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Permeability of Roads to Movement of Scrubland Lizards and Small Mammals

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Abstract: *A primary objective of road ecology is to understand and predict how roads affect connectivity of wildlife populations. Road avoidance behavior can fragment populations, whereas lack of road avoidance can result in high mortality due to wildlife-vehicle collisions. Many small animal species focus their activities to particular microhabitats within their larger habitat. We sought to assess how different types of roads affect the movement of small vertebrates and to explore whether responses to roads may be predictable on the basis of animal life history or microhabitat preferences preferences. We tracked the movements of fluorescently marked animals at 24 sites distributed among 3 road types: low-use dirt, low-use secondary paved, and rural 2-lane highway. Most data we collected were on the San Diego pocket mouse (*Chaetodipus fallax*), cactus mouse (*Peromyscus eremicus*), western fence lizard (*Sceloporus occidentalis*), orange-throated whiptail (*Aspidoscelis hyperythra*), Dulzura kangaroo rat (*Dipodomys simulans*) (dirt, secondary paved), and deer mouse (*Peromyscus maniculatus*) (highway only). San Diego pocket mice and cactus mice moved onto dirt roads but not onto a low-use paved road of similar width or onto the highway, indicating they avoid paved road substrate. Both lizard species moved onto the dirt and secondary paved roads but avoided the rural 2-lane rural highway, indicating they may avoid noise, vibration, or visual disturbance from a steady flow of traffic. Kangaroo rats did not avoid the dirt or secondary paved roads. Overall, dirt and secondary roads were more permeable to species that prefer to forage or bask in open areas of their habitat, rather than under the cover of rocks or shrubs. However, all study species avoided the rural 2-lane highway. Our results suggest that microhabitat use preferences and road substrate help predict species responses to low-use roads, but roads with heavy traffic may deter movement of a much wider range of small animal species.*

Keywords: avoidance, connectivity, conservation planning, habitat fragmentation, heteromyid, reptiles, road ecology, urban ecology

Resumen: *Un objetivo principal de la ecología de caminos es entender y predecir como afectan los caminos la conectividad de las poblaciones silvestres. El comportamiento de evitación de caminos puede fragmentar poblaciones, mientras que la falta de evitación puede resultar en alta mortandad debido a colisiones. Muchas especies animales pequeñas enfocan sus actividades a microhábitats particulares dentro de su hábitat mayor. Buscamos estudiar como los diferentes tipos de caminos afectan el movimiento de pequeños vertebrados y conocer si ciertas respuestas hacia los caminos pueden ser predecibles basándose en la historia de vida del animal o el microhábitat. Rastreamos los movimientos de animales marcados con fluorescencia en 24 sitios distribuidos entre 3 tipos de caminos: tierra de bajo uso, camino secundario pavimentado de bajo uso, y carretera rural de 2 carriles. La mayoría de los datos que colectamos fueron sobre* Chaetodipus fallax, Peromyscus eremicus, Sceloporus occidentalis, Aspidoscelis hyperythra, Dipodomys simulans *(tierra, pavimentación secundaria), y* P. maniculatus *(solamente en carretera).* C. fallax *y* P. eremicus *se movían hacia los caminos de tierra pero no hacia una carretera de baja pavimentación de anchura similar o hacia la carretera, indicando que evitan los caminos con sustrato pavimentado.* S. occidentalis *y* A. hyperythra *se movían hacia la tierra y los caminos secundarios pavimentados pero evitaban la carretera rural de 2 carriles, indicando que pueden evitar el ruido, las vibraciones o el disturbio visual de un constante flujo de tráfico.* D. simulans *no evitaba el camino de tierra ni los caminos secundarios con pavimento. En general, el camino de tierra y los caminos*

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secundarios fueron más permeables para las especies que prefieren forrajear o tomar el sol en áreas abiertas de su hábitat en lugar de bajo rocas o arbustos. D. simulans *no evitó el camino de tierra ni los caminos secundarios pavimentados. Sin embargo todas las especies estudiadas evitaron la carretera de 2 carriles. Nuestros resultados sugieren que las preferencias de uso de microhábitat y sustrato de caminos ayudan a predecir las respuestas de las especies hacia caminos de bajo uso, pero los caminos con tráfico pesado pueden disuadir el movimiento de un rango mucho mayor de especies animales pequeñas.*

Palabras Clave: conectividad, ecología de caminos, ecología urbana, evitación, fragmentación de hábitat, heterómido, planificación de la conservación, reptiles

Introduction

Terrestrial and aquatic areas have become increasingly permeated by roads. Roads affect movement patterns, demographics, and spatial distribution of local species. They can adversely affect wildlife by fragmenting habitats, creating population sinks, and acting as conduits for the spread of invasive species (e.g., Forman et al. 2003; Fahrig & Rytwinski 2009; Taylor & Goldingay 2010). They can positively affect wildlife by increasing connectivity between suitable habitat patches and food resources (e.g., Huey 1941; Getz et al. 1978; Forman et al. 2003).

A current need in the field of road ecology is to understand and predict how roads affect the probability wildlife populations will persist (Roedenbeck et al. 2007; Fahrig & Rytwinski 2009; Rytwinski & Fahrig 2012). This will likely require the development of demographic and spatial-movement models that incorporate behavioral responses to roads (e.g., Jaeger et al. 2005; Tracey 2006; Frair et al. 2008). Roads are highly variable, ranging from rarely traveled dirt roads to multilane highways with heavy traffic. Correspondingly, the responses of animals to different road types are expected to be highly variable.

To address variation in animal responses to different road attributes and traffic patterns, Jaeger et al. (2005) incorporated 3 types of road-specific avoidance behavior (road-surface avoidance related to road substrate and width, and, noise and car avoidance related to traffic) in their model for predicting when animal populations are at risk from roads. However, data to test these models are lacking because much of the current literature on road-related movement behavior typically focuses on either a single species or road type (e.g., Fahrig & Rytwinski 2009; Taylor & Goldingay 2010). There are also relatively few data available on reptiles, although this taxon is thought to be substantially and negatively affected by roads (Andrews et al. 2008). Finally, few researchers have incorporated both multiple road types and taxonomic classes in their studies to ascertain how animal communities respond to these linear features of the landscape.

