

# Research, part of a Special Feature on Effects of Roads and Traffic on Wildlife Populations and Landscape Function Road Zone Effects in Small-Mammal Communities

John A. Bissonette<sup>1</sup> and Silvia A. Rosa<sup>2</sup>

ABSTRACT. Our study focused on the putative effects of roads on small-mammal communities in a high desert region of southern Utah. Specifically, we tested whether or not roads create adjacent zones characterized by lower small- mammal densities, abundance, and diversity. We sampled abundance of small mammals at increasing distances from Interstate 15 during two summers. We recorded 11 genera and 13 species. We detected no clear abundance, density, or diversity effects relative to distance from the road. Only two of 13 species were never captured near roads. The abundance of the remaining 11 small mammal species was either similar at different distances from the road or higher closer to the road. We conclude that although roads may act as barriers and possible sources of mortality, adjacent zones of vegetation often provide favorable microhabitat in the desert landscape for many small mammals.

Key Words: density; desert; habitat quality; road ecology; species abundance; Utah; vertebrate abundance.

## **INTRODUCTION**

Roads represent a considerable concern for wildlife conservation globally (Forman and Alexander 1998, Trombulak and Frissell 2000, Jaeger et al. 2005). The most visible effect of roads on wildlife is direct mortality from collisions with vehicles. Road influences on landscapes extend much further than their physical boundaries (Reijnen et al. 1995, Forman 2000, Forman and Deblinger 2000, Bissonette 2002, Riitters and Wickham 2003). Other species-specific effects include changes in habitat quality, loss of connectivity, or barrier effects (Forman et al. 2003, Jaeger and Fahrig 2004, Jaeger et al. 2005, Row et al. 2007) and movement dynamics (Shine et al. 2004, Fahrig 2007). Underhill and Angold (2000) described an effect zone of up to 100 m as causing visible impacts on roadside ecological communities.

Small-mammal communities provide good models for studying such impacts because species in these communities generally use a wide variety of resources, have short generation times that allow for quick detection of environmental changes, may be permanent residents of a site, and usually respond to disturbances in a perceptible and measurable way (Steele et al. 1984). Roads can impact smallmammal communities by: (1) creating an edge with different habitat characteristics (Garland and Bradley 1984, Tyser and Worley 1992, Bellamy et al. 2000); (2) promoting the introduction of exotic species (Getz et al. 1978, Vermeulen and Opdam 1995, Underhill and Angold 2000); (3) increasing stress and reducing survival (Benedict and Billeter 2004) through disturbance and contamination (Jefferies and French 1972, Williamson and Evans 1972, Quarles et al. 1974); (4) blocking movement, causing genetic barriers and home range rearrangements (Oxley et al. 1974, Garland and Bradley 1984, Mader 1984, Swihart and Slade 1984, 1990, Merriam et al. 1989, Gerlach and Musolf 2000); and finally, (5) causing direct road mortality (Wilkins and Schmidly 1980, Ashley and Robinson 1996, Mallick et al. 1998).

Although a large number of studies addressing the impact of roads on small mammals have assessed road barrier effects, less attention has been given to the effect of roads on the density and diversity of local communities. (However, see Goosem (2002) for a well-done study.) Some have mentioned the importance of road verges to small-mammal conservation but have not made reference to road

<sup>&</sup>lt;sup>1</sup>USGS Utah Cooperative Fish and Wildlife Research Unit, Department of Wildlands Resources, College of Natural Resources, Utah State University, <sup>2</sup>USGS-Utah Cooperative Fish and Wildlife Research Unit, Department of Wildlands Resources, College of Natural Resources, Utah State University

effects on diversity or density in adjacent habitats beyond the verge (Bennett 1988, Bellamy et al. 2000). Others have compared diversity and density between natural adjacent habitat and road verges/ medians (Douglass 1977, Adams and Geis 1983, Adams 1984, Garland and Bradley 1984, Meunier et al. 1999, Goosem 2000) but have not described community attributes in natural areas without road influences. Additionally, conclusions drawn from most road-ecology studies are often based on the use of count indices instead of mathematically derived estimators of abundance or density that are corrected by capture probability estimates. In studies of this nature, capture probability may be radically affected at different levels of human disturbance. Animals not accustomed to human disturbance may be more prone to avoiding traps than animals living in more disturbed areas, thus having a lower probability of capture. Therefore, data concerning numbers of animals captured need to be corrected by capture probability at different sites. Without correction for capture probability, the use of indices to estimate accurate population sizes is flawed (McKelvey and Pearson 2001), preventing accurate conclusions about road effects. Indeed, Roedenbeck et al. (2007) have argued for a more rigorous approach to road-ecology studies.

