RESPONSES OF SMALL TERRESTRIAL VERTEBRATES TO ROADS IN A COASTAL SAGE SCRUB ECOSYSTEM

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INTRODUCTION

Terrestrial and aquatic habitats have become increasingly permeated by a myriad of roads. Currently, the United States contains 6.2 million kilometers of public roads. While these roads only cover 1% of the total area of the country, Forman (2000) estimated they ecologically affect 19%. This estimate does not include the millions of kilometers of private roads. Roads can affect the movement patterns, demographics, and spatial distribution of local flora and fauna (Trombulak and Frissel 2000). They can have adverse effects on wildlife by fragmenting habitats, creating population sinks, acting as conduits for the spread of non-native species, and decreasing species diversity (Findlay and Houlahan 1996). They can have positive effects on wildlife by increasing connectivity and food resources and by creating edge habitats, which can add to spatial heterogeneity and thus to the local diversity of wildlife communities (Leopold 1933; Harris 1988).

In order to determine how roads will potentially affect population dynamics, one needs to know the behavioral response of a species when encountering a road. A response to a road could be thought of as a response to a habitat edge. Lidicker and Peterson (1999) proposed seven behavioral responses of an animal to a habitat edge ranging from avoidance of an edge zone to crossing an edge without inhibitions. Thus, roads could range from being impermeable to animal movement to having no effect on movement patterns. Regarding roads as edges only, however, ignores their linear properties along the landscape and their potential use as movement corridors. While boundaries redirect flow and decrease the rate of animal movement through a landscape, corridors increase the rate of movement in comparison to the adjacent landscape. Thought of in this way, roads can act on a continuum between being movement boundaries to movement corridors (Puth and Wilson 2001). These are not mutually exclusive, however, because by redirecting flow, an impermeable road boundary can potentially create a corridor along side it (Forman and Moore 1992).

Roads of different sizes, substrates, and traffic volumes have been shown to inhibit movement of large mammals (McLellan and Shackleton 1988; Brody and Pelton 1989; Mech 1989; Mladenhoff et al. 1995) small mammals (Oxley et. al. 1974; Kozel and Feharty 1979; Adams and Geis 1983; Garland and Bradley 1984; Mader 1984; Swihart and Slade 1984) snakes (Weatherhead and Prior 1992), amphibians (Gibbs 1998; deMaynadier and Hunter 2000), and arthropods (Mader 1984; Mader et al. 1990). In most of these studies, permeability decreased with increased road improvement and traffic volume. The resulting decrease in connectivity may negatively affect local demographic parameters such as decrease the chance of finding a mate, dispersal success, or locating spatially and temporally variable habitat and food resources (Soule 1991). If a road creates an impermeable barrier to animal movement, populations can become isolated or fragmented. Fragmented populations are more vulnerable to negative effects from demographic and environmental stochasticity, as well as from increased inbreeding and genetic drift (Noss and Csuti 1997). Increased genetic structuring due to fragmentation by roads has been documented for populations of the common frog, *Rana temporaria*, (Reh and Seitz 1990) and the bank vole, *Clethrionomys glareolus*, (Gerlach and Musolf 2000).

On the other side of the continuum, roads may provide efficient movement corridors for home range movements, migration, and dispersal of wildlife (see review by Trombulak and Frissel 2000). Many animals use unimproved roads to travel within their ranges. In addition, roadside habitats may function as edge habitats which often have vegetative differences in comparison to the interior. These often support many species that would not otherwise be present or exist in low numbers. In contrast to barrier effects, the resulting increase in connectivity resulting from use of roads or roadside habitats as corridors may have positive effects on population demographics. Range extensions correlated to dispersal on or next to roads have been documented for the meadow vole (Getz et al. 1978), pocket gophers (Huey 1941), cane toads (Seabrook and Dettman 1996), the Argentine ant (Suarez et al. 1998) and numerous species of plants (Greenberg et al. 1997).

In addition to use of roads for movement, many animals are attracted to roads for food or other resources. Many predators and scavengers may preferentially or opportunistically hunt along roads including wolves (Thurber et al. 1994), coyotes (May and Norton 1996), and birds of prey. Amphibians are often attracted to road ruts for use as breeding pools. Additionally, paved roads typically absorb and retain more heat than the surrounding habitat, making them “heat islands”. Because of this, many reptiles may be attracted to roads for thermoregulation (Klauber 1939; Case and Fisher 2001; review by Jochimsen and Peterson *in press*).

Animals that do not avoid roads may be in danger of increased mortality due to predation and/or vehicular traffic. As a result, roads also have the potential to become population sinks. The increased use of roads by native predators can expose local prey populations to greater predation rates (Andren and Angelstam 1988; May and Norton 1996). The use of roads by vehicular traffic, however, may have a much more significant effect on mortality rates. Motor vehicles kill an estimated one million vertebrates a day in the United States (Lalo 1987). They have been shown to be a major cause of increased death rates for many species of mammals and reptiles (Siebert and Conover 1991; Smith 1999; Trombulak and Frissell 2000) and have been linked to declines in some amphibian populations (Fahrig et al. 1993). Snakes typically comprise a major fraction of vertebrate road kills and are therefore of special concern (Siebert and Conover 1991; Rosen and Lowe 1994; Smith 1999; Case and Fisher 2001, review by Reed et al. 2003).

Currently, there are many published reports and journal articles on the effects of roads on wildlife. Surprisingly, however, there are few studies or reviews that attempt to predict animal responses based on life history characteristics. There are little data available on reptiles, although they are thought to be a taxon that may be significantly impacted (Jochimsen and Peterson *in press*). There is a lack of studies which incorporate the factors of road use, roadside habitat use, multiple road types, and multiple species to ascertain how different wildlife species respond to these linear features of the landscape. In addition, few studies have coupled these types of data with monitoring of road activity and mortality.

It has been widely reported that habitat generalists and edge specialists benefit from edges while habitat specialists suffer (Laurance and Yensen 1991; Lidicker and Koenig 1996; Lidicker 1999; Bentley et al. 2000). Similar responses have been documented for rodent communities along road edges (Getz 1978; Adams and Geis 1983; Goosem 2000). Is this a predictive trait for road responses? If not, what other predictive traits may be important for predicting species responses? How do they change in relation to road type (i.e from unimproved dirt access road to a multi-lane highway) and habitat type (open desert to closed forest)?

Coastal sage scrub is one of the most endangered ecosystems of the United States, with approximately 70 to 90% of the habitat having been destroyed by agriculture and development (Noss et al. 2000). Nearly 100 species of plants and animals associated with coastal sage scrub in California are currently classified as rare, sensitive, threatened, or endangered by state and federal agencies (O'Leary 1995). Additionally, much of the remaining habitat is fragmented, disturbed, and/or permeated by highways, secondary roads, dirt roads, and trails. The effects of roads on the fauna associated with coastal sage scrub vegetation have not yet been studied.

In this study, I assessed the activity patterns of four small mammal and two reptile species in relation to three types of roads transecting coastal sage scrub habitats. The species studied were a mixture of habitat generalists and specialists. I characterized both individual movement patterns in relation to multiple road types and the relative abundance of species at two distances from each road in order to explore the relationship between road type and species movement and spatial dynamics. I examined whether response patterns exist among multiple species with different life history strategies and whether habitat specialization may be used a predictive factor for responses to roads. For small mammals and reptiles, I also investigated the relationship between road type and road mortality.

The results of this study should further understanding by the scientific community of how animals respond to roads. By studying small mammals and reptiles, direct comparisons of behavior can be made between taxa with different life history strategies. If generalizations are found, it may help to predict behavior of unstudied species (Laurance and Yensen 1991; Lidicker and Koenig 1996). The results of this study should also aid in conservation planning of coastal sage scrub and other ecosystems by identifying focal vertebrate species that may be impacted by roads.

METHODS AND MATERIALS

I begin my methods section by introducing my study site and focal species. I then explain how the road activity and roadside habitat abundance data were collected and analyzed.

Study Site

The study area was in Jamul, San Diego County, California, within the San Diego National Wildlife Refuge (Otay-Sweetwater Unit) and in Rancho Jamul, a 1915 ha ecological preserve managed by California Department of Fish and Game. The preserves are dominated by coastal sage scrub with chaparral, oak and riparian woodland, and vernal pool habitats also present. The region has a Mediterranean-type climate characterized by hot, dry summers and cool, wet winters. Average annual precipitation is approximately 350 mm with approximately 95% of the annual mean rainfall occurring from November through April.

Assessment of Roadside Habitat Abundance

Three roads transecting coastal sage scrub (CSS) habitats were chosen for the study; a primary two-lane highway (State Highway 94), a secondary two-lane paved road (Millar Ranch Road), and several unimproved dirt roads (Fig. 1, Table 1, and Fig. 2). For the placement of trapping arrays, sites were chosen where the CSS extended at least 110 m from the side of the road on which the paired trapping arrays were to be located and 50 m from the opposite side of the road. Thus, all arrays were constructed at least 50 m away from any other habitat edges so as not to confound the presence of a road with any other habitat edge.

Eight paired trapping arrays were installed along each road (Fig. 3 and Appendix). Each pair of arrays consisted of a roadside and an interior array. The roadside array was placed within one meter of the road, while the interior array was placed at least 60 meters from the road. Trapping arrays were placed at least 50 meters apart from one another to minimize recaptures due to overlapping home ranges of animals. Each array consisted of three 5-gallon pitfall traps connected by a 15 meter drift fence (7.5 meters between each

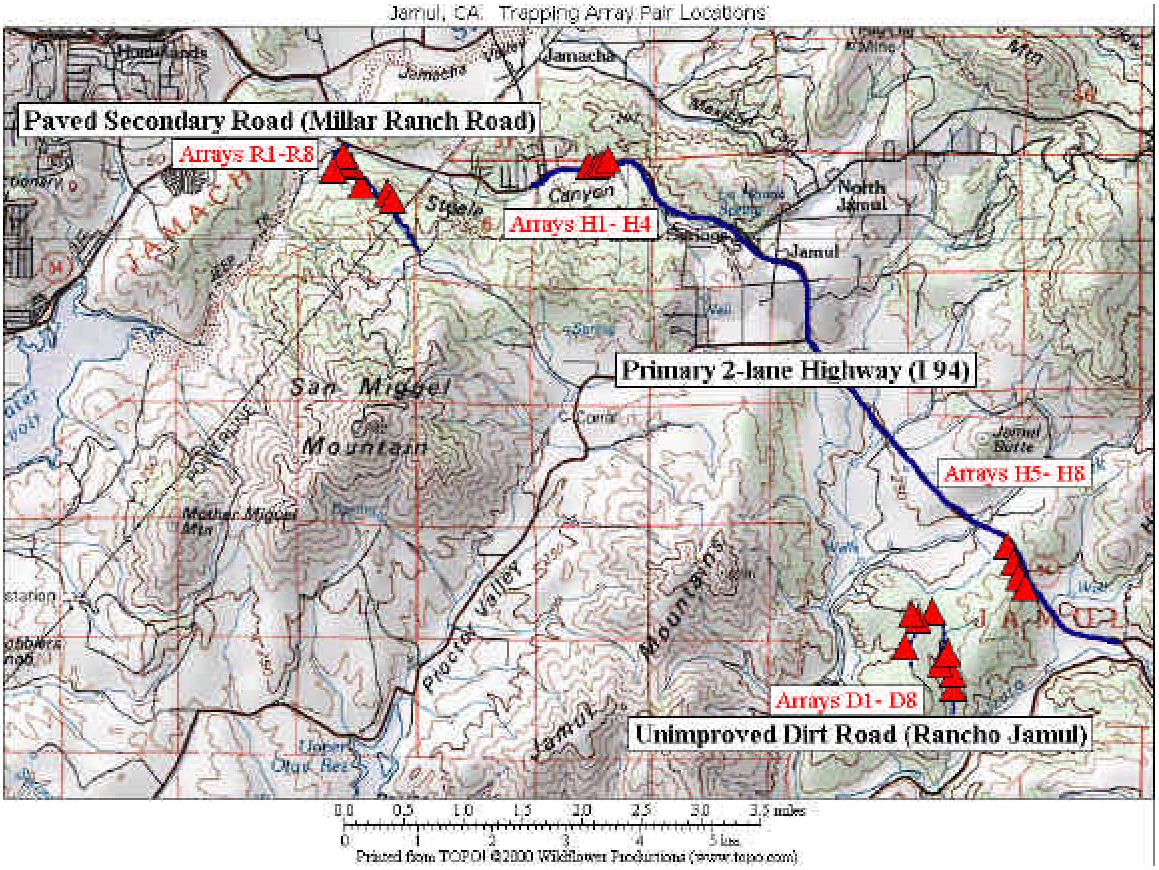

Fig. 1. Roads and trapping array pair locations in Jamul, San Diego County, California.