Scrublands are distributed throughout mid-latitude deserts and areas with Mediterranean-type climates. Scrublands are characterized by low-growing shrubs adapted to arid conditions and range from open habitats with sparse vegetation cover to areas with dense vegetation (Kellman 1980). Our study area was in coastal sage scrubland of southern California (U.S.A.). Much of this area is fragmented by urbanization, disturbed, or permeated with highways, secondary roads, dirt roads, and trails (O'Leary 1995; Noss et al. 2000).

We sought to understand how roads affect habitat connectivity for small vertebrate populations within these scrublands. We assessed the movement patterns of 4 small-mammal species and 2 lizard species relative to 3 types of roads: low-use dirt roads, a secondary paved road, and a primary paved highway. We also examined whether animal responses to roads differed among species with different life-history strategies and whether species' microhabitat-use preferences could be used to predict their responses to roads.

Methods

Study Site

Our study area was in 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 the California Department of Fish and Game. The coastal sage scrub (CSS) vegetation was dominated by California sagebrush (*Artemisia californica*), buckwheat (*Eriogonum fasciculatum*), and a variety of herbs and grasses. The region has a Mediterranean-type climate characterized by hot, dry summers and cool, wet winters. Average annual precipitation is 350 mm, and approximately 95% of the annual mean rainfall occurs from November through April. The CSS vegetation averaged 63% shrub cover, 30% grass and herb cover, and 28% open ground (total greater than 100% due to measures at multiple height categories [Brehme 2003]). There were 3 road types in the study area: 1.8 km of low-use unimproved dirt roads with an average width of 4.7 m (SD 1.3) and traffic volume of 0–20 vehicles/day; a 1.6-km low-use, secondary, 2-lane paved road (Millar Ranch Road) with an average width of 6.6 m (SD 0.2) and traffic volume of 200–500 vehicles/day (Traffic Section of San Diego County Public Works); and over 24 km of high-use, primary, 2-lane paved highway (State Highway 94) with an average width of 11.2 m (SD 0.9) and traffic volume of 7,400–18,000 vehicles/day

(California Department of Transportation). Road widths were measured as the width of grading for dirt roads and width of pavement for paved roads. Native soil or vegetation extended to the road edge for all unimproved and improved road types. During the study, there was no evidence of mowing or other vegetation-management activities.

Data Collection

Eight linear trapping arrays were installed along the length of each of the 3 road types. We chose sites where CSS vegetation extended at least 50 m from both sides of the road to avoid confounding the presence of a road with any other edge. Linear trapping arrays consisted of 3, 9-L pitfall traps connected by a 15-m drift fence (7.5 m between each bucket), 4 Sherman live traps (along both sides of fence halfway between each bucket), and one funnel trap. We baited all traps with birdseed and rolled oats. Arrays were diagonal to the road to increase effectiveness of intercepting animals moving both parallel and perpendicular to the road. At one end of the array, the pitfall trap was 1 m from the road edge, and at the other end, the pitfall trap was 11 m from the road edge. The middle pitfall trap was 5 m from the road edge. Pitfall-array materials and installation procedures are described in Fisher et al. (2008). Trap arrays remained open during each trapping period and were checked every morning at sunrise. We conducted ten 3-night trapping sessions at each array from April to December of 2001.

We used fluorescent-powder tracking (Lemen & Freeman 1985; Fellers & Drost 1989) to track the movements of small mammals and reptiles captured in the trap arrays. The fluorescent powder (Radiant Color, Richmond, California, U.S.A.) is nontoxic and is a safe and effective means of tracking small-scale animal movements (Stapp et al. 1994). The powder-tracking technique allowed us to study species' direct responses to roads. Tracking movements over longer distances and periods of time (e.g., with radiotelemetry) would better document infrequent crossings, but the use of fluorescent dye allows for documentation of fine-scale movement activity that telemetry does not (Lemen & Freeman 1985).

To differentiate among individuals, we dusted each animal released from an array with 1 of 20 base colors or unique mixtures of base colors. We were careful to dust only the body and to avoid the head area to prevent the animal from breathing in the powder (Stapp et al. 1994). Prior to their natural activity period, we placed it on the lid of the center bucket 5 m from the road edge. This allowed for a standard release distance from the road for all animals without the drift fence acting as a barrier to movement in any direction. When releasing an animal, the handler crouched down parallel to the animal and the road, released the animal, slowly backed away staying parallel to the road, and then left the area. This release strategy was to prevent the handler from scaring the animal toward or away from the road. We traced the fluorescent powder tracks at night with a portable 12-watt long-wave ultraviolet lamp. We laid a 50-m measuring tape over the trail until the powder could no longer be traced. For each animal, we recorded the total distance of the fluorescent track and made a diagram of the animal's movements in relation to the road. We recorded locations of burrows where tracks ended at burrow entrances. We tracked the movement of most individuals only one time to avoid problems with pseudoreplication (Hurlbert 1984). We traced a small number of animals on several occasions to examine the variability of results for individuals. For these animals, only the result of their first tracking occasion was used in statistical analyses.

We categorized all movements as either road use or habitat use. Road use was when an animal moved over the road for any distance of the track length. Habitat use was when an animal stayed in the scrubland during the entire tracking period. We included in our analyses only animals tracked for a minimum of 10 m. For the Dulzura kangaroo rat (*Dipodomys simulans*), we included 2 movements of approximately 9.5 m because there were a low number of total tracks. Because all animals were released within 5 m of the road, this minimum track distance allowed us to document movements relative to the road or well away from the array in any direction. We calculated permeability as the number of animals that exhibited road use divided by the total numbers of animals tracked for each species and road type.