Importantly, McGregor et al. (2008), working with translocated white-footed mice (Peromyscus *leucopus*) and eastern chipmunks (*Tamias striatus*), found that although these species tended to avoid crossing the road surface, their densities were not lower near roads. We wondered if these results would be the same for a broader community of small mammals. Using appropriate estimators of abundance and density, our objective was to assess and compare density and diversity estimators of small-mammal communities (corrected by capture probability estimates) in areas influenced by roads, with areas having no road influence. In using the term "road influence", we have assessed whether there were predictable patterns of higher or lower small-mammal densities within 600 m from the road. Because we were unsure if a road zone effect existed, we did not propose or test any of the current mechanisms that have been suggested (e.g., Fahrig et al. 1995, Goosem 2002, Jaeger et al. 2005, McGregor et al. 2008). We restricted our study to testing whether density and species diversity changed at increasing distances from the road. We were interested in determining whether a putative road zone effect, in fact, existed.

## METHODS

#### **Study Area**

This study was conducted in the high-elevation desert region of southwestern Utah, USA. This area is included in the Great Basin geographic region (Durrant 1952, Barosh 1960, Cronquist 1978). The study area is located near Beaver, Utah (38°16'N latitude and 112°37'W longitude). It is adjacent to Interstate 15 (I-15) (Fig. 1) and extends to the intersection with I-70, approximately 32 km to the north. Elevation in the study area ranges from 1700 to 1900 m (Department of Natural Resources 1978). The I-15 is a four-lane divided interstate highway. The average annual daily traffic (AADT) measured during our study period was essentially continuous, with volumes exceeding 16 115 vehicles per 24 h in 2005 and 16 535 vehicles per 24 h in 2006. Mean maximum noise level readings (dBA) (taken 9, 10, and 11 July 2008 at three locations separated by several kilometers along the study site on the I-15 and at three time periods (early morning 0450–0815 h, evening 1700–1100 h, and night 1145–0130 h) were: 74.50, 74.75, and 75.30 dBA (maximum value recorded), respectively. Equivalent average sound (LEQ) measured during the same time periods and in the same locations were: 59.9, 58.5, and 56.3 dBA, respectively. Based on these measurements, we concluded that the noise levels along the I-15 appear to be relatively consistent over time. The "A" weighted scale is used for all sound measurements for roadway projects because it most closely represents the human hearing response to sound (J. Cheney, UDOT, personal communication). The range of sound frequencies heard by small mammals is unknown.

The habitat characterizing the study area is dominated by big sagebrush (Artemisia tridentata) with occasional patches of pinyon pine (Juniperus osteosperma) and juniper (Pinus edulis). The road verge is either covered by sagebrush and grasses or nonvegetated. Weather is characteristic of highelevation intermountain desert with below freezing temperatures and snow cover during the winter, and high temperatures during the summer. Maximum temperatures during our research period rarely exceeded 38°C and minimum temperatures were usually above -23°C; the annual mean temperature was 8.6°C. Annual precipitation in the form of rain and snow is less than 305 mm, occurring primarily during winter, early spring, and late summer (Department of Natural Resources 1978). Relative **Figure 1.** Study-area map with trapping location in 2004 and 2005 and geographic areas (A, B, and C) used for comparison of densities in 2004 in southern Utah, USA.



humidity is very low and evaporation potential is high (Durrant 1952, Zeveloff and Collet 1988). Prolonged periods of drought are frequent in this region (Durrant 1952). The soil on trapping sites is composed mainly of fine sand deposits with occasional volcanic rocky areas (Chronic 1990).

## **Field Methods**

Small-mammal sampling was conducted exclusively in sagebrush habitat on both sides of the road during the summer periods of 2004 and 2005 and extended over the 32-km section of road from Beaver, almost to the intersection with the I-70. This was done to ensure that trapping sites were well dispersed. Trapping was conducted both close to and at a distance from the road in order to sample communities with and without putative road influence. Different sites placed >600 m apart were used for each trapping effort. During the first year (2004), we established 12 transects, each with two webs. The webs were placed on a perpendicular transect from the road at each site (Fig. 2). The first webs were centered at 50 m from the road (defined as close) and the second webs were centered, on average, 400 m from the road (defined as distant). Each web was composed of eight arms extending 50 m outward from a central point. Each arm had six trapping stations (5, 10, 20, 30, 40, and 50 m), plus one trapping station with two traps located at the center of the web. One snap trap and one Sherman trap were set at each trapping station. In total, each web had 98 traps that we checked for 3 consecutive nights, for a total of 7056 trap nights. In 2004, trapping was conducted from late May to late August. We used both lethal (snap traps) and nonlethal (Sherman) traps to maximize the number of species we might detect (especially trap-shy species) and to allow sampling during the diurnal period. We did not expect to catch the one or two larger mammalian species in the area, but were concentrating on small mammals. We calculated that the 50-m diameter webs sampled approximately a 7854 m<sup>2</sup> area plus half the diameter of any smallmammal home range in the vicinity. This would typically be about 0.5 ha (Nowak and Paradiso 1983).