Table 1
Road characteristics

Road Type	Name	Width (m) +/-1 sd	Traffic Volume (vehicles/day)
Secondary-Dirt	Access-Rancho Jamul	4.7 +/-1.3	0-20
Secondary- Paved	Millar Ranch Road	6.6 +/- 0.2	200-500[1]
Primary- Paved	Interstate 94	11.2 +/- 0.9	7400-18000[2]

[1] Traffic Section of San Diego County Department of Public Works (estimate)
[2] California Department of Transportation

bucket) and four Sherman live traps. A single funnel trap was also placed by each array to capture large snakes. Although the Sherman live traps are limited to capturing 4 individuals within the array, pitfall traps and funnel traps are not limited in the number of animals they can capture and have been shown to be effective in trapping both small mammals and reptiles (Case and Fisher 2001). Pitfall array materials and installation procedures were the same as

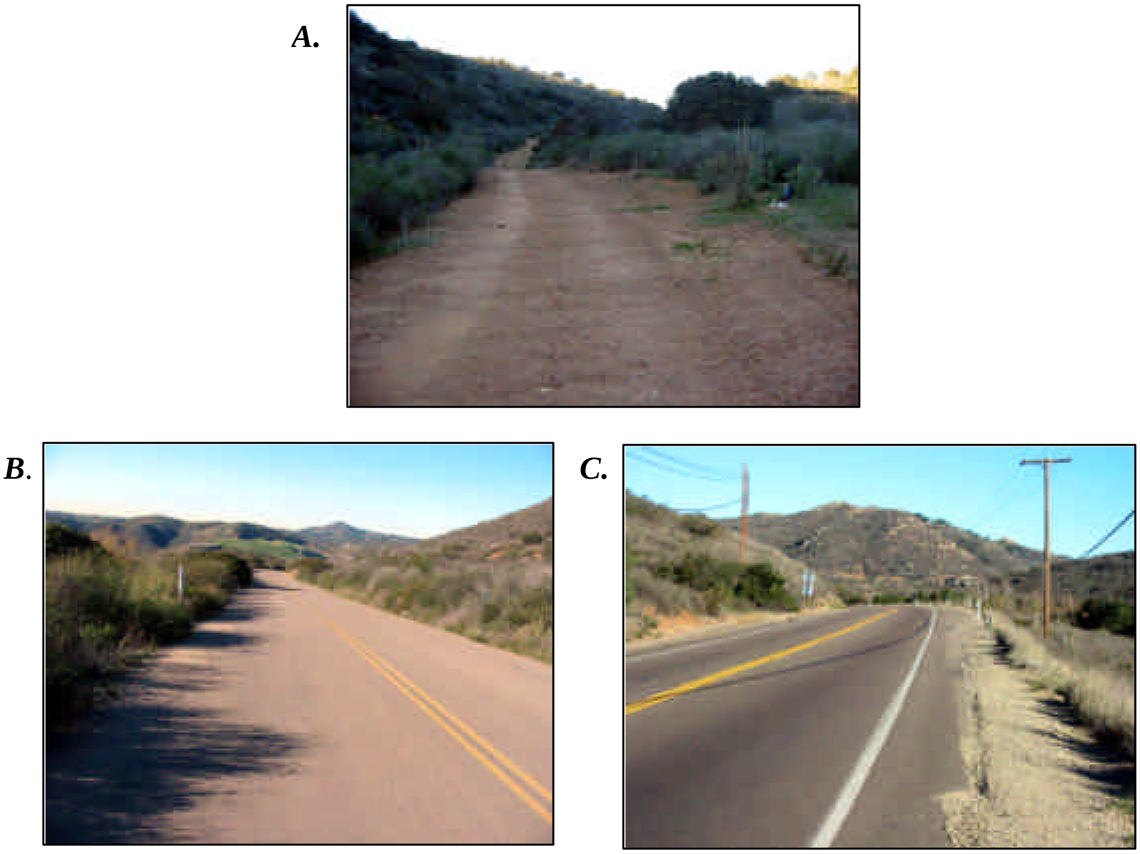

Fig. 2. Photographs of roads used in study. A) unimproved dirt, B) secondary paved, C) primary highway.

those described by Stokes et al. (2003).

All Sherman live traps were baited with birdseed and rolled oats. Traps were opened in the afternoon and checked every morning at sunrise. Pitfall traps were also baited with birdseed and rolled oats. They remained open during each trapping period and were checked every morning at sunrise. A total of ten trapping sessions were performed at each trapping array between April and December of 2001. Due to the intensive amount of work required to sample all arrays at once, arrays were split up into two groups for sampling. Each group consisted of four pairs of arrays by each road. Each session consisted of 2-3 trap nights (Table 2, p. 9). Thus, each of the 48 arrays was sampled a total of 200 trap-nights (8 traps X 25 nights). Sampling for the entire study consisted of 9600 trap-nights.

Each captured animal was identified to species, measured (body, tail, ear, and hind

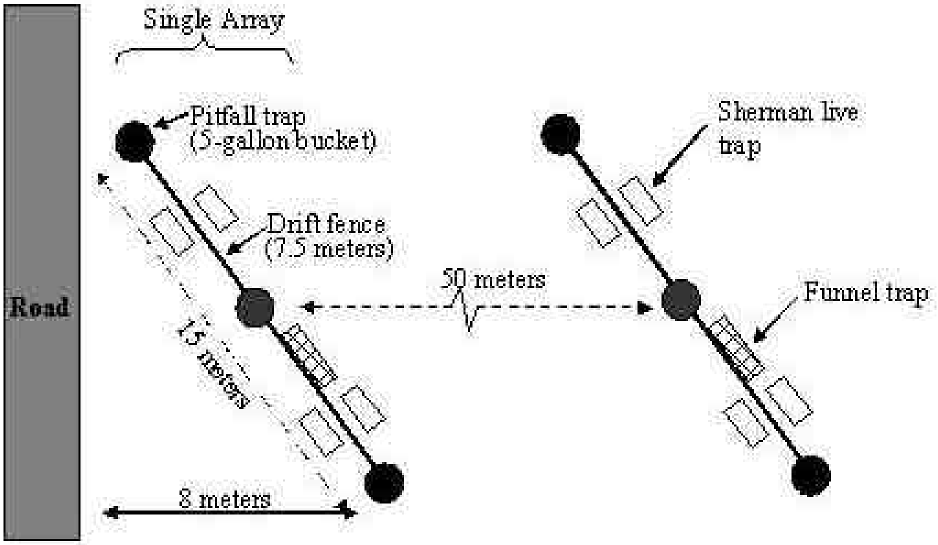

Fig. 3: Trapping array pair (roadside and interior).

foot lengths in mammals, snout-vent length for reptiles and salamanders, and snout-urostyle length for anurans), weighed (using a Pesola spring scale), assessed for reproductive condition (Stebbins 1985; Kunz et al. 1996), marked (by toe clipping or ear tags, American Society of Mammologists 1998; Stokes et. al. 2003), and released.

To determine if there were any differences in vegetation among the arrays that may account for differences in animal abundance, the vegetation around each array was surveyed between June and October, 2002. A 10m X 15m plot surrounding each array was surveyed using a stratified random sampling method with point intercepts (Sawyer and Keeler-Wolf 1995, Fig. 4). The plot was stratified into five equal longitudinal sections, perpendicular to the road edge. A random starting point (1 to 3 meters) within each section was chosen by a roll of a die. A 15 m transect line was then extended perpendicular to the road and sampled every 1 m. At each sample point, a thin measuring rod was placed on the ground. Plant height and height class (low herb, medium herb, low shrub, medium shrub, and high shrub (Sawyer and Keeler-Wolf 1995) were recorded for each plant that came into contact with the rod. All shrubs and perennial vegetation were identified to species. Grasses and forbs were identified to species, if known. A total of 55 sampling points per array were recorded.

Table 2
Dates of field data collection

		Trapping Arrays	
Season	Session	Group 1	Group 2
Spring	1	April 13-15	April 13-15
	2	May 4-6	May 4-6
	3	May 29- 31	June 5-7
Summer	4	June 19- 21	June 27- 29
	5	July 17- 19	July 24- 26
	6	Aug 7- 8	Aug 15- 16
	7	Sep 14- 15	Sep 21- 22
Fall	8	Oct 5- 6	Oct 19- 20
	9	Nov 2- 3	Nov 16- 17
	10	Dec 7- 8	Dec 19- 20

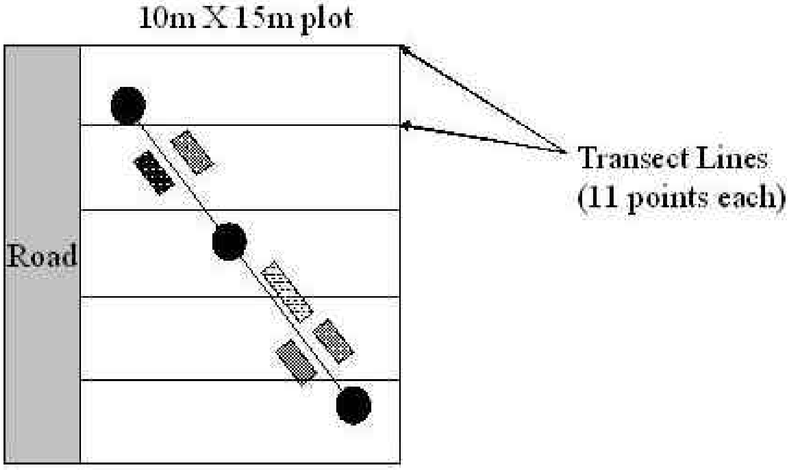

Fig. 4. Vegetation survey plot with transect lines.

Assessment of Road Activity and Mortality

For roadside trapping arrays, movement data for small mammals and reptiles were collected using the fluorescent powder tracking technique (Lemen and Freeman 1985; Fellers and Drost 1989; Manning and Ehmann 1991; Bestelmeyer and Stevenson 1998). The fluorescent powder is non-toxic (Radiant Color Inc.) and has been recommended as a safe and effective means of tracking small-scale animal movements (Stapp et al. 1994). In order to differentiate individuals, each animal released at an array was dusted with one of approximately twenty base colors or unique mixtures of the base colors. Special care was taken to dust only the body and to avoid the head area, to prevent the animal from breathing in the powder which, in a small percentage of cases, can cause short term respiratory distress (Stapp et al. 1994). Once an animal was dusted with fluorescent powder, it was carefully released within 5 meters of the road edge. Precautions were taken to minimize any effects of the handler on the direction of animal movements in relation to the road. When releasing an animal, the handler would crouch down parallel to the animal and the road and slowly back away, staying parallel to the road. This would prevent the handler from scaring the animal toward or away from the road. On the same or following evening after release, the fluorescent powder tracks were traced using a portable 12 watt long-wave UV lamp. A 50-meter measuring tape was laid over the trail until the powder could no longer be traced. For each animal, the total distance followed was recorded and a drawing was made of the animal's movements in relation to the road. Any information on location of burrow or use of open areas, covered areas, and vegetation for movement was also recorded. For the majority of animals, movement data were collected one time per individual. This was to avoid problems with pseudoreplication as well as to minimize any possible negative effects from the dye. A small proportion of animals were tracked on several occasions for validation of the tracking technique. For these animals, only the results of their first tracking occasion were used for analysis.

All movements recorded longer than 10 m were categorized as either "road use" or "habitat use". "Road use" was defined for any animal that stepped out onto the road for any distance of the track length. "Habitat use" was defined for any animal that stayed within the coastal sage scrub habitat during the tracking period. Only animals tracked for a minimum of 10 m were used in the analysis. Since all animals were released within 5 m of the road, this allowed sufficient distance to track the animal well away from the array in any direction.

As a secondary measure of road activity, any animals observed on the roads within 25 meters of any array were documented. During the daytime trapping sessions, roads were checked for the presence of animals when walking and driving between arrays. During the nighttime tracking sessions, roads were driven at a speed under 48 kmph and a spotlight was used to observe any animals on the roads. Both live and dead animals were identified to species or genus and recorded.

Statistical Analysis

For each trapping array site, the following vegetation indices were calculated: 1) percent ground covered by vegetation (PGC); 2) percent herb cover (PHC); 3) percent shrub cover (PSC); 4) perennial plant cover diversity (PPD), using the Shannon's index (Shannon 1948); 5) foliage height diversity (FHD), using Shannon's index of the five recorded height classes (Holbrook 1978; Beauchamp 1983); 6) and 7) percentages of the dominant shrubs, *Artemisia californica* (ARCA) and *Eriogonum fasciculatum* (ERFA), respectively.

I tested for the effects of road type, distance, and road type X distance on each vegetation index using analysis of variance (ANOVA) with distance as the within-subject factor and road type as the between-subject factor.

One and 2-way within and between-subject ANOVAs were also used to test for effects of road type, distance from road edge, and road X distance interactions on the abundance, sex ratios (male/female), and proportion of new captures (individuals captured once/total individuals captured) of individual species. This proportion will be higher where either survivorship is decreased in the habitat or more transient individuals are emigrating from the trapping array. For all analyses, the trapping array pair was treated as the subject. Distance from road was the within-subject factor and road type was the between-subject factor. The dependant variable was the total number of captures at each array. To minimize pseudoreplication (Hurlbert 1984) and the influence of "trap-happy" or "trap-shy" individuals on summed capture numbers, recaptures within each trapping session were removed before the analysis. An iterative approach was taken in order to ensure the most appropriate analysis was performed for each data set. For species with sufficient capture data throughout the study (*C. fallax and P. eremicus*), season was also included as a within-subject factor. To normalize for the different number of nights trapped per season, the dependent variable for these analyses was capture rate (number of captures per day). To account for any variance of animal captures due to vegetation, correlations were run between species capture data and vegetation indices. If there was a significant correlation between a species and any vegetation index ($p<.05$), the most significant index was included in the abundance analysis as a covariate. Since vegetation indices varied for the within-subject factor of distance, a restricted maximum likelihood model was used to fit the data using unstructured covariance estimates. If the covariate did not account for a significant portion of the variation in the model, it was subsequently removed and reanalyzed by ANOVA.

For ANOVA's, if the assumptions of a univariate analysis were not met, the multivariate approach of Wilk's lambda was used. For all analyses, if homogeneity of variance assumptions were not met, follow-up contrasts were conducted with separate variance estimates. For analysis with covariates, interactions between covariates and main effects were included to test for assumptions of equality of slopes. All counts were square root transformed (SQRT(x + 0.5)) and proportions were arcsine-square root transformed (ACS (SQRT(x))) to normalize skewed distributions before analysis (Krebs 1987). Residuals were checked for assumptions of normality and homogeneity of variance by examining probability plots and residual versus observed plots. Homogeneity of variance was also tested using Levene's test of equality of error variances. The method of Fishers Least Squares Difference (LSD) was used for Type I error protection. Thus, if the initial ANOVA resulted in no significant effects, no further contrasts were conducted. If the ANOVA resulted in a significant effect, follow-up contrasts were conducted to explore the effect with no additional Type I error protection.

RESULTS

Between April and December 2001, there were 1,704 animal captures in 9,600 trap-nights. For small mammals, there were 1,185 captures representing 14 species (Table 3a). San Diego pocket mice (*Chaetodipus fallax*) and cactus mice (*Peromyscus eremicus*) were the most abundant species, accounting for 43.5% and 35.8% of all captures, respectively. Deer mice (*Peromyscus maniculatus*) were the next most abundant species, accounting for 8.7% of all captures. All other species comprised less than 4% of the mammal captures individually. For reptiles, there were 519 captures representing 22 species (Table 3b). The orange-throated whiptail (*Cnemidophorus hyperythrus)* and western fence lizard (*Sceloporus occidentalis*) were the most abundant species, accounting for 49.9% and 22.5% of all captures, respectively. The side-blotched lizard (*Uta stansburiana*) was the next most abundant species, accounting for 6.6% of all captures. All other species comprised less than 4% of the reptile captures individually.