Analyses

To test whether animals avoided or used the roads more than expected by chance, we compared observed species movement paths with paths simulated from species-specific correlated random walk (CRW) models. The CRW models represent predicted movement without any behavioral response to the roads. We parameterized CRW models with tracking data from at least 3 individuals of each species. We used only paths within the interior scrubland and well away from the road to represent typical movements within an animal's habitat. We used recorded spatial coordinates at 1.0-m intervals along the path to calculate move and turn angles. The move angle was the direction of movement, and the turn angle was the angle of the current move step minus the angle of the previous move step.

We parameterized the simulations in 2 stages. First, for each individual animal's movement path, we estimated the mean turn angle and concentration parameter that determined the dispersion of a von Mises distribution (Fisher 1993). Second, we fitted a von Mises distribution to the mean turn angles for all paths and a gamma distribution to the concentration parameter of the turn angles for all paths. When simulating a path, we randomly drew a mean turn angle from the von Mises distribution and a concentration parameter from the gamma distribution. We added the turn angle to the move angle of the previous move step to obtain the move angle for the current move step. The move-step length was 1.0 m, and the total length was constrained to the average length of the observed paths for each species. We simulated 1000 paths for each species. To determine the expected number of animal movements onto roads if there was no barrier effect, we determined the number of CRW paths that transected a line 5 m from the start point. We parameterized and simulated all CRW models with a program written in R (R Development Core Team 2010). We compared the number of observed versus expected road movements with Fishers' exact tests. A significant result suggested the animals moved onto roads more or less than expected under the null hypothesis.

Individual animal movement behavior may be affected by population density (Swihart & Slade 1984; Hanski 1999). Therefore, we determined whether relative abundance differed among the roadside habitats with one-way analysis of variation for each species. For our index of species abundance, we used the minimum number of animals known alive. We calculated this index by removing all recaptures within each 3-day trapping session at each array. Although minimum number known alive can be biased as an abundance estimator, it is proportional to population sizes and is thus a reasonable index of abundance (Slade & Blair 2012).

Results

We dusted 306 animals with fluorescent powder and released them 5 m from the road edge. One-third of the animals were not included in our analyses because their track lengths were <10 m. Most of the small mammals that were not used in the analyses were tracked to a nearby burrow on the side of the road on which they were released, and there were no obvious tracks coming out of the burrow. Small reptiles and those with smooth scales (many snakes, skinks, side-blotched lizards [*Uta stansburiana*], and whiptails [*Aspidoscelis* spp.]) did not retain the powder dye well; thus, many of their tracks were lost within several meters. Some species were excluded due to too few captures. The 181 individuals we used in the analyses (125 small mammals, 56 lizards) were followed an average of 20.7 m (SE 0.8).

We also tracked 19 animals on a second occasion to test the repeatability of individual results. All these animals repeated their initial movement types. Seventeen (12 mammals and 5 lizards) stayed within the scrubland on both tracking occasions, whereas 2 (1 mammal and 1 lizard) repeatedly crossed the road. We present the results for 4 small mammal species and 2 lizard species. These species represent movements of 54 San Diego pocket mice (*Chaetodipus fallax*), 57 cactus mice (*Peromyscus eremicus*), 6 Dulzura kangaroo rats (dirt and secondary paved road only), 8 deer mice (*Peromyscus maniculatus*) (highway only), 26 western fence lizards (*Sceloporus occidentalis*), and 30 orange-throated whiptail lizards (*Aspidoscelis hyperythra*) (secondary paved road and highway only).

Small Mammals

San Diego pocket mice were tracked an average distance of 25.1 m (SE 1.6) from the point of release. Species-specific movement simulations predicted a permeability of 42% (percentage of animals moving onto road) if the roads had no effect on movement. Twenty-seven percent of San Diego pocket mice movements were tracked onto the dirt roads (Fisher's exact test, $n = 22$, $p = 0.194$). The majority of these movements (4 out of 5) were crossing events to the habitat on the other side of the road. The percentage of movements onto the secondary road was significantly lower than expected at 9.5% ($n = 21$, $p = 0.003$). The 2 movements onto the secondary road were not crossings, but along the edge of the road returning to the habitat on the same side of the road. There were no movements of San Diego pocket mice onto the primary highway ($n = 11$, $p = 0.004$) (Fig. 1). The relative abundance of pocket mice did not differ significantly among the 3 road types ($F_{2,21} = 1.493, p = 0.248$).

Cactus mice were tracked an average distance of 19.0 m (SE 1.2). Species-specific movement simulations predicted an expected road permeability of 30%. All the movements onto the dirt road were direct crossing events to the other side of the road (Fig. 2). Although 25% of the individuals went onto the dirt road (meaning there was no significant barrier effect [$n = 20$, $p = 0.626$]), no individuals were tracked onto the secondary paved road or primary highway ($n = 18$, $p = 0.003$ and $n = 19$, $p = 0.002$, respectively). Relative abundance of cactus mice did not differ significantly among the 3 road types ($F_{2,21} = 0.676, p = 0.522$).

Dulzura kangaroo rats were tracked an average of 14.6 m (SE 2.4). Movement simulations for this species predicted a road permeability of 41%. Although there were few animals tracked, most of them went onto the roadways. Of the 3 individuals tracked near the dirt road, all went onto the road ($n = 3, p = 0.070$), which indicates the road was more permeable to this species than the surrounding habitat. One individual's burrow entrance was in the middle of the roadway. Two out of 3 individuals tracked went onto the secondary paved road ($n = 3, p = 0.572$), which indicates this road was not a barrier to movement. One individual ran along the length of the road and the other crossed the road (Fig. 3).