Results from 2004 convinced us that we needed to use a different trapping design in 2005 in order to detect whether a finer-scale discrimination of smallmammal densities existed nearer the road. Therefore, we used trapping lines to obtain a finer spatial resolution of trapping results. Three trapping lines were placed in a transect perpendicular to the road (Fig. 2), allowing a more intensive effort nearer the road. Lines were set parallel and at increasing distances from the road verge (0 m = close, 200 m= mid, 600 m = distant). We established five transects, each with three lines. Trapping was conducted from late June to mid August 2005. Each line had 30 traps checked over 3 consecutive nights and mid mornings, for a total of 1350 trap nights. Trapping was conducted according to the Utah State University Institutional Animal Care and Use Committee (IACUC) animal welfare protocol #1139. All traps were baited with a mixture of horse feed and peanut butter. Upon capture, all animals were identified and measured, their gender was determined, and they were marked with a magic marker and released. Dead animals were removed from the study site. Due to differences in trapping design, we analyzed the data by year using the appropriate estimator and associated tests for each design. Yearly results were then compared to assess whether densities differed by proximity to the road. The short time period we trapped in each area (3) nights) guaranteed the data would not be compromised by density dependent responses.

# **Data Analysis**

## Diversity

We used the Shannon-Wiener diversity index (H')to compare community diversity at different distances from the road (Begon et al. 2006). The index was calculated for each web and trap line in all transects. We tested diversity differences at different distances from the road using the Wilcoxon paired sample test for 2004 data, and Friedman's test for 2005 data (Zar 1996). A least significance difference (LSD) multiple comparison test for Friedman's test (Sprent 1989) was used with 2005 data to determine whether pairs of distances (close vs. mid; close vs. distant; mid vs. distant) were significantly different. The choice of test was based on the number of samples and comparisons in each case; in 2004, we were comparing two samples (close vs. distant) and in 2005, we were comparing three samples (close vs. mid, close vs. distant, mid vs. distant).

## Abundance and density estimation

We employed a distance method described by Anderson et al. (1983) for the 2004 web data and accounted for first capture locations for each



Fig. 2. Schematic representation of trapping schemes in 2004 and 2005 used in southern Utah, USA.

individual and their distances to the center. We used Distance 4.1 (Buckland et al. 1993, 2001) to calculate densities and variance estimates. For analysis purposes, capture data in different transects were pooled by close webs and distant webs. Estimation was possible for all small mammals combined (all species) and for the most abundant species (i.e., >30 captured individuals per pooled database). We conducted an additional analysis for the 2004 data by pooling groups of transects set in similar geographic areas (A, B, and C; see Fig. 1). Grouping of these transects was done to account for biologically meaningful factors observed in the field (viz., vegetation and soil differences). We compared differences between and within areas at different distances. Density estimations were obtained by testing all available combinations of models in Distance 4.1 (uniform, half-normal, hazard, and negative exponential), with adjustment terms (cosine, simple polynomial, or hermite polynomial). Final model selection was based on Akaike's Information Criterion ( $\Delta AIC$ ) value and on model performance (i.e., models running without warnings; see Buckland et al. 2001). Because the amount of data was scarce, data sets were used in their entirety (i.e., without truncation). Intervals used in Distance 4.1 (0, 7.5, 15, 25, 35, and 45 m)

were the midpoints between trap stations. "0" was the name we attributed in Distance 4.1 to a class of captures made at the traps located at the center of each web. Resulting densities in close and distant webs were tested for significant differences with a Wald test.

We analyzed the 2005 trapping-line-based data in Mark 4.3 using a closed population mark-recapture method (White and Burnham 1999). Closure was assumed given that: (a) trapping occurred in a sufficiently brief interval (3 nights), and (b) the removals were known and accounted for. This is required by the analysis protocol (Williams et al. 2001). The Huggins closed-capture estimator was used to obtain abundance estimates. Capture data were pooled into three groups representing increasing distances from the road (close, mid, and distant). Estimates were obtained for the null model and other models that accounted for variability in capture probabilities due to behavior, heterogeneity, and time (values calculated automatically by the software). Models that did not converge were discarded. Remaining models with the lowest  $\Delta AIC$ value were averaged to obtain final estimates of abundance. Differences in abundance estimates from the road were tested using a Wald test.