There were only four amphibian captures; three pacific tree frogs (*Hyla regilla*) and a single spadefoot toad (*Spea hammondii*). There was a total of 5.6 cm of rain during the study period (Western Regional Climate Center 2003).

Because many species had too few captures for subsequent analyses, the focus of the results are on the three most frequently captured small mammals (*C. fallax*, *P. eremicus*, *P. maniculatus*) and the two most frequently captured lizards (*S. occidentalis, C. hyperythrus*). Other species or groups are presented where sufficient data exists in one or more parts of the study.

Because road type is largely confounded with site, there may be larger unknown landscape variables that differ between the road types. So the main effect of road is reported, but not interpreted as an effect due to the road itself. Instead, the focus of the results and interpretation are on the main effect of distance from the road (0 vs. 60 m) on animal abundance and any interaction effects that indicate that the effect of distance is dependant upon road type.

Table 3
Total number of captures for small mammal (A) and reptile species (B)

A. Small Mammals

Common name	Scientific name	No. Captured	% of Total
San Diego pocket mouse	*Chaetodipus fallax*	516	43.5%
Cactus mouse	*Peromyscus eremicus*	424	35.8%
Deer mouse	*Peromyscus maniculatus*	103	8.7%
Western harvest mouse	*Reithrodontomys megalotis*	38	3.2%
Desert shrew	*Notiosorex crawfordii*	27	2.3%
Dulzura kangaroo rat	*Dipodomys simulans*	25	2.1%
Desert woodrat	*Neotoma lepida*	14	1.2%
Dusky-footed woodrat	*Neotoma fuscipes*	13	1.1%
California mouse	*Peromyscus californicus*	7	0.6%
Ornate shrew	*Sorex ornatus*	5	0.4%
California vole	*Microtus californicus*	4	0.3%
House mouse	*Mus musculus*	4	0.3%
Botta's pocket gopher	*Thomomys bottae*	4	0.3%
California pocket mouse	*Chaetodipus californicus*	1	0.1%
	Total	1185	100.0%

B. Reptiles

Common name	Scientific name	No. Captured	% of Total
Orange-throated whiptail	*Cnemidophorus hyperythrus*	259	49.9%
Western fence lizard	*Sceloporus occidentalis*	117	22.5%
Side-blotched lizard	*Uta stansburiana*	34	6.6%
Southern alligator lizard	*Elgaria multicarinatus*	16	3.1%
Western skink	*Eumeces skiltonianus*	15	2.9%
California whiptail	*Cnemidophorus tigris*	14	2.7%
Striped racer	*Masticophis lateralis*	12	2.3%
Coast horned lizard	*Phrynosoma coronatum*	11	2.1%
California kingsnake	*Lampropeltis getulus*	6	1.2%
Southern pacific rattlesnake	*Crotalus viridis*	6	1.2%
Blind snake	*Leptotyphlops humilis*	5	1.0%
Red diamond rattlesnake	*Crotalus ruber*	3	0.6%
Gopher snake	*Pituophis melanoleucus*	3	0.6%
Long-nosed snake	*Rhinocheilus lecontei*	3	0.6%
Granite spiny lizard	*Sceloporus orcutti*	3	0.6%
Black-headed snake	*Tantilla planiceps*	3	0.6%
California legless lizard	*Anniella pulchra*	2	0.4%
Ringneck snake	*Diadophis punctatus*	2	0.4%
Western patch-nosed snake	*Salvadora hexalepis*	2	0.4%
Gilberts skink	*Eumeces gilberti*	1	0.2%
Night snake	*Hypsiglena torquata*	1	0.2%
Granite night lizard	*Xantusia henshawi*	1	0.2%
	Total	519	100.0%

Vegetative Cover

In individual ANOVA's, not one of the seven vegetation indices (percent ground cover, percent herb cover, percent shrub cover, foliage height diversity, perennial plant diversity, percent California sagebrush, percent buckwheat) differed with respect to distance (near vs. far) from the road. Only one index (percent California sagebrush, *Artemisia californica*) was significantly different ($F_{2,21}$= 9.285, p=.0013) between road types (Table 4). Individual contrasts showed that the average percentage of the sagebrush was lower at the secondary paved road site (CI_{95}: 7.2- 17.4) than at the sites with the dirt road (CI_{95}: 23.2- 37.9) and highway (CI_{95}: 15.7- 28.9). Overall, this indicates that coastal sage scrub vegetation at all trapping sites was largely the same, so that the effects of interest, distance and distance X road, are not confounded with any major differences in vegetation.

Table 4
Results of ANOVAs testing the effects of distance (near vs. far) and road (dirt, secondary paved, primary highway) on seven vegetation indices

		Distance		Road		Distance*road	
Vegetation Index	95% Confidence Interval	$F_{1,21}$	p	$F_{2,21}$	p	$F_{2,21}$	p
Percent ground cover	69.2- 75.1	3.178	0.089	0.692	0.512	0.037	0.964
Percent herb cover	23.5- 36.0	1.025	0.323	0.762	0.479	3.082	0.067
Percent shrub cover	58.9- 67.7	0.345	0.563	2.651	0.094	0.791	0.467
Foliage height diversity	1.209- 1.301	0.413	0.528	0.945	0.405	1.490	0.248
Perennial plant diversity	0.820- 1.016	0.788	0.385	1.816	0.187	0.987	0.389
Percent *A. californica*	17.2- 24.7	1.097	0.307	9.285	0.001*	0.265	0.770
Percent *E. fasciculatum*	19.5- 28.8	0.853	0.366	0.515	0.605	0.168	0.846

*result is significant at the 95% confidence level

Small Mammal Abundance in Roadside Habitat

Results of statistical analyses of the effects of road, distance, and road X distance on the relative abundance of small mammals are presented in Table 5. Seasonal trends in captures varied for the three most abundant species (Fig. 5).

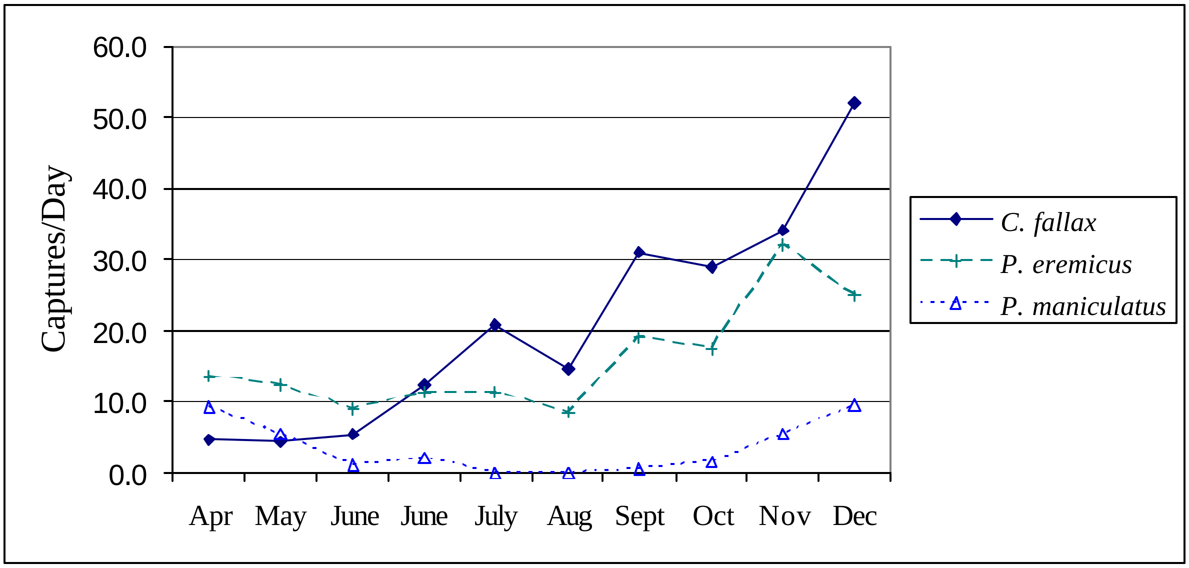

Fig. 5. Number of captures by time graphed for three small mammal species.

Abundance of the San Diego pocket mouse, *C. fallax*, showed considerable variation among seasons (Fig. 5). There were low numbers of captures in spring ($CI_{95\%}$: 0.09-0.17 array/day), with increasing numbers in summer ($CI_{95\%}$: 0.30-0.43 array/day) and fall ($CI_{95\%}$: 0.63-0.91 array/day). The majority juveniles and sub-adults (45/63) were captured during the summer months following breeding activity in the spring. Spring data were excluded from subsequent analysis due to too few captures. ANOVA of summed summer and fall abundance data revealed that there was a significant road X distance interaction ($F_{2,21}$ = 3.827, p= 0.038). Therefore, the effect of distance was dependent upon road type. They were less active near the dirt road than 60 m to the interior (t_7=2.386, p=0.048), but did not differ in their response to the paved road (t_7= 0.095, p= 0.927) or highway (t_7=0.781, p=0.461, Fig. 6A). There were also a higher proportion of young individuals (juveniles and sub-adults) near the dirt road versus 60 m to the interior (Fisher's exact test, p=0.022), while there were no age class differences by the secondary road or highway (Fisher's exact test, p= 0.622 and p= 0.148, respectively). So that along with decreased abundance by the dirt road,

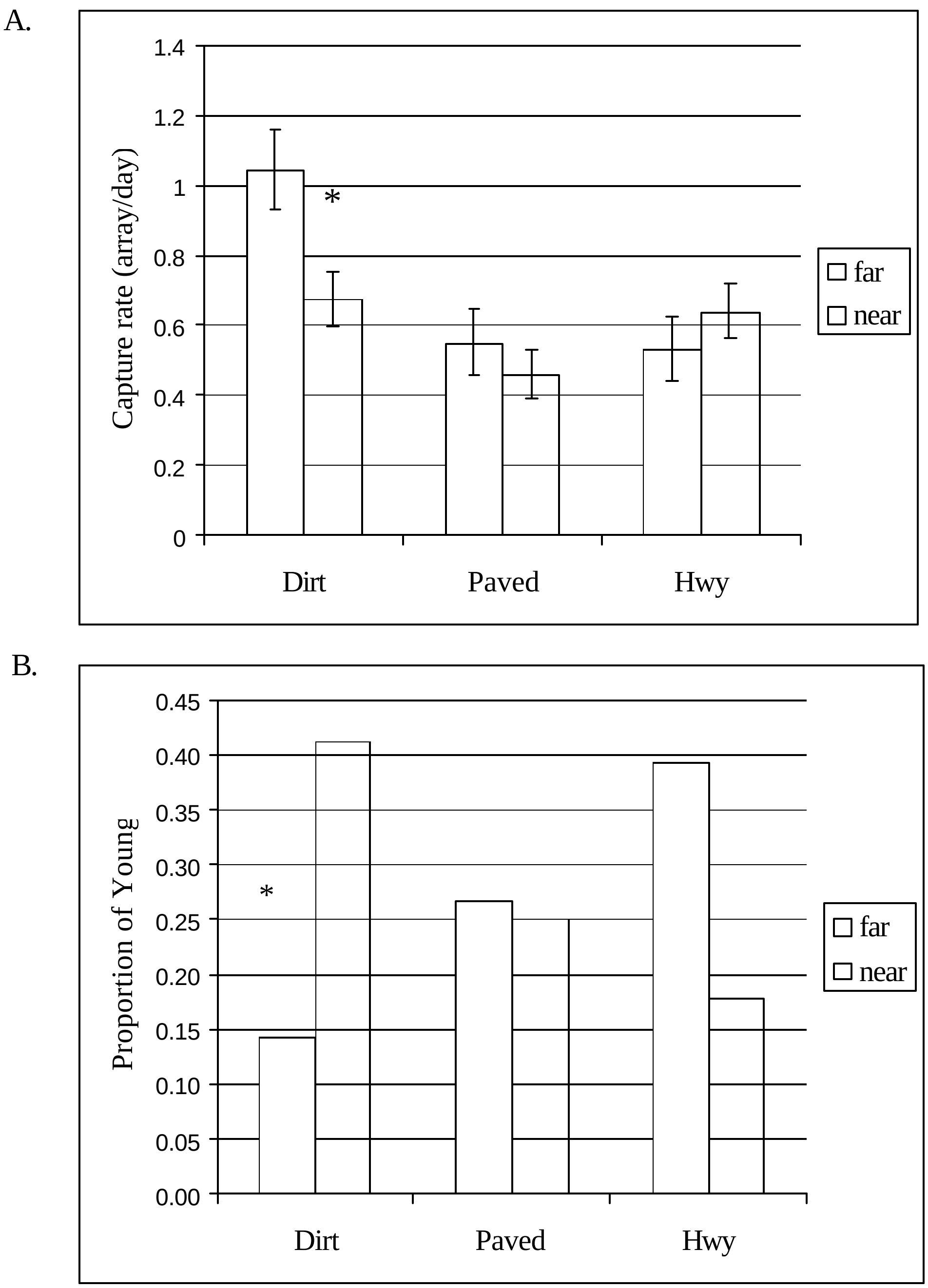

Fig. 6. Capture rate (± 1 standard error) of *C. fallax* by road type and distance (A). Proportion of young captured by road type and distance (B). All data transformed back to original units. *mean difference is significant at the 95% confidence level by Fisher's LSD (A) and Fisher's exact test (B).

there was a concomitant increase in the ratio of young (Fig. 6B).

Abundance of the cactus mouse, *P. eremicus*, did not vary significantly between seasons, road types, or distance from road (Fig. 7). It did have a positive correlation (r=0.40, p=0.005) to abundance of California sagebrush, *Artemisia californica*, and this covariate accounted for a significant proportion of the variation in the REML model ($F_{1,34.75}$=6.841, p= 0.013).