Deer mice were tracked adjacent to the highway for an average length of 19.9 m (SE 2.3). Species-specific

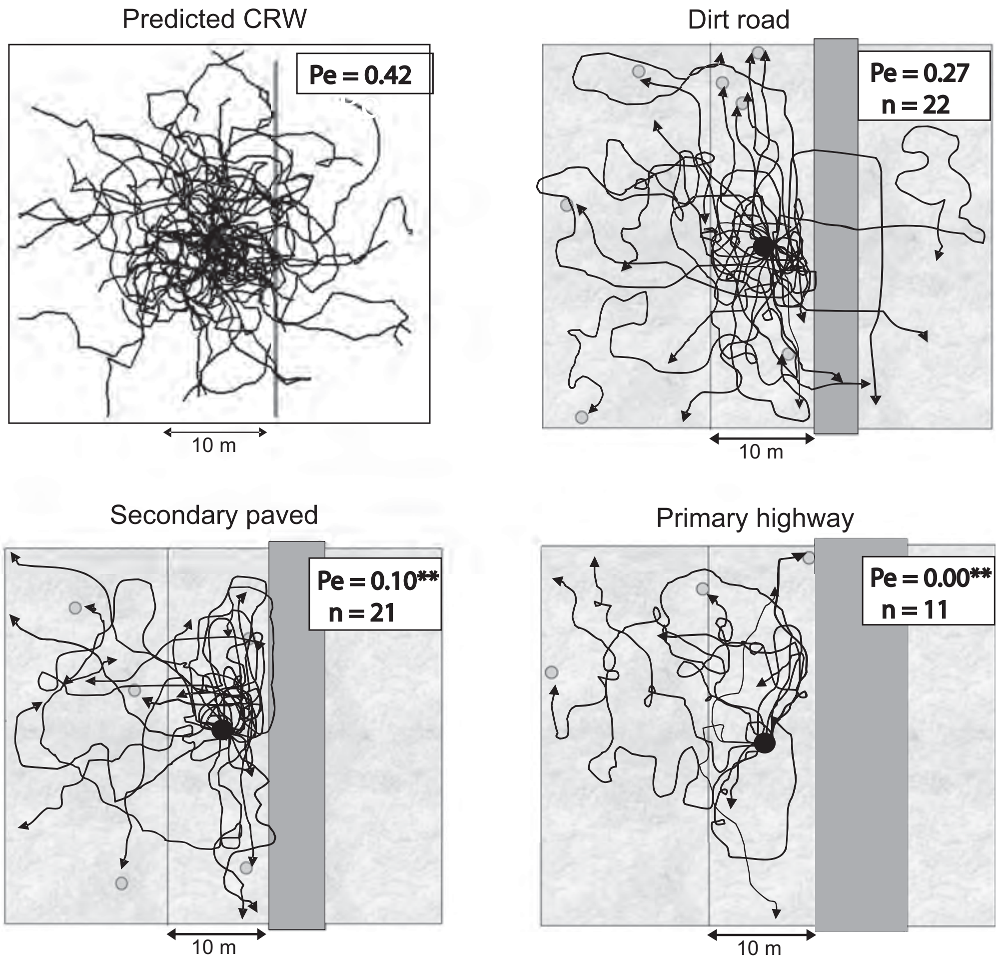

Figure 1. Predicted (correlated random walk, CRW) and observed permeability (Pe) of road types to movement of the San Diego pocket mouse (Chaetodipus fallax). Each drawing shows movements tracked at multiple independent release sites superimposed onto a single frame (gray circles, burrows; $^{**}p < 0.01$).

movement simulations predicted a road permeability of 37%. No deer mice went out onto the road, which indicates the rural highway was a significant barrier for this species ($n = 8, p = 0.030$). Many individuals were tracked to burrow entrances that were within a few meters of the road.

Lizards

Western fence lizards were tracked an average distance of 17.4 m (SE 2.2) from point of release. Species-specific movement simulations predicted an expected road permeability of 31%. The permeability of the dirt roads to movement of western fence lizards was higher than expected; 66% of lizards went onto the dirt road ($n = 9$, $p = 0.030$). These were a mixture of crossing events and movement along the road. A high percentage (56%) of individuals also went onto the secondary paved road ($n = 9$, $p = 0.146$). These movements were all along the road and no crossing events were recorded. However, most of these tracks were lost on the pavement, so we could not determine which side of the road the animal went to. In comparison, not a single western fence lizard went onto the highway (Fig. 4). Although permeability between the expected and observed values for the highway was not significant ($n = 6, p = 0.186$), the permeability of the highway to fence lizard movements was significantly lower than permeability of the dirt ($p = 0.028$) and secondary paved roads ($p = 0.044$) to movements of fence lizards. Their relative abundance did not differ among road types ($F_{2,21} = 0.006, p = 0.994$).

Movement simulations predicted road permeability of 31% for orange-throated whiptail if the roads had no effect on movement behavior. The average track length was 17.0 m (SE 1.3) by the secondary and primary paved roads. Although 33.3% of orange-throated whiptails crossed the secondary paved road ($n = 6$, $p = 1.00$), none were tracked out onto the highway ($n = 24$, $p \leq 0.001$) (Fig. 5). Only one whiptail was captured by the dirt road, and its track length was <10 m. Whiptail abundance next to the paved road and highway did not differ significantly ($t_{14} = 1.612, p = 0.129$). However, the