## RESULTS

#### Trapping

Our research involved completing a total of 8406 trap nights (7056 were webs and 1350 were trap lines), during which we captured 478 individual small mammals (420 were webs and 58 were trap lines) comprising 13 species and 11 genera. In 2004, we had 513 captures with 93 recaptures; in 2005, we had 70 captures with 12 recaptures. The species trapped most often were deer mice (*Peromyscus maniculatus*) and great-basin pocket mice (*Perognathus parvus*).

In 2004, we captured a total of 11 species (Table 1). Two of the species (rock squirrel (Spermophilus *variegatus*) and sagebrush vole (*Lemmiscus curtatus*)) were captured only in the webs closer to the road, whereas two other species (pinyon mouse (Peromyscus truei) and white-tailed antelope squirrel (Ammospermophilus leucurus)) were captured only at sites distant from the road. The remaining seven species were captured at distances both close to and distant from the road. During 2005, we captured a total of seven species (Table 1). Three of the species (desert cottontail (Sylvilagus audubonii), jackrabbit (Lepus californicus), and desert woodrat (Neotoma lepida)) were only caught near the road. The number of species decreased as distances to the road increased. For example, we captured seven species close to the road, four species at mid distances, and three species at transects farthest from the road (Table 1). All species detected at mid and far distances were also present at close distances. Uniquely located species were detected either close to or far from the road.

We noted that some species were detected only in areas with unique microhabitat characteristics. For example, desert woodrats were only captured close to pinyon-juniper habitat or areas with rocky substrate; chisel-toothed kangaroo rats (*Dipodomys* microps) were only detected in the southern portion of the study area near the town of Beaver; cottontail rabbits and jackrabbit juveniles were only detected in road verge habitat; and rock squirrels and sagebrush voles were caught only at higher elevations in a transect with more structurally complex vegetation (Fig. 1, area B). The transect sampled in area B was distinct from the others because of its habitat features (e.g., qualitatively different vegetation and greater abundance of woody debris). It also had a disproportionately high

number of organisms (132 individuals in total, of which the number of removals was 32). Three species were found only here (Fig. 1, area B).

#### **Diversity Analysis**

Results of the Shannon-Wiener diversity index (*H*') analysis showed different results in diversity according to different sampling years (Table 2). For 2004, the diversity of small mammals was 43.2% higher in areas distant from the road (*Z* = -2.224, *P* = 0.026) vs. for 2005, where diversity was 57-87% lower farther from the road (Friedman test  $\chi^2 = 6$ , *P* = 0.05).

#### **Abundance and Density Analysis**

Our analysis of total small-mammal distribution relative to road distance showed different results for different years. In 2004 (Fig. 3), there was no significant difference in densities (number per hectare) at distant vs. closer webs (Z = -0.49, P =0.63); however, densities were 28.9% higher at distant webs. In 2005, comparisons between close, mid, and distant webs found lower abundances of small mammals as a group at distant transects (Fig. 3). An 87.3% difference between abundances at close and distant webs was highly significant (Z =3.99, P < 0.001). The difference between mid and any other distance was non significant, perhaps because the low capture and recapture rates at the mid distance resulted in less precise estimates  $(CV_{MID} = 0.84).$ 

Despite the fact that trapping areas were chosen carefully for vegetation consistency, observations in the field suggest that sites may have had relevant differences in microhabitat characteristics. Observed differences (e.g., volcanic rocky substrate, proximity of pinyon-juniper, higher elevation, and a greater amount of woody debris) may have influenced trapping outcomes in some transects (e. g., Fig. 1, area B). For these reasons, we pooled data only from transects with similar characteristics that corresponded to similar geographic areas and compared densities between areas to test whether differences in habitat influenced density (Fig. 4a). Area B had higher densities of organisms both in webs near and farther from the highway than areas A or C. Densities at area B were significantly different from densities at area A (for both close (Z

Distance to Road	2004	2005	
CLOSE	Peromyscus maniculatus (124) Perognathus parvus (39) Tamias minimus (27) Dipodomys microps (5) Rethrodontomys megalotis (4) Peromyscus boylii (3) Neotoma lepida (2) Lemmiscus curtatus (1) * Spermophilus variegatus (1) *	Perognathus parvus (12) Peromyscus maniculatus (10) Dipodomys microps (8) Tamias minimus (2) Sylvilagus audubonii (2) * Lepus californicus (1) * Neotoma lepida (1) *	
MID	_	Dipodomys microps (11) Perognathus parvus (4) Peromyscus maniculatus (1) Tamias minimus(1)	
DISTANT Peromyscus maniculatus (120) Perognathus parvus (54) Tamias minimus (18) Peromyscus boylii (11) Ammospermophilus leucurus (4) * Rethrodontomys megalotis (3) Peromyscus truei (2) * Neotoma lepida (1) Dipodomys microps(1)		Dipodomys microps (2) Perognathus parvus (2) Peromyscus maniculatus (1)	

**Table 1.** Species detected at different distances from the I-15 in 2004 and 2005 in southern Utah, USA; number of individual captures of each species.

