadside fencing installed on that side of the road

Percentages correspond to the distances at which counts of tortoise sign are estimated to reach that percentage of total estimated abundance away from roads

Road type	Amount of habitat (ha) recovered from roadside fencing			
	50%	75%	90%	95%
County road	4.6	11.3	20.1	26.7
Interstate	11.9	28.9	51.5	68.5

Reduced wildlife abundances near roads may result from behavioural avoidance or mortality. Behavioural avoidance of roads has been observed in grizzly bears (*Ursus arctos*) outfitted with GPS collars in Montana, where roadway crossings occurred less frequently than did simulated movements of equal length (Waller and Servheen 2005). Furthermore, 85% of observed road crossings occurred at night when traffic volume was lower, even though bears in the study area were equally active during the day. Grizzly bears ultimately lost 8.7% of available habitat because of road avoidance (McLellan and Shackleton 1988). Gray wolves (*Canis lupus*) show similar avoidance of roads, tending not to establish pack home ranges within 250 m of road edges (Kaartinen *et al.* 2005). In contrast, freshwater turtles are known to seek out roads for the associated open-canopy habitats, which provide thermal characteristics suitable for nesting (Steen and Gibbs 2004). However, desert tortoises typically nest in their home burrows (Ernst and Lovich 2009), and are unlikely to choose to nest along roads. There are few data on the movements and behaviours of tortoises along roads and we cannot rule out behavioural avoidance of roads as a possible mechanism responsible for road-effect zones that we found. Future studies that examine the behaviour of tortoises along roads would add greatly to our understanding of the processes giving rise to the patterns we observed. However, as discussed

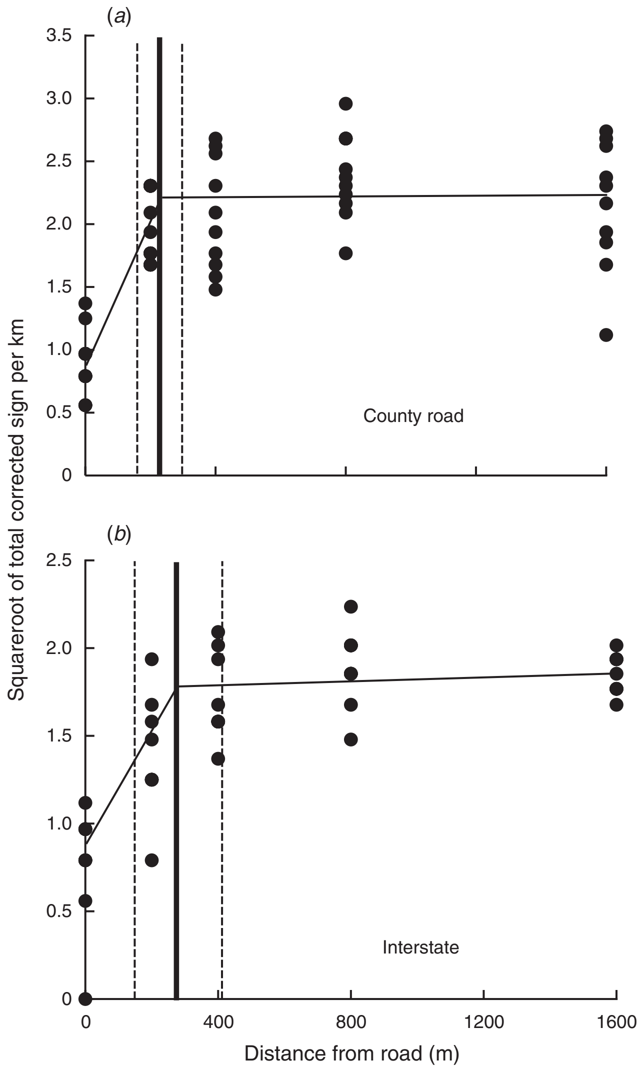

Fig. 5. Plots of the square-root-transformed total corrected sign for each transect that was conducted along (*a*) county roads or (*b*) interstate roads, showing best fit lines from piecewise regression models. The location of the estimated breakpoint is indicated with the thick solid line and the dashed lines represent ± 1 s.e.

below, mortality is likely to be a leading factor contributing to reduced abundances of tortoises along roads.