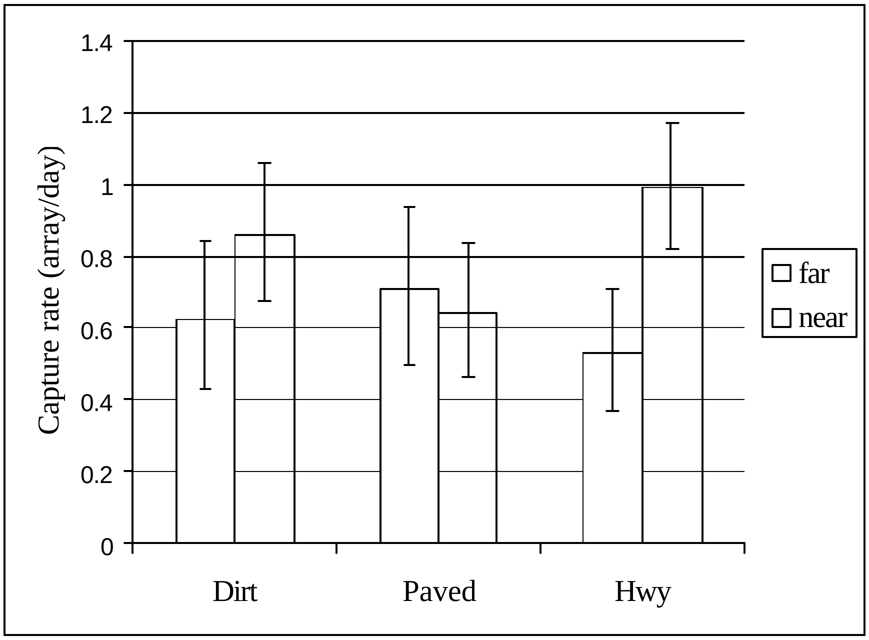

Fig. 7. Capture rate (± 1 standard error) of *P. eremicus* by road type and distance. All data transformed back to original units.

A third pattern of abundance by season was observed with the deer mouse, *P. maniculatus*. Captures were high in the spring (n=49), very low in the summer (n=4), and high again in the fall (n=33). Summer data were excluded from the analysis due to too few captures. Grouped analysis of spring and fall data resulted in an almost significant road X distance interaction ($F_{1,21}$=3.299, p= 0.057) and significant main effects of road and distance ($F_{2,21}$=4.706, p= 0.020 and $F_{1,21}$=6.333, p= 0.020, respectively). Follow-up contrasts revealed that there was increased deer mouse abundance at the highway sites compared to the dirt or secondary paved road ($F_{1,22}$=4.706, p= 0.031 and $F_{1,22}$=6.333, p= 0.009, respectively). Within the highway sites, the abundance of the deer mouse was significantly greater next to the road than 60 m to the interior (t_7=2.805, p= 0.026, Fig. 8).

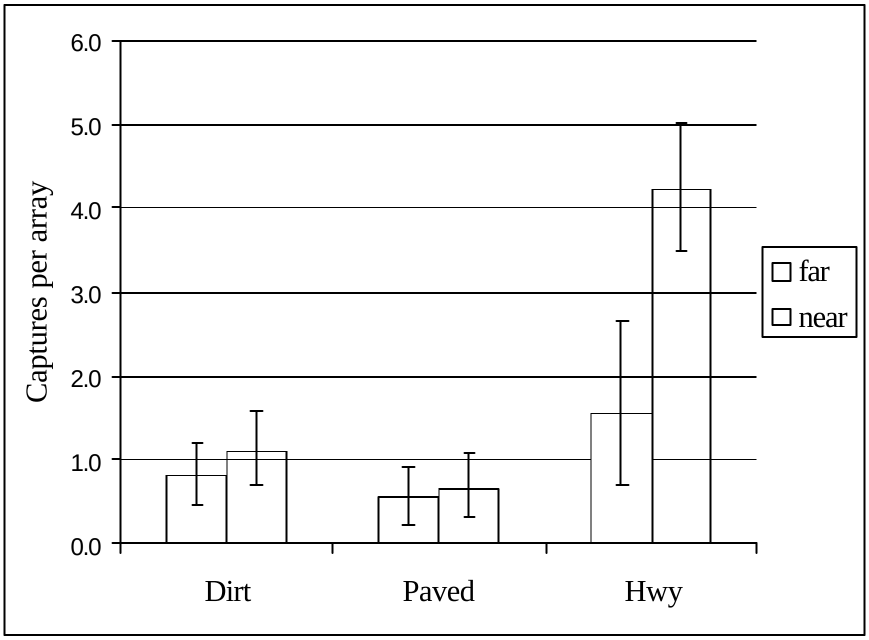

Fig. 8. Mean number of captures of *P. maniculatus* (± 1 standard error) by road type and distance. All data transformed back to original units. * the mean difference is significant at the 95% confidence level calculated with separate variance estimates.

Reptile Abundance in Roadside Habitat

Reptile abundance was variable through the year for different species (Fig. 9). Because overall reptile captures were relatively low, all individual and grouped reptile data were summed over seasons to increase the power of the analysis.

There were two peaks in abundance of the orange-throated whiptail, *C. hyperythrus*, over time (Fig. 9). The first peak took place in June, July, and August, where captures were primarily reproductive adults. The second peak in October represents primarily juvenile captures. Since the trends in juvenile and adult data were the same with respect to distance from road and road type, these were grouped together for analyses. *Cnemidophorus hyperythrus* captures were also variable over space. There were few captures (14 captures) at the dirt road site, so this road was removed in subsequent REML analyses. The results showed that abundance was reduced at the paved road site in comparison to the highway ($F_{1,27}$ =8.033, p= 0.009) and reduced near versus far from the roads ($F_{1,27}$ =4.488, p= 0.043, Fig. 10). There was a modest correlation between whiptail abundance and perennial plant diversity (r= .437, p=.002) and this covariate subsequently accounted for a significant amount of variation ($F_{1,27}$ =10.876, p= 0.003) in the model. There were no significant results with individual contrasts of distance within road type.

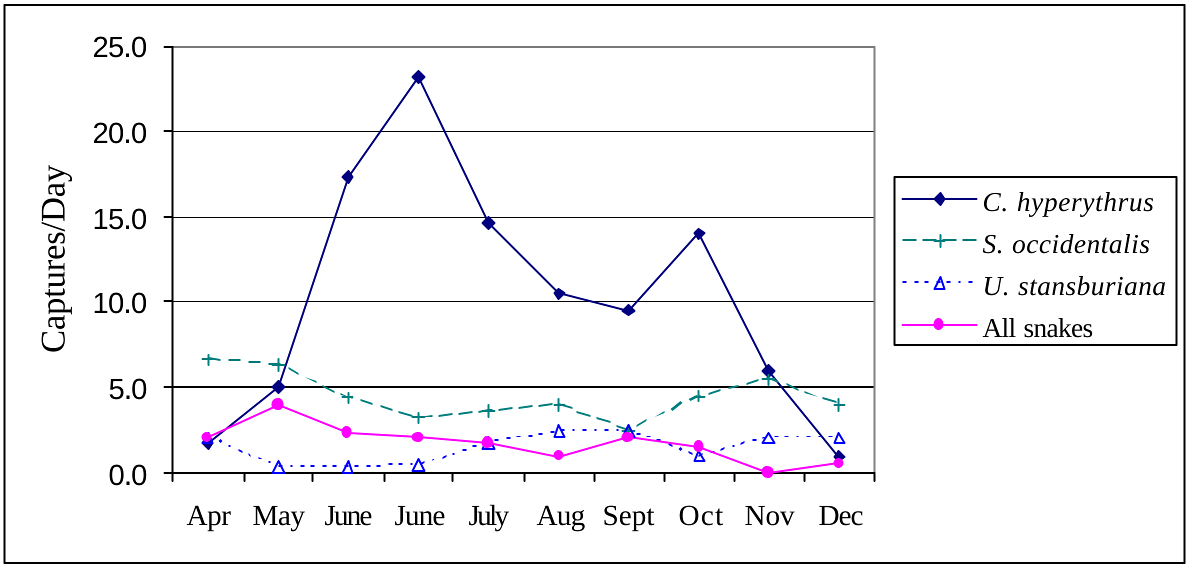

Fig. 9. Number of reptile captures by time graphed for three lizard species and the group ‘all snakes’.

There were two peaks in abundance of the orange-throated whiptail, *C. hyperythrus*, over time (Fig. 9). The first peak took place in June, July, and August, where captures were primarily reproductive adults. The second peak in October represents primarily juvenile captures. Since the trends in juvenile and adult data were the same with respect to distance from road and road type, these were grouped together for analyses. *Cnemidophorus hyperythrus* captures were also variable over space. There were few captures (14 captures) at the dirt road site, so this road was removed in subsequent REML analyses. The results showed that abundance was reduced at the paved road site in comparison to the highway ($F_{1,27}$ =8.033, p= 0.009) and reduced near versus far from the roads ($F_{1,27}$ =4.488, p= 0.043, Fig. 10). There was a modest correlation between whiptail abundance and perennial plant diversity (r= .437, p=.002) and this covariate subsequently accounted for a significant amount of variation ($F_{1,27}$ =10.876, p= 0.003) in the model. There were no significant results with individual contrasts of distance within road type.

In contrast to *C. hyperythrus*, road type or distance from the road did not explain a significant amount of variation in the abundance of the western fence lizard, *S. occidentalis* ($F_{1,21}$ =1.158, p= 0.294 and $F_{1,21}$ =0.484, p= 0.480, respectively, Fig. 11). In addition,

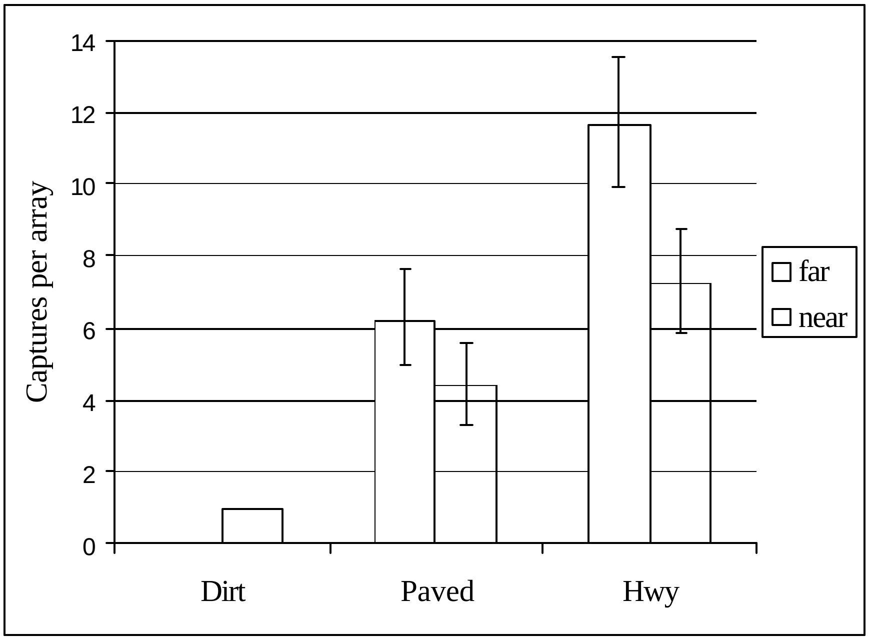

Fig. 10. Mean number of captures (± 1 standard error) of *C. hyperythrus* by road type and distance. Means are adjusted for the covariate, perennial plant diversity, set at .9788. All data transformed back to original units.

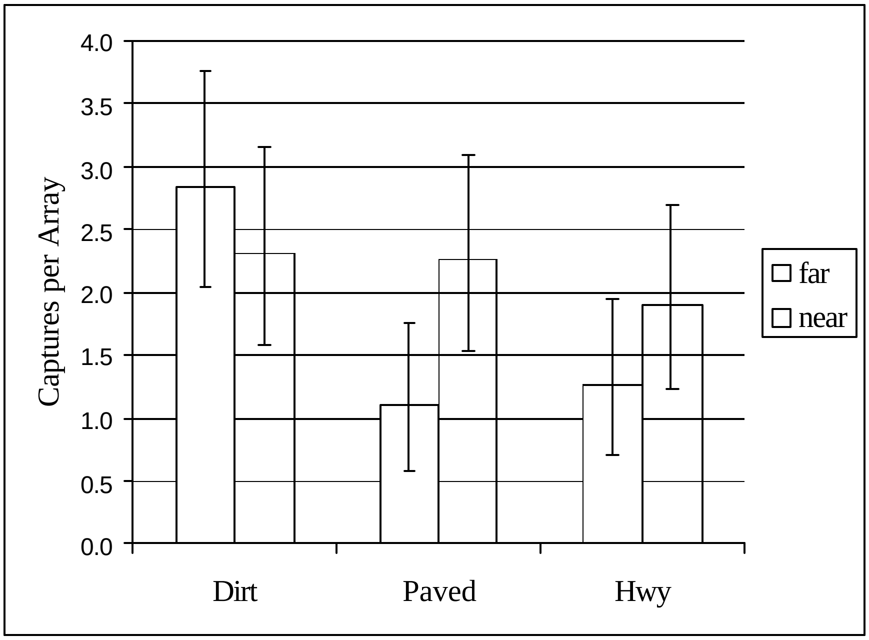

Fig. 11. Mean number of captures (± 1 standard error) of *S. occidentalis* by road type and distance. All data transformed back to original units.

analyses of snakes (as a group) and the side-blotched lizard, *U. stansburiana*, revealed no differences in abundance in relation to distance or road type (Exact tests, p=0.610 and p=0.100, respectively).

Movements of Small Mammals in Relation to Roads

A total of 306 animals were dusted with fluorescent powder and released within 5 m of the road. Generally, the fluorescent powder was effective for tracking fine-scale movements. However, one-third of the animals were not included in the analysis because their track lengths were less than the cut-off of 10 m. Most of the small mammals (44/73) that were not used in the analyses were tracked into a nearby burrow, with no obvious tracks coming back out. All of these were tracked into burrows on the same side of the road. Small reptiles and those with smooth scales (many snakes, skink, side-blotched lizard, and whiptail) did not hold the powder dye very well and many of their tracks were lost within several meters. The 204 animals that were used in the analyses (135 small mammals, 65 lizards, four snakes) were followed an average of 20.7 m (se=0.75). To test the repeatability of results, 19 animals were followed more than once for greater than 10 m. All of these animals repeated their initial movement types. Seventeen (12 mammals and five lizards) stayed within the habitat on both tracking occasions, while two (one mammal and one lizard) repeatedly crossed the road.