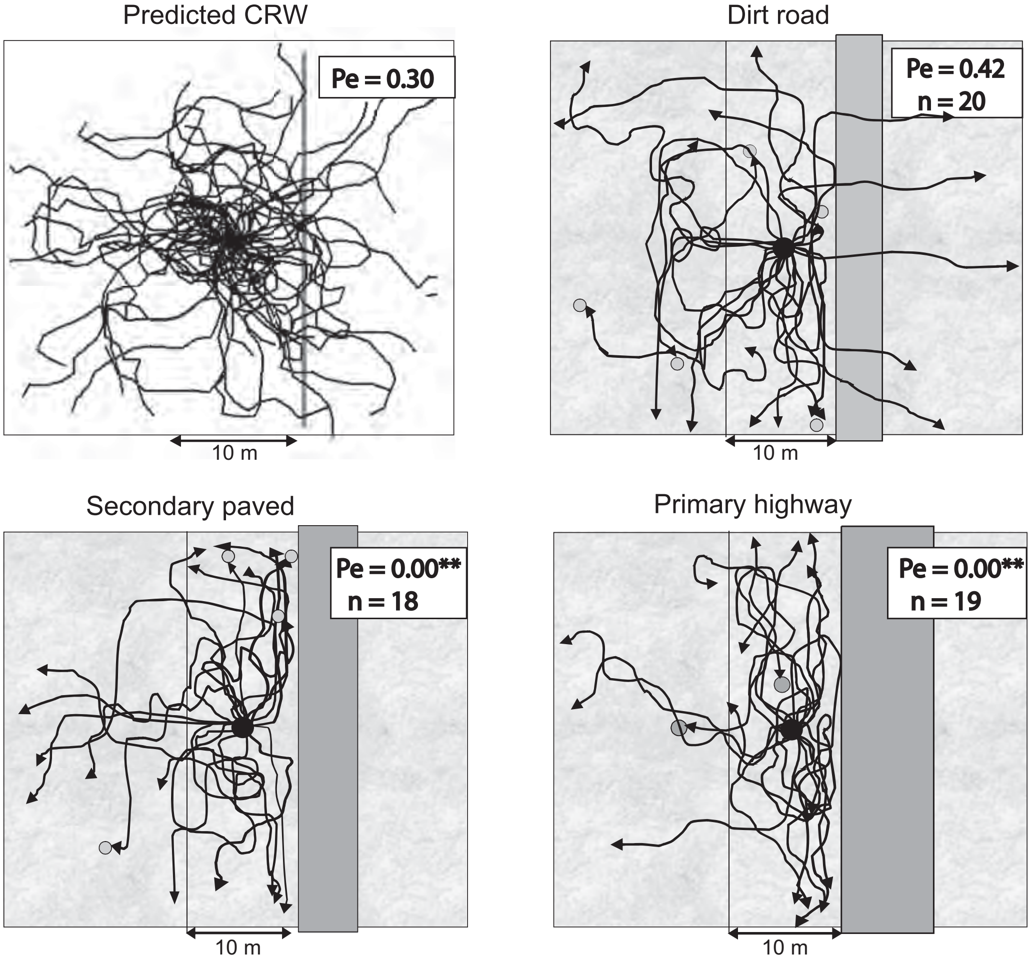

Figure 2. Predicted (correlated random walk, CRW) and observed permeability (Pe) of road types to movement of the cactus mouse (Peromyscus eremicus). Each drawing shows movements tracked at multiple independent release sites superimposed onto a single frame (gray circles, burrows; $^{**}p < 0.01$).

success rate in tracking the whiptail for distances >10 m was significantly greater by the highway (24/32) than by the paved road (6/20, $p = 0.002$).

Discussion

Although they live in open scrub habitats, San Diego pocket mice and cactus mice prefer to move and forage under microhabitats of shrub and rock cover rather than open areas (Meserve 1976; Price & Kramer 1984). Thus, they may quickly pass through or avoid areas of open ground. This is consistent with their movements relative to the dirt road, which were primarily direct crossings to shrub and rock cover on the other side of the road. One cactus mouse crossed the dirt road on 2 occasions. This result indicates the dirt road was within its home range. 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. The secondary road differed from the dirt roads by an average added width of 1.9 m, the addition of pavement, and an increased traffic volume averaging one vehicle every 5 minutes. It is unknown which of these factors or combination thereof resulted in their avoidance of this road. However, because of the low traffic volume and little difference in width, it is likely that these species were avoiding the road substrate. White-footed mice (*Peromyscus leucopus*) and eastern chipmunks (*Tamias striatus*) avoid crossing paved roads regardless of traffic volume (McGregor et al. 2008). By comparing roads with different substrates and traffic volumes, our results support the hypothesis that many small mammal species avoid paved road substrates. The reasons for this are not understood and deserve further study. However, mammals are particularly sensitive to odors in their environment. Road pavement surfaces, such as asphalt and coal tar, contain complex mixtures of volatile and non-volatile compounds. Even very minute concentrations of smells and chemicals that mimic pheromones may elicit instinctive behavioral