\* = species caught only at these distances

= -2.15, P = 0.03) and distant webs (Z = -3.07, P = 0.002)) and area C (for both close (Z = -2.84, P =0.004) and distant webs (Z = -2.97, P = 0.003)). These results show that area B was significantly different from the remaining areas in terms of density of small mammals. When we compared close and distant abundances of all organisms within each of the geographic areas, we found no significant differences ( $Z_{\text{Area A}} = 1.33$ , P = 0.18;  $Z_{\text{Area B}} = -1.61$ , P = 0.11;  $Z_{\text{Area C}} = -1.12$ , P = 0.26). Even for the most frequently caught individual species (Fig. 4b), we were unable to reject the null hypothesis, indicating no significant differences in densities between close and distant trapping sites for either species (Peromyscus maniculatus Z = -1.06, P = 0.29; Perognathus parvus Z = 0.71, P= 0.48). However, there appear to be speciesspecific results for these two species: Peromyscus maniculatus density was 100.6% higher at distant

webs whereas *Perognathus parvus* density was 31.8% lower.

#### **DISCUSSION AND CONCLUSIONS**

The main objective of this study was to detect whether there was a road-zone effect on communities of small mammals that would be reflected in species abundances or density. The null hypothesis was that abundance and density would not vary significantly at increasing distances from the road. We did, however, expect that there would be species-specific differences (Jaeger et al. 2005). Any measureable differences were expected to be consistent over the time period of the study. Our results showed no clear road-zone effects on the community of small mammals over time. However,

Year	Comparison	Trend in Diversity	Difference between H Estimates (%)	Significance
2004	$H_{close}$ vs. $H_{distant}$	Distant > Close	43.2%	*
	$H_{close}$ vs. $H_{mid}$	Close > Mid	57.3%	*
	$H_{close}$ vs. $H_{distant}$	Close > Distant	87.2%	*
	$H_{mid}$ vs. $H_{distant}$	Mid > Distant	70.1%	NS

**Table 2.** Changes in small-mammal diversity H' (Shannon-Wiener index) in 2004 and 2005 at different distances from the I-15 in southern Utah, USA.

\* differences significant at P < 0.05;

NS = not significant

we did note that there were two species each that were found only at close (rock squirrel and sagebrush vole) or far (pinyon mouse and whitetailed antelope squirrel) distances from the road. Translocation studies and additional trapping over a period of years are needed to demonstrate whether these patterns are persistent. For several species found both close and far from the road, our results suggest that it would take more time to demonstrate whether a road-zone effect (i.e., higher or lower densities and abundances) exists. Clearly, the species we caught were reacting in a speciesspecific manner. We are aware that differences in sampling methods could also have influenced our results; not necessarily because of their statistical properties, but perhaps more significantly because of the nature of their geometry relative to the road edge. Transects that parallel the road are more likely to capture more of the species present than are circular trapping webs where the edge only comes close to the road. As Elphick (2008) argued: "How you count counts."

Of the species we captured near the road (Table 1), only *Lemmiscus curtatus*, *Spermophilus variegatus*, *Sylvilagus audubonii*, and *Lepus californicus* were not found at sites far from the road. However, our observations as we walked through the study site suggested that at least *Sylvilagus audubonii* and *Lepus californicus* can be expected to occur almost anywhere in the area. What this suggests is that most of the species captured near the road are native to the area. The yearly differences in abundance and diversity suggest that other variables may have been influencing these patterns. Variation in precipitation volume is known to influence small-mammal life cycles in desert ecosystems (Beatley 1969); however, precipitation did not differ significantly between our sampling years. A severe multi-year drought period in Utah ended in 2004. It is possible that the precipitation during that year was readily absorbed by the dried soils with little runoff; 2005 was a wetter year and precipitation appeared to result in greener road verges. That higher diversity and abundance of small mammals were observed near the road in 2005 may be coincidental. Determining causality is not possible. The possible interaction between roads, precipitation, smallmammal abundance, and diversity patterns needs further testing. Microhabitat differences could have influenced organism abundances; however, our observations are qualitative and we cannot provide a definitive answer.

Although we captured only a few species, the species accumulation curve for 2005 (Appendix 1) suggests that we captured most of the species present in the area. Nonetheless, we suggest that further studies might consider trapping for a 5-night interval using live traps of suitable sizes. Increased sampling sites, although very time consuming to run, would appear to give a better estimation of the variability in species captures as well as differences in locations, especially if run for several years. Small-mammal populations can be notoriously

**Figure 3.** Density and abundance estimates of small mammals (95% confidence intervals) at different distances from the I-15 in southern Utah, USA, in: (a) 2004 and (b) 2005.