Overall, both mammals and reptiles showed decreasing road permeability (the proportion of movements onto the road) with increased improvement of the road. While most of the animals frequently used the dirt roads, they decreasingly used the secondary paved road, and none were tracked out onto the primary highway (Fig. 12). Movement data are presented individually for three small mammal species; *Chaetodipus fallax* (n= 54), *Peromyscus eremicus* (n=57), and *Peromyscus maniculatus* (highway only, n=8) and 2 lizard species; *Sceloporus occidentalis* (n=26) and *Cnemidophorus hyperythrus* (secondary paved road and highway, n=30). Drawings of all tracked movements in relation to the three roads are presented in Figures 13 to 17.

Cnemidophorus hyperythrus (secondary paved road and highway, n=30). Drawings of all tracked movements in relation to the three roads are presented in Figures 13 to 17.

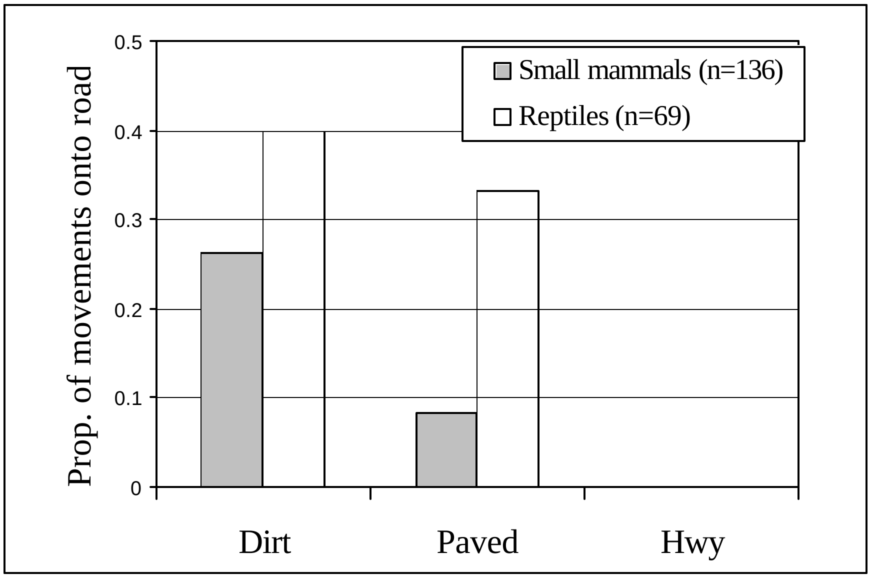

Fig. 12. Road Permeability. The proportion of movements onto three roads plotted for small mammals and reptiles.

The San Diego Pocket mouse, *C. fallax*, was tracked an average distance of 25.1 m (se= 1.6) from the point of release. On the dirt roads, 37.5% (n= 22) of *C. fallax* movements were tracked out onto the road. The majority of these movements were crossing events to the habitat on the other side of the road. On the secondary road, permeability decreased to 10.5% (Fisher's exact test, p=.067, n=21), with no recorded crossing events. The two movements onto the secondary road were both alongside and parallel to the road with a subsequent return to the habitat on the same side of the road. There were no movements of *C. fallax* onto the primary highway (Fisher's exact test, p=.042, n=11, Fig. 13). A one-way ANOVA comparing abundance of the pocket mice in the three roadside habitats resulted in no significant difference ($F_{2,21}$= 1.493, p= 0.248), indicating that differences in usage among the three roads were not a result of differences in animal abundance in the adjacent habitat.

The cactus mouse, *P. eremicus*, appeared to respond even more abruptly to the secondary paved road. Track lengths for this mouse averaged 19.0 m (se=1.2). While 33.3% (n=20) went onto the dirt road, none of these mice were tracked onto the secondary or primary roadways (Fisher's exact test, p=.001; n=18 and 19, respectively). All of the movements onto the dirt road were direct crossing events to the habitat on the other side of the road (Fig. 14). A one-way ANOVA comparing abundance of cactus mice in the three roadside habitats resulted in no significant difference ($F_{2,21}$= 0.676, p= 0.522), indicating that

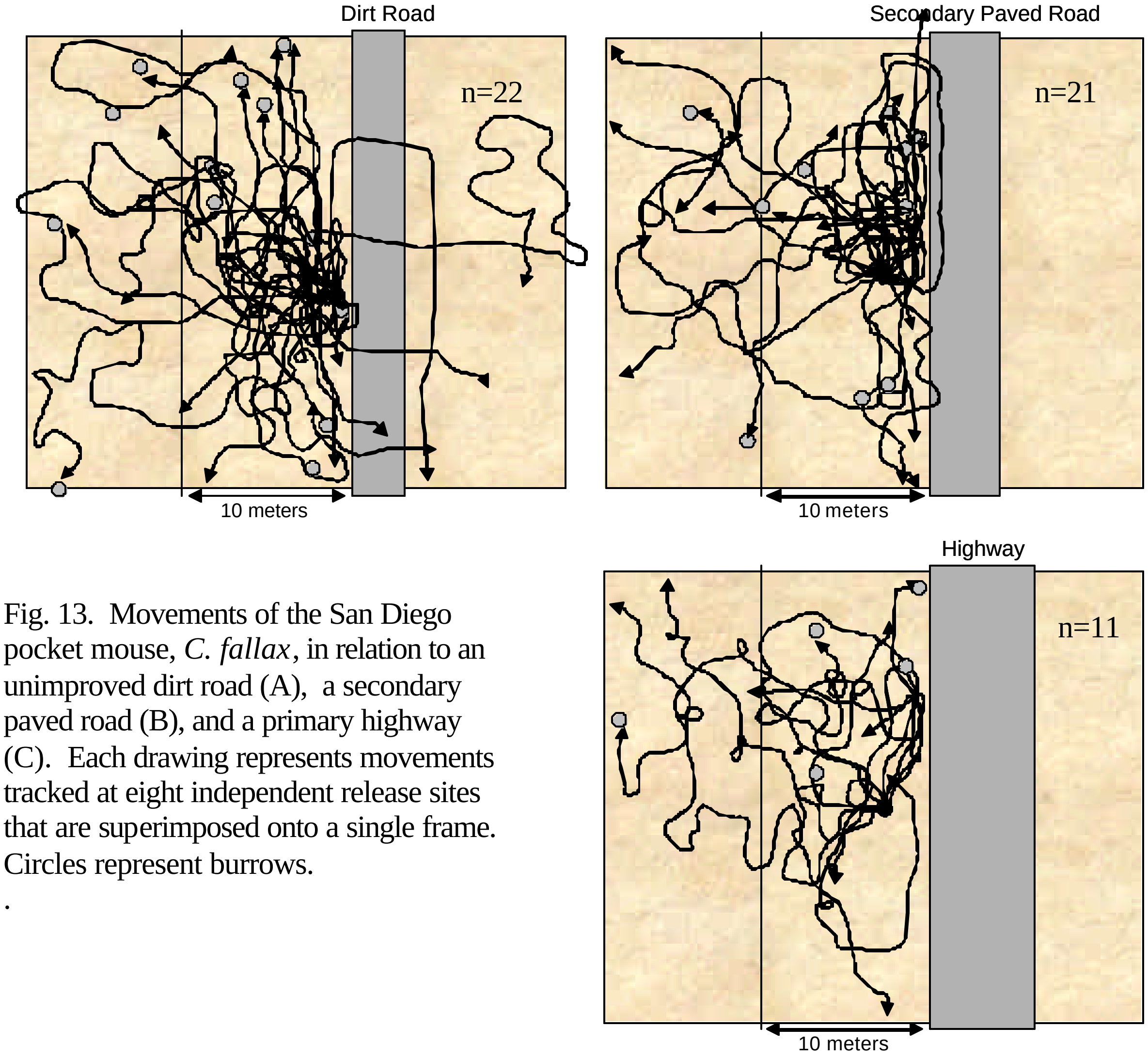

Fig. 13. Movements of the San Diego pocket mouse, *C. fallax*, in relation to an unimproved dirt road (A), a secondary paved road (B), and a primary highway (C). Each drawing represents movements tracked at eight independent release sites that are superimposed onto a single frame. Circles represent burrows.

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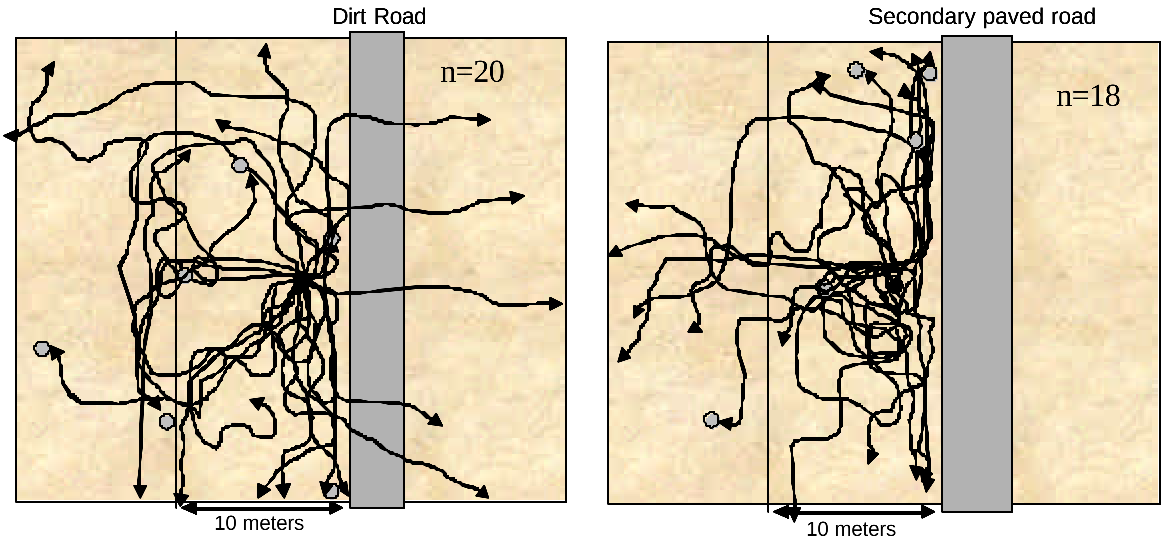
differences in usage among the three roads were not a result of differences in animal abundance in the adjacent habitat.

Eight deer mice, *P. maniculatus*, were tracked adjacent to the highway for an average length of 19.9 m (se= 2.3). None went out onto the road. Many were tracked into burrows that were within a few meters of the road, often on road verges (Fig. 15).

A total of four individuals of *D. simulans* were tracked an average of 17.3 m (se= 2.6). All of these animals went out onto the roadways. Of the three individuals tracked by the dirt road, two ran along the road and one crossed the road. The one individual released by the paved road immediately crossed the road.



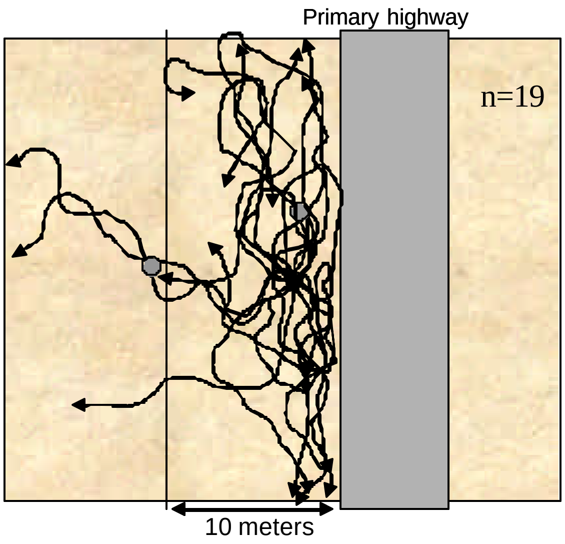


Fig. 14. Movements of the cactus mouse, *P. eremicus*, in relation to an unimproved dirt road (A), a secondary paved road (B), and a primary highway (C). Each drawing represents movements tracked at eight independent release sites that are superimposed onto a single frame. Circles represent burrows.

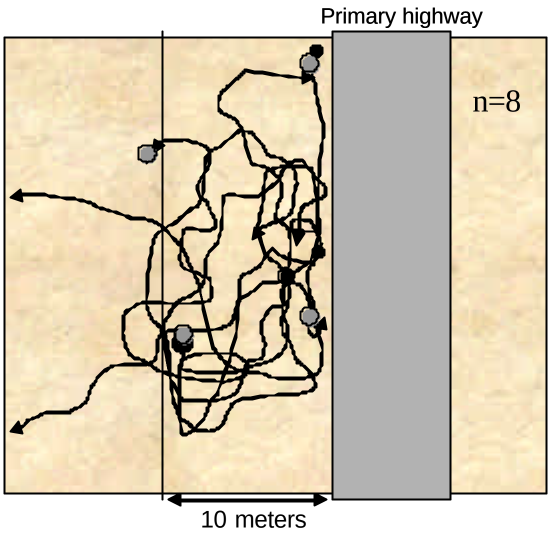


Fig. 15. Movements of the deer mouse, *P. maniculatus*, in relation to a primary highway. Each drawing represents movements tracked at eight independent release sites that are superimposed onto a single frame. Circles represent burrows.

Movements of Reptiles in Relation to Roads

The Western fence lizard, *S. occidentalis*, was tracked an average distance of 17.4 m (se=2.2) from point of release. It exhibited much higher road permeability to the dirt road than either of the mice, as 66% (n=9) of the lizard movements transected the dirt road. These were a mixture of crossing events and movements along the road. A slightly smaller percentage (44%, n=9) went out onto the secondary paved road (Fisher's exact test, p=0.319). These movements were all along the road and no crossing events were recorded. However, many of these tracks were lost on the pavement, so that it was not determined on which side of the road the animal ended up. In comparison, not a single fence lizard went out onto the highway (Fisher's exact test, p=.017, Fig. 16). A one-way ANOVA comparing abundance of the fence lizard in the three roadside habitats resulted in no significant difference ($F_{2,21}$= .006, p= 0.994), indicating that differences in usage among the three roads were not a result of differences in animal abundance in the adjacent habitat.