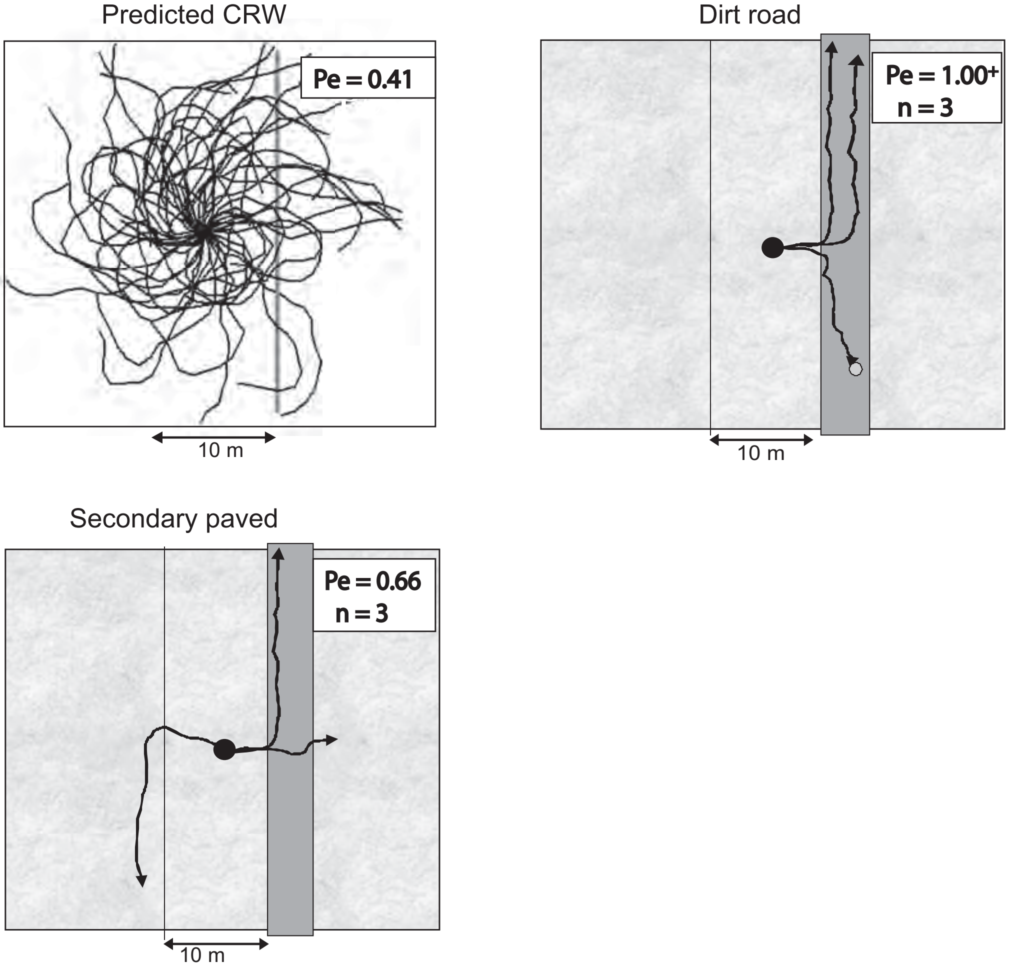

Figure 3. Predicted (correlated random walk, CRW) and observed permeability (Pe) of road types to movement of Dulzura kangaroo rat (Dipodomys simulans). Each drawing shows movements tracked at multiple independent release sites superimposed onto a single frame (gray circle, burrows; $+p < 0.10$).

responses in some species (e.g., Leinders-Zufall et al. 2000).

However, the avoidance of pavement is not generalizable to all species of small mammals. The yellow-necked mouse (*Apodemus flavicollis*) regularly crossed both dirt and paved roads of similar width (Rico et al. 2007). In our study, 2 out of 3 Dulzura kangaroo rats went out onto the secondary paved road. Although we did not capture any Dulzura kangaroo rats by the highway, this species accounted for the majority of dead animals we observed on the highway (3 out of 7) (Brehme 2003), which indicates the highway was also somewhat permeable to movement for this species. The higher than expected permeability of dirt roads to movements of the Dulzura kangaroo rat is consistent with results of a previous study on the Stephens' kangaroo rat (*D. stephensi*) (Brock & Kelt 2004). Kangaroo rats may preferentially use dirt roads for movement within their habitat. These bipedal heteromyids prefer to move and forage within open-ground areas of scrub habitats and respond positively to disturbances such as fire (e.g., Meserve 1976; Price & Kramer 1984; Brehme et al. 2011). In areas with denser vegetation, low-use dirt roads and trails may provide an increased opportunity for kangaroo rats to disperse to open scrub habitats. Alternately, we would expect negative effects from high-traffic roads on kangaroo rats. Traffic noise can disrupt communication in kangaroo rats (Shier et al. 2012) and nonavoidance of these roads would very likely result in increased mortality rates from vehicular traffic.

Because many reptiles may be attracted to open spaces and paved surfaces for thermoregulatory purposes, it is often hypothesized that these animals do not avoid roads (e.g., Klauber 1939; Jochimsen et al. 2004; Andrews et al. 2008). The dirt and secondary paved roads in our study were highly permeable to movement of western fence lizards (67% and 56%, respectively). Their movements on the dirt roads consisted of crossings and movements along the road; thus, the road was in part used as a conduit for movement. In contrast, their