**Figure 4.** (a) Density estimates of small mammals (95% confidence intervals) in 2004 at different distances from the I-15 in three distinct geographic areas (A, B, C); (b) Density estimates of *Peromyscus maniculatus* and *Perognathus parvus* (95% confidence intervals) in 2004 at different distances from the I-15, southern Utah, USA.



dynamic and capturing the nature of the dynamic would appear to be quite time consuming. We think that well-designed transplant experiments of small mammals in relation to the road would aid in our understanding. Obviously, controlling for microhabitat structure is important, especially in dry areas. Small mammals are known to respond strongly to plantcommunity structure. This may prove to be an especially difficult task in arid communities, where plant structure is heavily related to rainfall.

The use of trap type (lethal vs. live) is controversial. Most have eschewed the use of snap traps, and perhaps rightly so. But a problem arises with species that may be normally trap shy. How does one go about capturing reputedly trap-shy animals? This question is a moral and ethical one for many scientists, and a source for dialog. We suggest that one approach is to list those species expected or shown to be trap shy and then conduct experiments in field enclosures with a known number of each species (itself a significant task) to see how effective live trapping is with these reputedly trap-shy species. We are unfamiliar with any existing study in this area, although some work may have been done in this regard.

Assessing whether road effects are present in smallmammal communities is a non-trivial exercise and one that is set in a much broader landscape context. Do the animals avoid the road surface itself or the traffic? Are there threshold effects? For example, are lower traffic volumes more conducive to road crossing (and possibly, mortality) than higher traffic volumes? Which species appear to be positively rather than negatively influenced by roads? How does the scientist interpret results when a significant number of individuals within a species respond differently? What is the decision rule? Can we even speak of a group response (e.g., "small mammals") when results from several studies show speciesspecific responses? If we find that our results are totally mixed, what are the implications for interpreting the environmental impacts? What recommendations can the scientist make for decision making and mitigation? Are impacts on a few (but not all) species sufficient for a proposed mitigation? These are questions that road ecologists do not appear to have settled among themselves, and yet, some consensus would appear to be necessary. An even broader and more difficult question is: "how do human-altered landscapes change animal movement patterns?" (Fahrig 2007). This concern broadens the scope from roads to changes in the patterns and processes of altered landscapes. We believe this is where the most serious effects will be found.

# CAVEAT

According to van Horne (1983), survival is a more reliable indicator of habitat quality than numbers or abundance. Therefore, studies on small-mammal survival at increasing distances from roads could provide a more reliable measure of the real impact of roads (although measuring fitness and survival is a much more onerous task than just counting animals). Additionally, conclusions tend to be biased toward abundant species due to the difficulty of using statistical analysis with low abundances. This compromises the understanding of road effects on rare and probably more sensitive species.

Responses to this article can be read online at: http://www.ecologyandsociety.org/vol14/iss1/art27/ responses/

## **Acknowledgments:**

We thank the Utah Department of Transportation, the Utah Division of Wildlife Resources, and the Bureau of Land Management for the funding provided for this research. Many thanks go to C. Boal, M. Conner, R. Cutler, S. Durham, P. Cramer, C. Kassar, and D. Ferreira. Three anonymous reviewers as well as the subject editor made valuable and significant comments. We thank them for their comments and close reading of the manuscript.

# LITERATURE CITED

Adams, L. W. 1984. Small mammal use of an interstate highway median strip. *Journal of Applied Ecology* **21**:175–178.

Adams, L. W., and A. D. Geis. 1983. Effects of roads on small mammals. *Journal of Applied Ecology* **20**:403–415.

Anderson, D. R., K. P. Burnham, G. C. White, and D. L. Otis. 1983. Density estimation of small-

mammal populations using a trapping web and distance sampling methods. *Ecology* **64**:674–680.

Ashley, P. E., and J. T. Robinson. 1996. Road mortality of amphibians, reptiles and other wildlife on the Long Point causeway, Lake Erie, Ontario. *The Canadian Field Naturalist* **110**:403–412.

**Barosh, P. J.** 1960. Beaver lake mountains, Beaver County, Utah. Their geology and ore deposits. Utah Geological and Mineralogical Survey. *University of Utah Bulletin* **68**.

**Beatley, J. C.** 1969. Dependence of desert rodents on winter annuals and precipitation. *Ecology* **50**:721–724.

**Begon, M., C. R. Townsend, and J. L. Harper.** 2006. *Ecology: from individuals to ecosystems.* Fourth edition. Blackwell, Oxford, UK.

Bellamy, P. E., R. F. Shore, D. Ardeshir, J. R. Treweek, and T. H. Sparks. 2000. Road verges as habitat for small mammals in Britain. *Mammal Review* **30**:131–139.