Only a single orange-throated whiptail, *C. hyperythrus*, was captured by the dirt road and its track length was not long enough to be used in the analysis. However, this species exhibited the same pattern of decreased permeability from the secondary to the primary paved roads (Fig. 17). While 33.3% (n=6) of the whiptails crossed the secondary paved road, none (n=24) were tracked out onto the highway (Fisher's exact test, p=.0022). The average track length for this species was 17.0 m (se= 1.3). A t-test comparing abundance in the habitat next to these two roads resulted in no significant difference (t_{14}=1.612, p= 0.129), indicating that the difference in usage of the two roads was not due to a difference in abundance in the adjacent habitat. However, the success rate in tracking the whiptail for distances greater than 10 m was significantly greater by the highway (24/32) than the paved road (6/20; Fisher's exact test, p= 0.002).

Small Mammal and Reptile Activity on Roads

There were a total of 103 small mammal and 28 reptile live observations on the roads during the course of the study. The totals were calculated over 44 days and nights, so that the same individuals could have been counted on several occasions. All observations were made within 25 m of the arrays, so the total distance of road covered (400 m) was equivalent for

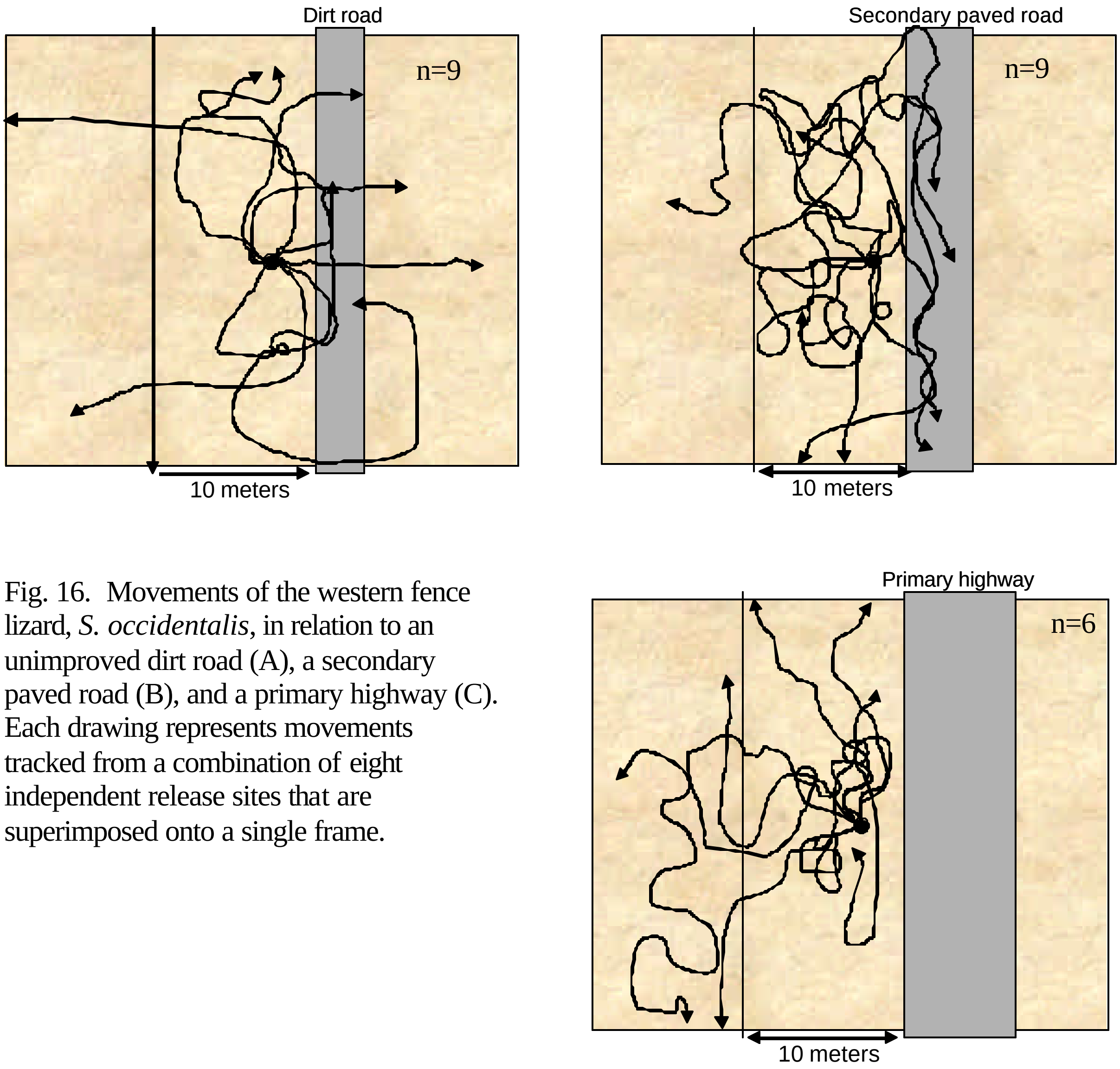


Fig. 16. Movements of the western fence lizard, *S. occidentalis*, in relation to an unimproved dirt road (A), a secondary paved road (B), and a primary highway (C). Each drawing represents movements tracked from a combination of eight independent release sites that are superimposed onto a single frame.

each road type. Overall, these data corresponded to the road permeability data in that there were more observations of animals on the dirt road than either of the paved roads. The total number of small mammals and reptiles observed running, sitting, or basking on the roads decreased with increased improvement of the road (Fig. 18). Most genera and/or guilds showed this same pattern, but to differing degrees.

All small mammals were observed at night and a disproportionately large number (87) were observed on the dirt roads. Approximately half (43) of these observations were of the Dulzura kangaroo rat, *Dipodomys simulans*. The majority of these were running along the roads, rather than across, and often jumped into burrows in the middle of the roads. There were no live observations of this species along the other two road types. There were

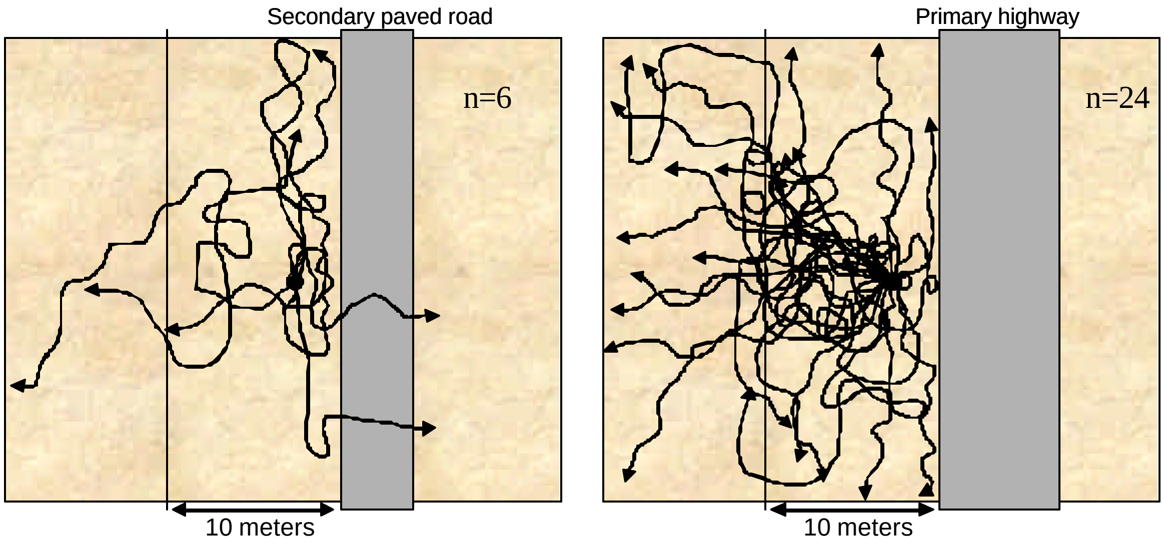


Fig. 17. Movements of the orange-throated whiptail, *C. hyperythrus*, in relation to a secondary paved road (A), and a primary highway (B). Each drawing represents movements tracked from a combination of eight independent release sites that are superimposed onto a single frame.

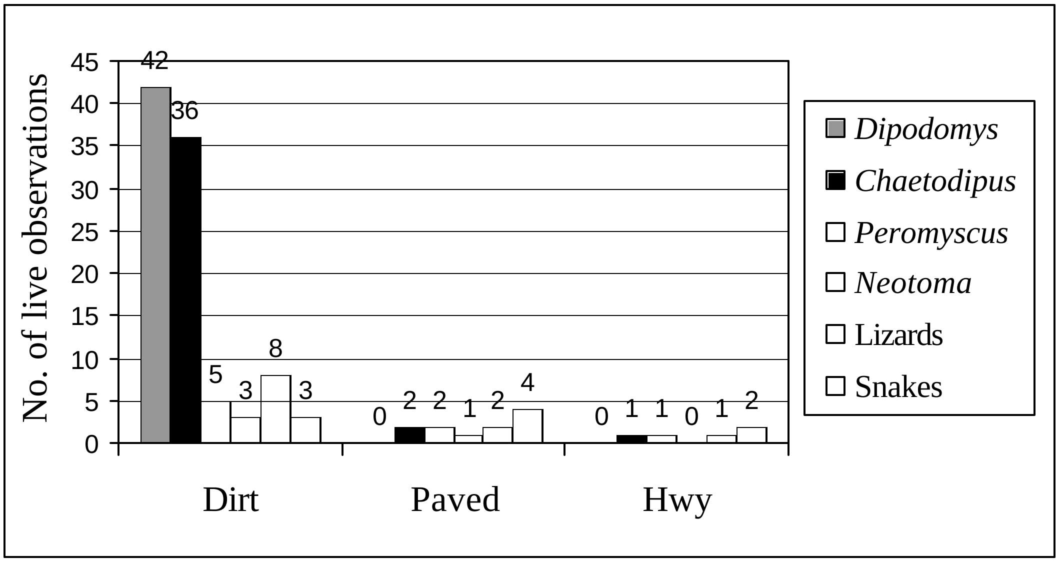


Fig. 18. Total number of live observations of small mammals and reptiles on the roads during the course of the study.

also many (36) observations of the San Diego pocket mouse, *C. fallax*, on the dirt road. Of these, most were observed in the spring, sitting or running along the side of the road, and many appeared to be juveniles. Only three pocket mice were observed on the paved roads (2 secondary road and 1 highway), and all were running alongside the edge of the road. Woodrats (*Neotoma* sp.) and white-footed mice (*Peromyscus* sp.) were observed in fewer numbers overall, almost always running directly across the roadways.

Most of the lizard observations (7/10) consisted of western fence lizards, *S. occidentalis*, running along or across the dirt road during the day. The other three observations were of an orange-throated whiptail (*C. hyperythrus*) and a California whiptail (*C. tigris*) on the secondary paved road and a side-blotched lizard (*U. stansburiana*) on the highway. Snakes were the only group that did not show a decreasing trend in activity from the dirt road to the highway, but there were only a total of nine observations. A king snake (*L. getulus*), striped racer (*M. lateralis*) and gopher snake (*P. melanoleucus*) were observed on the dirt road. Four red diamond rattlesnakes (*C. ruber*) were observed on the secondary paved road and a single *L. getulus* and *C. ruber* were observed on the highway. All were crossing the road or basking alongside.

The number of dead animals observed on the roads exhibited the opposite trend. Road mortality increased for both small mammals (Fishers exact test, p<.001) and reptiles (Fishers exact test, p=.009) with increased improvement of the road (Table 5, Fig. 19). The dead animals found on the highway consisted of four snakes (3 *Crotalus viridis* and one *Lampropeltis getulus*), three kangaroo rats (*D. simulans*), 2 pocket mice (*C. fallax*), 1 white-footed mouse (*Peromyscus sp.*), one woodrat (*Neotoma sp.*), and one side-blotched lizard (*U. stansburiana*). On the secondary paved road, two snakes (*C. viridis* and *Pituophis melanoleucus*), two fence lizards (*S. occidentalis*), and one woodrat (*Neotoma fuscipes*) were found dead. One kangaroo rat (*D. simulans*) was found dead on the dirt road.