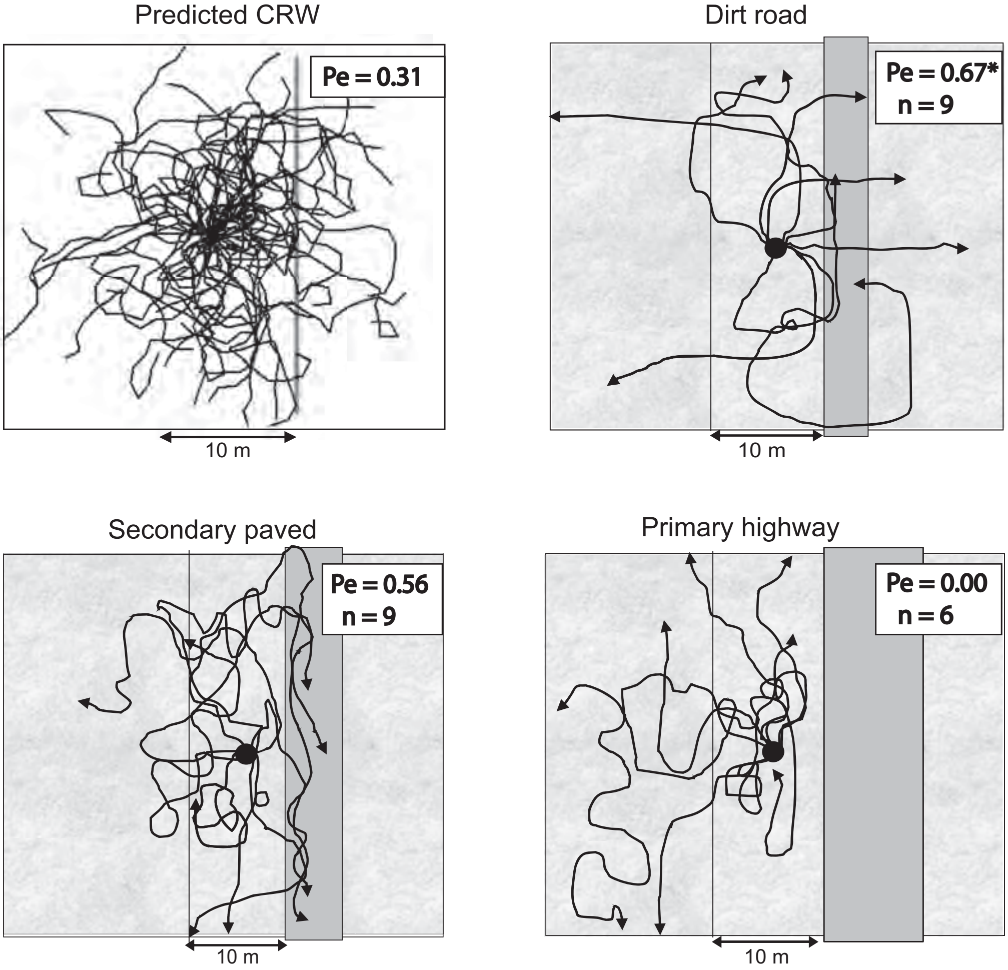

Figure 4. Predicted (correlated random walk, CRW) and observed permeability (Pe) of road types to movement of the western fence lizard (Sceloporus occidentalis). Each drawing represents movements tracked at multiple independent release sites that are superimposed onto a single frame ($^*p < 0.05$).

movements on the secondary road were often erratic and irregular along the road edge. This suggests the paved road was used for basking which was regularly observed during the study. The complete absence of movements onto the highway was in stark contrast to their response to the dirt and secondary paved roads. Similarly, although the secondary road was permeable to movement of the orange-throated whiptail, this species also completely avoided the highway.

Delaney et al (2010) found that genetic diversity is lower in populations of western fence lizards that are separated by a highway than in populations in continuous habitat. Because of the high permeability of the secondary paved road to these 2 species, we think it is unlikely that the additional width of the highway (4.6 m) alone adequately explains their marked avoidance of the highway. However, the level of traffic (average 1 vehicle/7 seconds) was 40-fold higher on the highway than on the secondary paved road; thus, the constant stream of vehicular traffic and corresponding noise and vibration may have been sufficient to deter use of the highway. On the basis of our own literature search and recent reviews on responses of reptiles to roads (Andrews et al. 2008; Rytwinski & Fahrig 2012), we believe ours is the first study to document behavioral road avoidance in lizards.

All the study species exhibited increased road avoidance and thus experienced decreased connectivity as road improvement and traffic increased. By studying both small mammals and reptiles we were able to make direct comparisons of behavior between taxa with different microhabitat preferences and life-history strategies. Species microhabitat-use preferences within their habitat may be an important predictive factor for road permeability (Fig. 6). Animals that are more likely to focus their activities in open areas within their habitat were more likely to venture out onto low-use roads. In our study, the 3 species (Dulzura kangaroo rat, western fence lizard, orange-throated whiptail) that use open areas for foraging

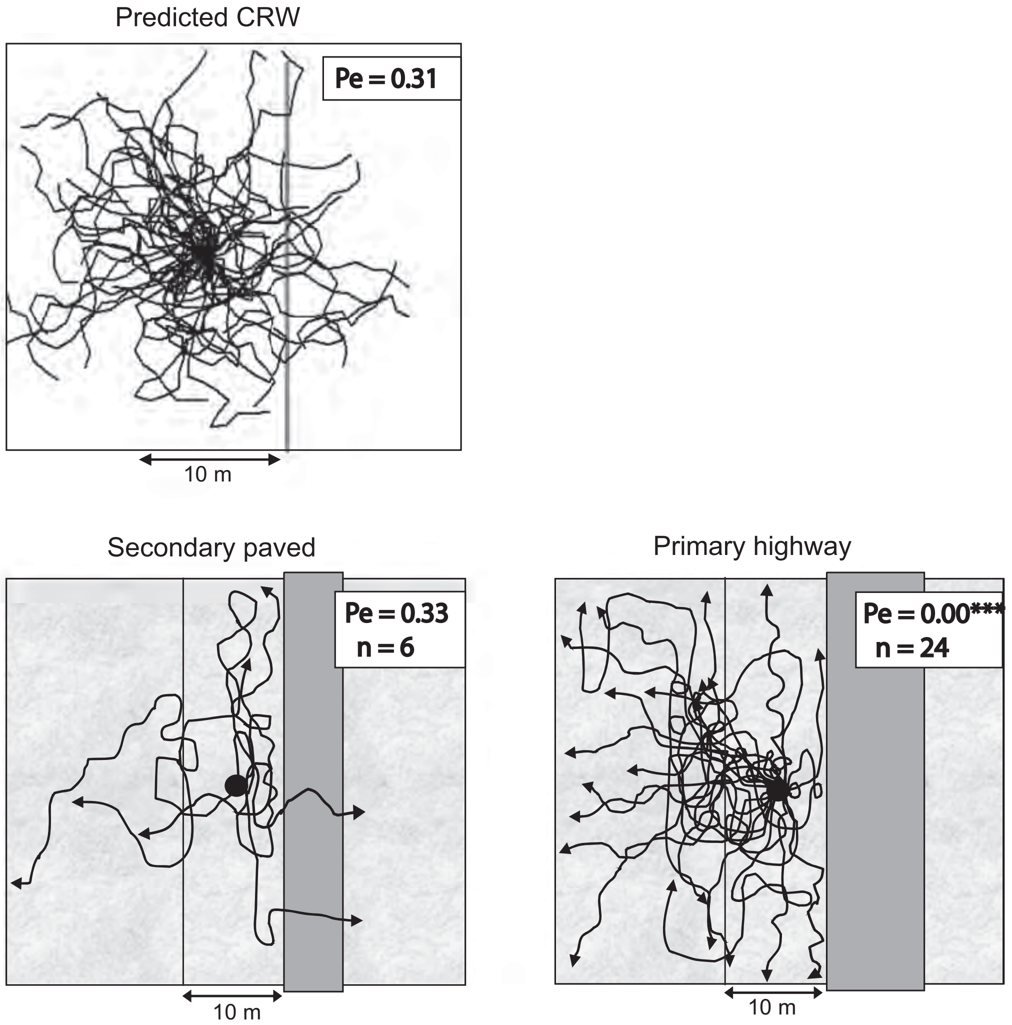

Figure 5. Predicted (correlated random walk, CRW) and observed permeability (Pe) of road types to movement of orange-throated whiptail lizard (Aspedoscelis hyperythra). Each drawing shows movements tracked at multiple independent release sites superimposed onto a single frame ($^{***}p < 0.001$).