**Benedict, R. A., and M. C. Billeter.** 2004. Discarded bottles as a cause of mortality in small vertebrates. *Southeastern Naturalist* **3**:371–377.

**Bennett, A. F.** 1988. Roadside vegetation: a habitat for mammals at Naringal, southwestern Victoria. *The Victorian Naturalist* **105**:106–113.

**Bissonette, J. A.** 2002. Scaling roads and wildlife: the Cinderella principle. *Zeitschrift für Jagdwissenschaft* **48**:208–214.

Buckland, S. T., D. R. Anderson, K. P. Burnham, and J. L. Laake. 1993. Distance sampling: estimating abundance of biological populations. Chapman and Hall, London, UK.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. *Introduction to distance sampling*. Oxford University Press, London, UK.

**Chronic, H.** 1990. *Roadside geology of Utah.* Second edition. Mountain Press, Missoula, Montana, USA.

**Cronquist, A.** 1978. The biota of the Intermountain Region in geohistorical context. *In* Intermountain

biogeography: a symposium. Great Basin Naturalist Memoirs 2.

**Department of Natural Resources.** 1978. *Hydrology of the Beaver Valley area, Beaver County, Utah, with emphasis on ground water.* Technical Publications Department of Natural Resources, Salt Lake City, Utah, USA.

**Douglass, R. J.** 1977. Effects of a winter road on small mammals. *Journal of Applied Ecology* **14**:827–834.

**Durrant, S. D.** 1952. *Mammals of Utah—taxonomy and distribution*. Museum of Natural History. University of Kansas Press, Lawrence, Kansas, USA.

**Elphick, C. S.** 2008. How you count counts: the importance of methods research in applied ecology. *Journal of Applied Ecology* **45**:1313–1320.

**Fahrig, L.** 2007. Non-optimal animal movement in human-altered landscapes. *Functional Ecology* **21**:1003–1017.

Fahrig, L., J. H. Pedlar, S. E. Pope, P. D.Taylor, and J. F. Wegner. 1995. Effects of road traffic on amphibian density. *Biological Conservation* 75:177–182.

**Forman, R. T. T.** 2000. Estimate of the area affected ecologically by the road system in the United States. *Conservation Biology* **14**:31–35.

Forman, R. T. T., and L. E. Alexander. 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* **29**:207–231.

Forman, R. T. T., and R. D. Deblinger. 2000. The ecological road-effect zone of a Massachusetts (USA) suburban highway. *Conservation Biology* 14:36–46.

Forman, R. T. T., D. Sperling, J. A. Bissonette, A. PClevenger, C. D. Cutshall, V. H. Dale, L. Fahrig, R. France, C. R. Goldman, K. Heanue, J. A. Jones, F. J. Swanson, T. Turrentine, and T. C. Winter. 2003. *Road ecology: science and solutions*. Island Press, Washington, D.C., USA.

Garland, T. J., and W. G. Bradley. 1984. Effects of a highway on Mojave Desert rodent populations. *American Midland Naturalist* **111**:47–56.

Gerlach, G., and K. Musolf. 2000. Fragmentation of landscape as a cause for genetic subdivision in bank voles. *Conservation Biology* **14**:1066–1074.

Getz, L. L., F. R. Cole, and D. L. Gates. 1978. Interstate roadsides as dispersal routes for *Microtus pennsylvanicus*. *Journal of Mammalogy* **59**:208– 212.

**Goosem, M.** 2000. Effects of tropical rainforest roads on small mammals: edge changes in community composition. *Wildlife Research* **27**:151–163.

———. 2002. Effects of tropical rainforest roads on small mammals: fragmentation, edge effects and traffic disturbance. *Wildlife Research* **29**:277–289.

Jaeger, J. A. G., J. Bowman, J. Brennan, L. Fahrig, D. Bert, J. Bouchard, N. Charbonneau, K. Frank, B. Gruber, and K. T. von Toschanowitz. 2005. Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. *Ecological Modelling* **185**:329–348.

Jaeger, J. A. G., and L. Fahrig. 2004. Effects of road fencing on population persistence. *Conservation Biology* **18**:1651–1657.

Jefferies, D. J., and M. C. French. 1972. Lead concentrations in small mammals trapped on roadside verges and field sites. *Environmental Pollution* **3**:147–156.

Mader, H. J. 1984. Animal habitat isolation by roads and agricultural fields. *Biological Conservation* **29**:81–96.

Mallick, S. A., G. H. Hocking, and M. M. Driessen. 1998. Road-kills of the eastern barred bandicoot (*Perameles gunnii*) in Tasmania: an index of abundance. *Wildlife Research* **25**:139–145.