Table 5
Results of contingency analyses to determine if the proportion of live versus dead animals were different for the three road types

Species	n	Statistical Analysis (Exact Test p-values)			
		All Roads	Dirt vs. Secondary	Dirt vs. Primary	Secondary vs. Primary
Small Mammals	100	.000*	.126	.000*	.059
Reptiles	28	.009*	.035*	.011*	.419

*mean difference is significant at the 95% confidence level

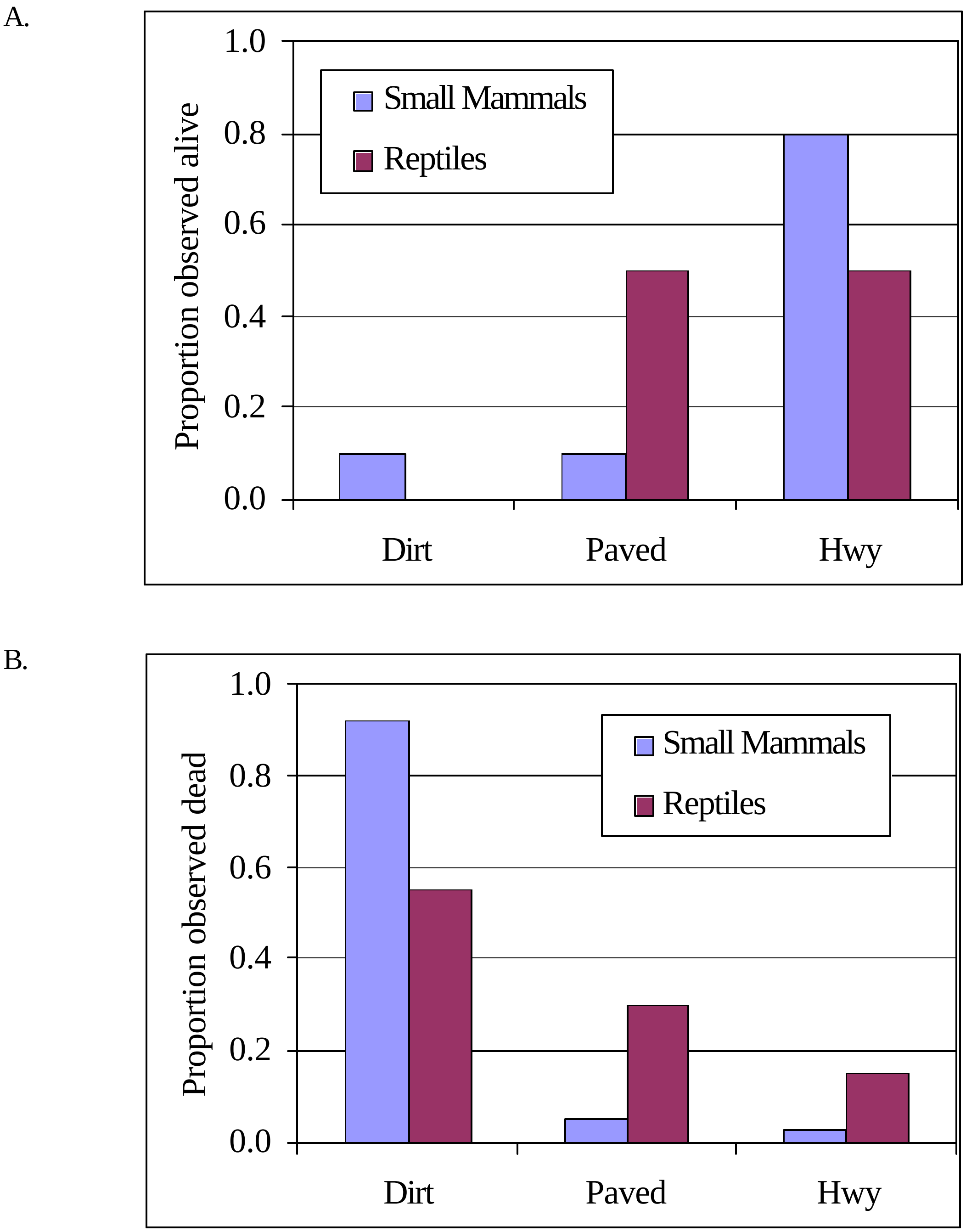


Fig. 19. Proportions small mammals and reptiles observed alive (A) and dead (B) on each of the three road types. Proportions were calculated by dividing the number of observations on each road type by the total number of observations on all roads.

DISCUSSION

Data were generated on six animal species. These were a combination of habitat generalists and specialists from two different animal taxa: small mammals and reptiles. Habitat generalists are defined as occurring in many habitat types over a wide geographic range, while habitat specialists are primarily restricted to a single habitat type and have a relatively small geographic range. Of the small mammals studied, two peromyscine rodents, *Peromyscus eremicus* and *P. maniculatus*, are habitat generalists. *Peromyscus maniculatus* is found throughout North America in a multitude of habitat types including alpine, northern boreal forest, desert, grassland, brushland, southern montane woodland, and arid upper tropical habitats (King 1968). *Peromyscus eremicus* is common in desert shrub and riparian habitats throughout the southwestern United States, north central Mexico, and Baja California (Veal and Caire 1979). The two heteromyids, C*haetodipus fallax* and *Dipodomys simulans*, on the other hand, are habitat specialists and primarily occur in coastal sage scrub habitats in southwestern California and northern Baja California (Schmidly et al. 1993, Lackey 1996). Of the two most frequently captured lizard species, *Sceloporus occidentalis* is the habitat generalist. This species is distributed throughout eastern Oregon, southwest Idaho, all of Nevada, western Utah, Southern California, and northwestern Baja California. It is commonly found from the coast to the highest mountain areas at over 6,000 feet. It thrives in a wide variety of low and high elevation habitats, including grassland, scrub, chaparral, woodland, and forested areas (Stebbins 1985). In contrast, *Cnemidophorus hyperythrus*, is a relative specialist existing primarily in coastal sage scrub and open chaparral habitats in southern California and Baja (Stebbins 1985). All of these species have relatively small home ranges averaging between 0.1 and 0.4 hectares (Storer et al. 1944; MacMillen 1964; Bostic 1965; Davis and Ford 1983). These species are discussed individually below.

Individual Species

Twenty-eight percent of the San Diego pocket mice, *Chaetodipus fallax,* and 25% of the cactus mice, *Peromyscus eremicus*, ventured out onto the dirt road. Using a random movement model, Stamps *et al.* (1987) predicted that a permeability of approximately 38%

reflects a habitat with no physical or psychological barriers to movement across the boundary. Thus, the dirt roads were not substantial boundaries to movement. These road movements were primarily direct crossings to the habitat on the other side of the road, indicating that the road was not used as a conduit for movement. Although they live in open scrub habitats, *C. fallax* and *P. eremicus* are known to prefer shrub and rock cover to open habitat (Meserve 1976; Price and Waser 1984). Thus, they may quickly pass through or avoid vast areas of open space. In contrast to the dirt road, there were no documented movements of either species across the secondary paved road or highway, even though the distances required to cross either road were well under the average tracked distances of the species. A single *P. eremicus* was documented crossing the road on two occasions, in June and July, indicating the road was within its home range. This indicates that both paved roads acted as boundaries for individual home ranges, while the dirt road likely fell within individual home ranges. In comparison to the dirt road, the secondary paved road differed by an average width of two meters, the addition of pavement, and an increased traffic volume averaging one vehicle every five minutes. It is unknown which of these factors or combination thereof resulted in their aversion to cross this road. Night-time road observations supported the tracking results for relative road permeability. The proportion of both rodent species observed on the roads decreased from the dirt road to the secondary paved road and highway, respectively. Although the proportion of observations on the dirt road were proportionately higher for *C. fallax* than *P. eremicus*, the majority of *C. fallax* observations occurred primarily in the early spring and appeared to be juveniles. After June, the number of sightings of both species was roughly equal. Thus, the dirt roads may be more permeable to juveniles of *C. fallax* than to adults.

Although their behavioral responses to the roads were similar, *C. fallax* and *P. eremicus* had different abundance patterns in roadside habitats. *Chaetodipus fallax* did not differ in abundance with the two distances from the secondary road and highway, indicating that the improved roadside habitats were not avoided or preferred. Interestingly, abundance did differ by distance from the dirt road. A significantly lower number of pocket mice were captured next to the dirt road trapping arrays compared to the interior arrays. In concert with this, there were proportionately more juveniles captured close to the dirt roads. Similar age structure responses to edges have been documented with gray-tailed voles *(Microtus* *canicaudus*, Lidicker and Peterson 1996). This indicates that the habitat adjacent to dirt roads may have been perceived as suboptimal to adult mice and may be associated with higher predation risk by the dirt road. Studies of carnivores on site showed increased coyote activity on the dirt roads in comparison to the adjacent highway (Hathaway et al. 2003). Coyotes frequently use dirt roads for movement within a landscape where they may opportunistically hunt small mammals (May and Norton 1996). In addition, more owls were observed perching or flying near the dirt road at night than were observed by either of the paved roads.

In contrast to *C. fallax*, the abundance of *P. eremicus* in roadside habitat was highly correlated to the abundance of California sage, *Artemisia californica*, a food plant (Meserve 1976), but had no relation to distance from any of the roads. In a study of effects of a highway on Mojave Desert rodent populations, Garland and Bradley (1984) found similar results for this species. Abundance of *P. eremicus* was correlated with abundance of *Yucca*, presumably used as nesting sites, but was not affected by proximity to the road.

The deer mouse, *Peromyscus maniculatus*, exhibited increased abundance in the habitat close to the highway, but no individuals were documented traveling onto the highway. This species is often captured in high numbers near urban edges or disturbed CSS habitats in southwestern San Diego County (pers. obs). For *P. maniculatus*, the road verge may provide suitable habitat and a serve as connecting route to other suitable habitat patches. Interestingly, the increase in *P. maniculatus* abundance by the highway did not result in a decrease in *P. eremicus* abundance. This indicates that the two may differ in some aspect of resource utilization. Meserve (1976) found that the two species shared many of the same dietary preferences, but a significant proportion of *P. eremicus* activity took place up in the shrub layer while all *P. maniculatus* activity occurred on the ground. The fluorescent dye tracks showed similar patterns of space in use in this study.

The Dulzura kangaroo rat, *Dipodomys simulans*, may have exhibited an alternate pattern of road use than the other small mammals. However, there were insufficient data to test this hypothesis. In contrast to the quadrapedal heteromyids (*Chaetodipus*), the bipedal heteromyids (*Dipodomys*) are known to prefer open areas of scrub habitats (Rosenzweig and Sterner 1970; Meserve 1976; Brown and Harney 1993; Price and Kramer 1984). There is reason to suspect that these animals do not avoid roads. Although there were relatively few captures of *Dipodomys*, they accounted for the majority of observations on the dirt roads, where they were frequently seen running along and across the roads. All individuals that were tracked (three dirt road, one secondary paved) went out onto the roads and in the first few years after the construction of the secondary paved road, it was reported that one could not drive down the road at night without running over numerous kangaroo rats (Millar Ranch road resident, observation). This species also accounted for the greatest number of road kill observations of small mammals on the highway. The trapping methodology used in this study has been shown to be highly effective in capturing *Dipodomys* (McClenaghan and Taylor 1993**,** Meserve 1976a, 1976b), so the lack of capture success should reflect a relatively low abundance of *Dipodomys* in the adjacent habitat. All together, these observations support the theory that *D. simulans* do not avoid roads, but may even use them as a conduit for movement. Price and Waser (1984) documented significant increases in abundance of *D simulans* (formerly *D. agilis*) in early successional burned sites compared to unburned sites. In coastal sage scrub, the density of vegetation is usually dependent upon the recency of fire. Dirt roads and trails may provide marginal habitat in denser scrub habitat and allow for increased potential for dispersal to newly created open scrub habitats. Under this hypothesis, dirt roads may have positive effects on population demographics of this species while heavily trafficked paved roads would certainly have negative effects.

The western fence lizard, *S. occidentalis*, had approximately double the permeability to the dirt (66%) and secondary paved roads (44%) than either of the mice. Its movements out onto the dirt road consisted of a mixture of crossings and movements down the road, indicating that they also used the road as a conduit for movement. Interestingly, most tracked movements onto the secondary paved road consisted of long distance, often irregular, movements along the road, suggesting that the paved road may have been used for basking, as well as a conduit for movement. The complete absence of movements out onto the highway was in stark contrast to this species' response to the other two roads. Because of the average track length and this species' response to the secondary paved road, there is no evidence to suggest that the width of the highway or the substrate resulted in the decreased permeability. The 40 to 90-fold increase in traffic volume resulting in an almost constant stream in traffic, however, may have been sufficient to deter road use. Again, road riding observations supported the tracking data. The greatest number of live observations were made on the dirt road, while the greatest number of road kills were documented on the paved road. There were no live or dead observations of this species on the highway, further substantiating avoidance of this road. Distance from the road was not a significant indicator of *S. occidentalis* abundance in roadside coastal sage scrub habitat.

The abundance of the orange-throated whiptail, *Cnemidophorus hyperythrus*, was highly variable in the roadside habitat. Abundance was positively correlated with perennial plant diversity which is consistent with its habitat and food requirements (Rowland 1992), however, this did not explain most of the variability between road sites. Ver Hoef et al. (2001) found the abundance of *C. hyperythrus* in southern California was correlated to the abundance of *Crematogaster* ants and sandier soils. Although these parameters were not measured in this study, a recent biodiversity inventory of Rancho Jamul (Hathaway et al. 2003) showed that the ants and soils were present at the dirt road sites where very few of these animals were captured. Thus, it is unknown what landscape level factors may have caused these discrepancies in capture rates among sites. In respect to distance from roads, abundance was significantly reduced adjacent to the paved road and highway versus the interior. Although not significant, abundance was also reduced next to the dirt roads. These results indicate that the lizard may avoid habitat adjacent to roads, but the reasons for this are unclear. Although no individuals were tracked by the dirt roads, *C. hyperythrus* is commonly found along trails and dirt roads (Brattstrom 2000), so it is likely that permeability to these types of roads high. Thirty-three percent of the individuals tracked went out onto the paved road. In contrast with *S. occidentalis*, these were direct crossings. This may be consistent with the animal's tendency to forage under plant cover (Bostic 1966b**,** personal observations of tracked movements). Like *S. occidentalis*, there were no movements recorded onto the highway, even though a high number of individuals (24) were tracked.

The data on snakes were sparse, due to few captures and a low success in tracking for long enough distances with fluorescent powder. Snakes were observed roughly equally on the three roads, either crossing or basking on the side of the road. They did, however, comprise the majority of road kill observations on the secondary road and highway.

Limitations

There are several limitations to the interpretation of these data. First, because of the limitations of the study area, there were either no or insufficient replicates for the factor of road type. The study encompassed approximately 2 km of dirt roads within a reserve, approximately 1 km of the same secondary paved road, and two groupings of trapping arrays along 10 km of a single rural highway. Because of the lack of replication and the spatial correlation of arrays within road types, no attempt was made to interpret road-to-road differences in abundance. In contrast to the large scale landscape variables which may affect direct road-to-road comparisons in habitat abundance, distance (0 vs. 60 m from a road) and road use are finer-scale responses to roads**.** Because of this, I interpret these effects both within and between road types. Since there were no differences in any of the vegetation indices when comparing distance within a road or the effect of distance between roads, it is reasonable to conclude that these results are most likely due to the attributes of the road itself. In the case of behavioral responses (i.e. permeability) to the three roads, animals are thought to directly respond to the habitat edge in the landscape (Stamps et al. 1987) and thus would be responding to the unique characteristics of each road. These characteristics include road matrix (dirt or pavement), road width, and traffic volume.