or thermoregulation ventured onto dirt and secondary paved roads more than the species (San Diego pocket mouse, cactus mouse) that prefer to forage within or under the cover of rocks and shrubs.

Thus, one would predict that the populations of small animals with closed microhabitat preferences would be in most danger of becoming fragmented by any type of road. For instance, small mammal and reptile species that avoid open ground, such as the cotton rat (*Sigmodon hispidus*), prairie vole (*Microtus ochrogaster*), Eastern massasauga rattlesnake (*Sistrurus c. catenus*), rosy boa (*Lichanura trivirgata*), and many rainforest species, avoid crossing even narrow dirt roads (Swihart & Slade 1984; Weatherhead & Prior 1992; Goosem 2001; Rochester et al. 2005). Whereas generalist species and those with open microhabitat preferences would be more likely to cross roads, use roads for activity, and as conduits for movement. However, even these species may avoid roads with heavy traffic due to the constant disturbance from noise, vibrations, and lights. Therefore, roads with moderate traffic would be expected to pose the greatest risk of vehicular mortality for generalists and open microhabitat specialists due to the use of roads by both animals and vehicles (Seiler 2003). Our results pertain to small mammals and lizards with home ranges that are small relative to the road matrices within the study area. It is expected that movements onto roads would be more common for animals that make long migratory movements or that have large home ranges relative to the road matrices within their habitat.

Our results show that a 2-lane rural highway through open scrubland can create a significant movement barrier for species of small mammals and reptiles. Behavioral mechanisms appear to be road surface avoidance for some small mammal species and traffic avoidance for lizard species. Avoidance of improved roads may be a beneficial response in that mortality from vehicular traffic is avoided or minimized. However, networks of

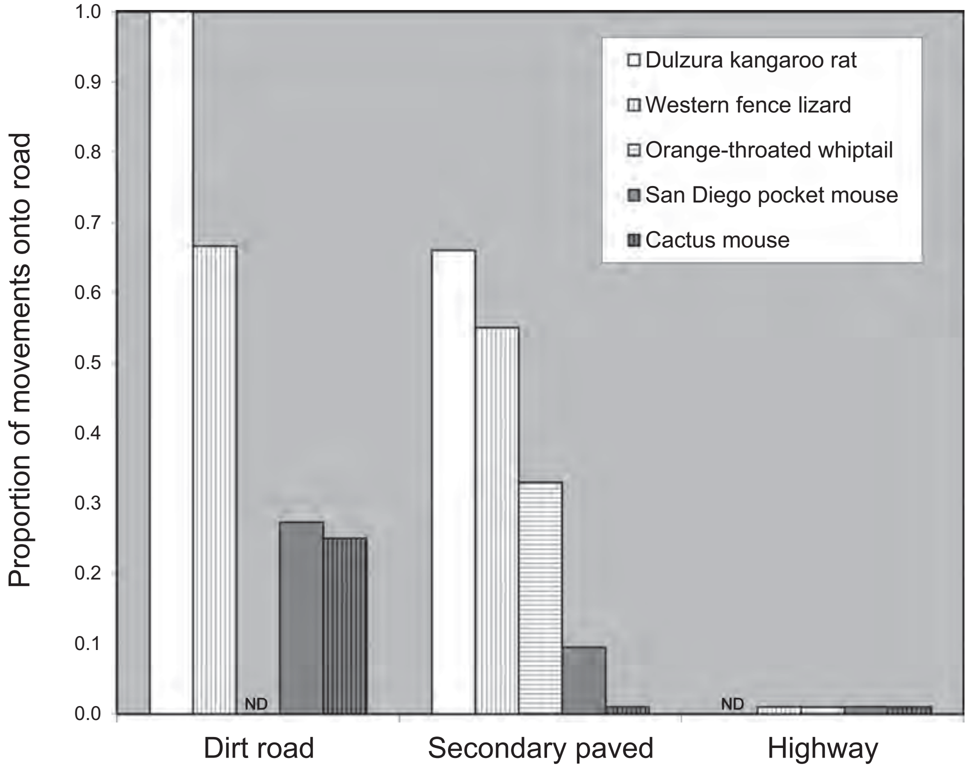

Figure 6. Road permeability relative to species microhabitat-use preferences (white bars, species that typically forage in and use open areas of their habitat; gray bars, species that primarily forage under vegetation cover; ND, no data for species at specific road type). Expected permeability range 0.30–0.41 with no road response.

roads throughout a landscape may divide habitat into fragments that are too small to sustain some populations over the long term. Barrier fencing and safe-crossing structures may reduce the effects of habitat fragmentation for species that avoid roads and reduce road mortality for species that do not avoid roads (e.g., Boarman & Sazaki 1996; Dodd et al. 2004).

More research is needed to determine whether road response patterns are consistent across other habitats and small animal species, whether microhabitat-use preferences can also help predict the use of road-crossing structures, and to further understand the population-level effects of movement-behavior decisions (Fahrig 2007; Rytwinski & Fahrig 2012). If generalizations are found, they will help us to identify vulnerable species and potentially detrimental roads within their habitat, inform population and spatial-movement models, and inform management decisions and mitigation measures for both studied and unstudied species.

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