**McGregor, R. L., D. J. Bender, and L. Fahrig.** 2008. Do small mammals avoid roads because of the traffic? *Journal of Applied Ecology* **45**:117–123.

McKelvey, K. S., and D. E. Pearson. 2001. Population estimation with sparse data: the role of estimators versus indices revisited. *Canadian Journal of Zoology* **79**:1754–1765.

Merriam, G., M. Kozakiewicz, E. Tsuchiya, and

**K. Hawley.** 1989. Barriers as boundaries for metapopulations and demes of *Peromyscus leucopus* in farm landscapes. *Landscape Ecology* **2**:227–235.

Meunier, F. D., J. Corbin, C. Verheyden, and P. Jouventin. 1999. Effects of landscape type and extensive management on use of motorway roadsides by small mammals. *Canadian Journal of Zoology* **77**:108–117.

Nowak, R. M., and J. L. Paradiso. 1983. *Walker's mammals of the world*. Johns Hopkins University Press, Baltimore, Maryland, USA and London, UK.

**Oxley, D. J., M. B. Fenton, and G. R. Carmody.** 1974. The effects of roads on populations of small mammals. *Journal of Applied Ecology* **11**:51–59.

Quarles, H. D. III, R. B. Hanawalt, and W. E. Odum. 1974. Lead in small mammals, plants, and soil at varying distances from a highway. *Journal of Applied Ecology* **11**:937–949.

**Reijnen, R., R. Foppen, C. T. Braak, and J. Thissen.** 1995. The effects of car traffic on breeding bird populations in woodland. III. Reduction of density in relation to the proximity of main roads. *Journal of Applied Ecology* **32**:187–202.

**Riitters, K. H., and J. D. Wickham.** 2003. How far to the nearest road? *Frontiers in Ecology and Environment* **1**:125–129.

Roedenbeck, I. A., L. Fahrig, C. S. Findlay, J. E. Houlahan, J. A. G. Jaeger, N. Klar, S. Kramer-Schadt, and E. A. van der Grift. 2007. The Rauischholzhausen agenda for road ecology. *Ecology and Society* **12**(1): 11. [online] URL: <u>http:</u> //www.ecologyandsociety.org/vol12/iss1/art11/.

Row, J. R., G. Blouin-Demers, and P. J. Weatherhead. 2007. Demographic effects of road mortality in black ratsnakes (*Elaphe obsoleta*). *Biological Conservation* **137**:117–124.

Shine, R., M. Lemaster, M. Wall, T. Langkilde, and R. Mason. 2004. Why did the snake cross the road? Effects of roads on movement and location of mates by garter snakes (*Thamnophis sirtalis* parietalis). Ecology and Society **9**(1): 9. [online] URL: <u>http://www.ecologyandsociety.org/vol9/iss1/</u> art9/. **Sprent, P.** 1989. *Applied nonparametric statistical methods*. First edition. Chapman and Hall, London, UK.

**Steele, B., R. Bayn, Jr., and V. C. Grant.** 1984. Environmental monitoring using populations of birds and small mammals: analyses of sampling effort. *Biological Conservation* **30**:157–172.

Swihart, R. K., and N. A. Slade. 1984. Road crossing in *Sigmodon hispidus* and *Microtus ochrogaster*. *Journal of Mammalogy* **65**:357–360.

Swihart, R. K., and N. A. Slade. 1990. Long-term dynamics of an early successional small mammal community. *American Midland Naturalist* **123**:372–382.

**Trombulak, S. C., and C.A. Frissell.** 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* **14**:18–30.

**Tyser, R. W., and C. A. Worley.** 1992. Alien flora in grasslands adjacent to road and trail corridors in Glacier National Park, Montana (USA). *Conservation Biology* **6**:253–262.

**Underhill, J. E., and P. G. Angold.** 2000. Effects of roads on wildlife in an intensively modified landscape. *Environmental Reviews* **8**:21–39.

van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47:893–901.

**Vermeulen, H. J. W., and P. F. M. Opdam.** 1995. Effectiveness of roadside verges as dispersal corridors for small ground-dwelling animals: a simulation study. *Landscape and Urban Planning* **31**:233–248.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**:120–138.

Wilkins, K. T., and D. J. Schmidly. 1980. Highway mortality of vertebrates in southeastern Texas. *Texas Journal of Science* **32**:343–350.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2001. Analysis and management of animal populations. Academic Press, San Diego, California, USA. Williamson, P., and P. R. Evans. 1972. Lead: levels in roadside invertebrates and small mammals. *Bulletin of Environmental Contamination and Toxicology* 8:280–288.

Zar, J. H. 1996. *Biostatistical analysis*. Third edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Zeveloff, S. L., and F. R. Collet. 1988. *Mammals of the Intermountain West*. University of Utah Press, Salt Lake City, Utah, USA.