The fluorescent powder was effective for monitoring short distance movements, with an average track length of approximately 20 m. This was sufficient distance for each animal to cross any of the roads. This does not mean that the animal never crosses the road. A study comparing track methods found that radiotelemetry documented a 50% road crossing rate over 30 days for two species of mice (*Peromyscus maniculatus* and *Reithrodontomys fulvescens*) versus a 3% crossing rate when using fluorescent powder for a single night (Clark et al. 2001). Thus, when tracking an animal over a longer period of time, more road crossings would be expected. Unfortunately, there were several problems with these data which make direct comparisons impossible. First, data for the two tracking methods were collected in different seasons and in different years. Second, powder tracks were not followed from point of release. Instead, the roads were scanned for dye and therefore it is unknown what distances the tracks could have been followed. Thirdly, a pocket black light was used to scan for the dye. In my preliminary tests, I found these to be very ineffective in following the dye for over a few meters and found only a modified 12 watt long-wave ultraviolet light to be adequate. Therefore, the low number of documented crossings by Clark et al. (2001) was probably an artifact of inadequate sensitivity. Nonetheless, the relative permeability to different roads showed the same pattern using either method. However, the use of fluorescent dye also allows for documentation of fine-scale movement activity that telemetry does not (Lemen and Freeman 1985). In this study, I was able to document species' direct responses to roads, including movements along the habitat edge, direct road crossing events, as well as movements along a road.

There were insufficient data to document factors that may affect road permeability within a species, such as season, density, age, and/or sex related differences. The differential abundance of juveniles by the dirt road exhibited by *C. fallax* is an indication that these intraspecific differences may exist. Density has been documented to affect road permeability in some species (Swihart and Slade 1984). Although the relationship between density and road permeability could not be tested in this study, the numbers of *C. fallax*, *P. eremicus*, and *S. occidentalis* captured by each type of road were not different within species. This allowed for calculation of relative permeability among roads without confounding density differences.

For roadside habitat, relative abundance was measured at two distances from the roadways, 0 and 60 m. In much literature, it has been estimated that roads can affect habitat up to hundreds of meters from the road (Saunders et al. 2002). This could mean that the interior distance analyzed in this study may have not been sufficient to truly test species responses to the road or to capture species that avoid any area greater than 60 m from a road. However, most of these higher estimates have been in forested or aquatic ecosystems (Forman 2000). Roads in forested areas result in increased exposure to sun and wind, resulting in vegetative differences near road edges. For open scrub vegetation, these factors are likely to have minimal depth of influence into the adjacent habitat. In this study, I found no difference in seven vegetation indices in relation to proximity to the three roads. On high traffic roads, however, road noise and chemical deposition could have farther reaching effects (Trombulak and Frissell 2000).

Overall Trends

All of the species that were sufficiently captured and tracked in this study (*C. fallax, P. eremicus, S. occidentalis,* and *C. hyperythrus*) exhibited the same basic response to the roads. They all increasingly avoided more improved roads. In general, they did not avoid crossing dirt roads and many animals likely incorporated these roads within their home ranges. Small mammals generally avoided crossing the secondary paved road, while the lizards did not. However, all species exhibited a strong aversion to the highway. To my knowledge and from a recent review on responses of reptiles to roads (Jochimsen and Peterson, *in press*), this is the first study to document road avoidance in lizards. Since these animals all increasingly avoided roads with increased traffic volume, this may indicate that they are perceived as acute sources of disturbance. Avoidance behavior of this type of disturbance may be innate, learned, and/or the result of intense selection pressure. Even though significantly lower number of animals went out onto the improved roads, the ones that did suffered a higher proportion of mortality due to vehicular traffic. Along the highway, a single species (*P. maniculatus)*, showed the combined response of road avoidance with increased abundance in the habitat immediately adjacent to the road. This indicates this species may use the habitat adjacent to the road as a movement corridor. *Peromyscus maniculatus* has the largest range of all species here and this type of behavioral response may benefit this species in finding and occupying new habitat patches without resulting mortality from vehicular traffic.

Habitat specialization did not appear to correlate with road permeability for the species monitored in this study, but may have a negative association with relative abundance in the roadside habitat (Table 6). The two specialists with adequate roadside habitat abundance data (*C. fallax, C. hyperythrus*) both exhibited decreased abundance next to a road, albeit their responses to different road types varied. This is in contrast to the generalists *(P. eremicus, P. maniculatus, and S. occidentalis),* which either had no change in abundance or increased abundance in habitat immediately adjacent to the roadways. Although there were too few species to test this hypothesis, these results generally support previous studies that conclude habitat specialists are more sensitive to edges (see review by Lidicker and and Koenig 1996). For road permeability, I suggest that microhabitat utilization may be more

Table 6
Space-use behavior versus abundance in roadside habitat

Species	Behavior		Roadside Habitat Abundance[1]		
	Habitat use	Microhabitat use	Unimproved dirt	Secondary paved	Primary highway
P. eremicus	Generalist	Closed	ND	ND	ND
P. maniculatus	Generalist	Closed	ND	ND	↑311%
C. fallax	Specialist	Closed	↓45%	ND	ND
S. occidentalis	Generalist	Open/closed	ND	ND	ND
C. hyperythrus	Specialist	Open/closed		↓30%	↓37%

[1] Percent change between roadside and interior habitat abundance
ND= No difference between roadside and interior habitat abundance

Table 7
Space-use behavior versus road permeability[1]

Species	Behavior		Road Permeability[1]		
	Habitat use	Microhabitat use	Unimproved dirt	Secondary paved	Primary highway
P. eremicus	Generalist	Closed	33.3	0	0
P. maniculatus	Generalist	Closed			0
C. fallax	Specialist	Closed	37.5	10.5	0
D. simulans	Specialist	Open	100.0[2]		
S. occidentalis	Generalist	Open/closed	66.7	44.4	0
C. hyperythrus	Specialist	Open/closed		33.3	0

[1] Proportion of animals that went out onto the roadways.
[2] (n=3)

important as a predictive factor (Table 7). Animals that are more likely to use open spaces for foraging or movement within a landscape may be more likely to venture out onto roads or to use them as movement corridors. These may be open habitat specialists or multi-habitat generalists. In this study, the three species (*D. simulans, S. occidentalis, C. hyperythrus*) known to use open areas of habitat for foraging and/or thermoregulation ventured out onto dirt and secondary paved roads a greater proportion of times than the species (*P. eremicus, C. fallax*) that are known to prefer cover.

In relation to the two-lane rural highway, all three of the mice and the two lizard species in this study appeared to perceive this as a boundary, regardless of their habitat preferences. Some animals may not avoid these roads, but there are several reasons why it might have been difficult to document this response. First, since the roads I studied have been in existence for greater than 10 years, the species that do not avoid roads may have already experienced a decline in population numbers, and thus were not captured in sufficient numbers. I believe from my sparse data and anecdotal observations by others that this may have been the case for the Dulzura kangaroo rat, *D. simulans*. This may also be the case for amphibian populations that must cross a road to move between upland and breeding sites. Although, in the case of this study, a year of low rainfall precluded monitoring of amphibian abundance. Second, many species may not avoid roads because of large home range requirements. These species are typically less abundant than those with smaller home ranges and thus would not have been captured in high enough numbers for statistical analysis in this study.

From this and previous data, one would predict that closed habitat specialists would be in most danger of becoming fragmented by the presence of a road. However, even these species may cross roads in order to meet resource requirements. In contrast, habitat generalists and open habitat specialists would be more likely to use roads for activity and conduits for movement. However, even these species may avoid heavily trafficked highways. Habitat use characteristics and, thus, road use behaviors may also vary within species. These may vary according to season, age, sex, population density, food availability, predation risk, and inter and intra-specific competition. Since reptiles typically use open habitats and heat absorbent elements of the landscape for basking, even if they forage in closed habitats, they may be a more likely taxon to use roads in their daily activity. Further research and a review of published data are needed to test these hypotheses.

MANAGEMENT RECOMMENDATIONS

These results indicate that even a simple 2-lane rural highway through coastal sage scrub habitat is sufficient to result in substantial road avoidance behavior in many species. These conclusions are not limited to highways, per se, as the width and traffic volume of the highway in this study are similar to many roads that are considered secondary roads. Avoidance of improved roads may be a beneficial response by many species in that increased mortality from vehicular traffic is avoided or minimized. However, matrices of roads throughout the landscape may divide habitat into fragments that are too small to sustain some populations over the long term (MacArthur and Wilson 1967). To reduce the effects of habitat fragmentation resulting from this, the availability of corridors or safe-crossing structures are needed (see reviews by Yanes et al. 1995, Jochimsen and Peterson *in press*). For those species which cannot or do not avoid roads, the use of barrier fencing along primary and secondary roadsides would be necessary to reduce road mortality and the possibility of species extirpation from the adjacent natural areas. Boarman and Sazaki (1996) found 88% fewer vertebrate carcasses along 24 km of a fenced highway in comparison to 24 km of a non-fenced highway in the Mojave Desert. They also found that many small-to-medium sized vertebrates, including coyote, fox, jackrabbit, ground squirrels, kangaroo rats, snakes, lizards, and desert tortoises used culverts along the fenced section to safely cross the highway.

In contrast to primary and secondary roads, low traffic dirt roads may be a beneficial for maintaining or enhancing movement for early successional facultative or obligate species (Litvaitis 2001), such as *Dipodomys simulans*. In coastal sage scrub habitat, most species in this study did not appear to negatively respond to these roads. However, even these roads may negatively affect some species that avoid all open areas or suffer increased mortality by opportunistic predators. Thus, management decisions should depend upon focal species.

More research is needed to characterize predictive traits of species and individuals to different road types. With a set of predictive traits, management efforts can immediately focus on those species that may benefit or are at most risk of extirpation from the presence of roads within their habitat. For well-trafficked roads in all habitats, particular conservation attention should be paid to large mammals, snakes, and amphibians. In coastal sage scrub habitat, the response of kangaroo rats to different road types deserves further study.

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APPENDIX

GPS COORDINATES FOR TRAPPING ARRAYS

GPS Data Format Deg NAD83

Road Type	Array	Distance	Latitude	Longitude
Unimproved dirt	1	Far	32.6650	-116.8499
		Near	32.6648	-116.8504
	2	Far	32.6662	-116.8502
		Near	32.6661	-116.8508
	3	Far	32.6674	-116.8518
		Near	32.6674	-116.8513
	4	Far	32.6688	-116.8507
		Near	32.6686	-116.8512
	5	Far	32.6735	-116.8529
		Near	32.6732	-116.8528
	6	Far	32.6730	-116.8553
		Near	32.6725	-116.8553
	7	Far	32.6732	-116.8558
		Near	32.6727	-116.8560
	8	Far	32.6693	-116.8566
		Near	32.6690	-116.8561
Secondary paved	9	Far	32.7292	-116.9391
		Near	32.7294	-116.9398
	10	Far	32.7283	-116.9402
		Near	32.7286	-116.9398
	11	Far	32.7288	-116.9389
		Near	32.7285	-116.9392
	12	Far	32.7285	-116.9381
		Near	32.7282	-116.9385
	13	Far	32.7265	-116.9363
		Near	32.7267	-116.9357
	14	Far	32.7254	-116.9332
		Near	32.7251	-116.9336
	15	Far	32.7250	-116.9329
		Near	32.7247	-116.9333
	16	Far	32.7247	-116.9321
		Near	32.7242	-116.9327
Primary highway	17	Far	32.7290	-116.9004
		Near	32.7284	-116.9001
	18	Far	32.7286	-116.9010
		Near	32.7283	-116.9009
	19	Far	32.7286	-116.9016
		Near	32.7281	-116.9015
	20	Far	32.7286	-116.9028
		Near	32.7281	-116.9027
	21	Far	32.6819	-116.8416
		Near	32.6823	-116.8412
	22	Far	32.6801	-116.8409
		Near	32.6801	-116.8404
	23	Far	32.6780	-116.8402
		Near	32.6783	-116.8399
	24	Far	32.6767	-116.8392
		Near	32.6771	-116.8387

ABSTRACT

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I assessed the activity pattern of small mammals and lizards in relation to three types of roads transecting coastal sage scrub habitats. The bulk of data were generated for three small mammal species (*Chaetodipus fallax, Peromyscus eremicus*, and *Peromyscus maniculatus*) and two lizard species (*Sceloporus occidentalis* and *Cnemidophorus hyperythrus*). I characterized both relative abundance at two distances from each road and individual movement patterns in relation to each road in order to explore the effects of roads on species spatial and movement dynamics. The two habitat specialists exhibited decreased abundance next to different road types. The three habitat generalists either showed no difference or increased abundance by a road. These data generally support previous studies that suggest habitat specialists are more sensitive to edges. All species exhibited decreased permeability to improved roads. The unimproved dirt road did not impede movement, while the primary highway was a barrier for all species. Responses to the secondary paved road differed among species. I suggest that species with open microhabitat preferences are more likely to venture out onto unimproved dirt and secondary paved roads. Those that did venture out onto improved roads suffered increased mortality due to vehicular traffic.

ABSTRACT OF THE THESIS

Responses of Terrestrial Vertebrates to Roads in a Coastal Sage Scrub Ecosystem

by
Cheryl Shaffer Brehme
Master of Science in Biology
San Diego State University, 2003

I assessed the activity pattern of small mammals and lizards in relation to three types of roads transecting coastal sage scrub habitats. The bulk of data were generated for three small mammal species (*Chaetodipus fallax, Peromyscus eremicus,* and *Peromyscus maniculatus*) and two lizard species (*Sceloporus occidentalis* and *Cnemidophorus hyperythrus*). I characterized both relative abundance at two distances from each road and individual movement patterns in relation to each road in order to explore the effects of roads on species spatial and movement dynamics. The two habitat specialists exhibited decreased abundance next to different road types. The three habitat generalists either showed no difference or increased abundance by a road. These data generally support previous studies that suggest habitat specialists are more sensitive to edges. All species exhibited decreased permeability to improved roads. The unimproved dirt road did not impede movement, while the primary highway was a barrier for all species. Responses to the secondary paved road differed among species. I suggest that species with open microhabitat preferences are more likely to venture out onto unimproved dirt and secondary paved roads. Those that did venture out onto improved roads suffered increased mortality due to vehicular traffic.