A second mechanism that can reduce wildlife abundance along roads is direct mortality (Forman and Alexander 1998; Forman *et al*. 2003). The large home ranges (14–26 km^2) of moose (*Alces alces*) result in a high frequency of road crossings and deaths from vehicles, a primary cause of mortality in some areas (Bangs *et al*. 1989; Cederlund and Sand 1994). Increased mortality from roads is also widespread for many amphibians and reptiles (reviewed in Fahrig and Rytwinski 2009). Female freshwater turtles, for example, are likely to encounter roads when nesting, resulting in increased mortality and male-biased sex ratios in populations (Gibbs and Steen 2005). Even in terrestrial turtles, demographic modelling has suggested that roads have the potential to limit populations through mortality (Gibbs and Shriver 2002). Indeed, mortality from vehicular collisions may be the greatest contributor to the road-effect zones in desert tortoises that we observed.

The installation of roadside fencing along existing roads could eliminate mortality and help recover the threatened desert tortoise. Over time, fencing could allow tortoises to recolonise habitat in road-effect zones, areas that appear otherwise suitable for desert tortoises (Nafus *et al*. 2013). Installing roadside fencing along interstate roads rather than along county roads would yield more reclaimed habitat. However, on the basis of our own observations and unpublished data on the movements of desert tortoises in our study area, these animals are encountered more often on county roads than on interstate roads, suggesting greater current risk of vehicular mortality on county roads. Presumably, lower current mortality and greater road-effect zones along interstate roads reflect high historical mortality and long-term impacts (e.g. Findlay and Bourdages 2000), resulting in reduced abundance in areas along interstate roads. Similarly, van Langevelde *et al*. (2009) found that European badgers (*Meles meles*) were more likely to be killed on minor roads than on major roads (64% versus 36% of all traffic-related deaths, respectively), leading those authors to conclude that minor roads have a greater current mortality impact on badger populations. Thus, managers must consider balancing the more immediate goal of eliminating current mortality along county roads with that of potentially reclaiming more habitat along interstate roads, a longer-term objective. The ‘slow’ life histories of tortoises require protecting current populations of tortoises along county roads, which may be a better conservation investment than is waiting for eventual recolonisation of depleted areas along established interstates.

Road-effect zones may also differ in size depending on the size of tortoise home ranges in different areas. For example, in areas with sparse vegetation, tortoises may range more widely to obtain adequate forage and refugia. Increased movement may increase road-crossing frequencies and, thus, increase the likelihood of a fatal encounter with a car. Thus, road-effect zones may vary depending on the surrounding habitat. Future studies should investigate the extent to which tortoises may avoid roads of different sizes and their behaviours when they encounter roads. Surface disturbances, vibrations or noise from vehicle traffic may contribute to road-effect zones by discouraging desert tortoises from settling close to highways or other roads (Baepler *et al*. 1994). There are no published data available to evaluate this possibility. Studying the behaviours of tortoises along roads will be important for future work to address; individual-based population models suggest that animal behaviour plays a critical role in the potential costs and benefits of road fencing (Jaeger and Fahrig 2004). In instances where mitigation fencing is installed, studies of habitat use pre- and post-installation should be prioritised. Evaluating the rate and degree to which habitat is reclaimed, as well as the capacity to maintain habitat connectivity through installation of passage corridors (Lesbarrères and Fahrig 2012; van der Grift *et al*. 2013; Rytwinski *et al*. 2015), will be critical to understanding the efficacy of road-side fencing as a mitigation and management strategy.

Road-effect zones are one of the most insidious forms of habitat loss that contributes to biodiversity declines globally (Forman and Alexander 1998; Forman *et al*. 2003). Although roads themselves may comprise only a small portion of land use in many areas, their cumulative impact can extend far beyond their physical footprint. In the present study, road effects on populations extended 5–8 times farther than the widths of the roads themselves. Quantifying the extent of road effects using methods such as ours can more accurately reveal the true impact of roads on populations and the extent to which habitat may be reclaimed. Such information may be particularly useful as land managers consider ways to reduce impacts to special status species.

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