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INFLUENCE OF ROADS ON MOVEMENTS OF SMALL MAMMALS

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ABSTRACT—The landscape of the world is becoming more dissected by roads each year due to the growing human population. Numerous studies have documented the direct impact of roads on wildlife by examining mortality caused by vehicles but few have investigated indirect effects of roads on animals. We used capture-mark-recapture (CMR), fluorescent pigments, and radiotelemetry techniques to assess the influence of roads on movements of rodents. During CMR, only 5 of 53 (9.4%) individuals captured more than once spontaneously crossed roads, whereas 21 of 51 (41.2%) rodents that were displaced across roads when released returned to the side of their original capture. Only 1 of 54 (1.9%) rodents powdered with fluorescent pigment moved across the road when released at their capture site. In contrast, 7 of 53 (13.2%) displaced and powdered animals crossed the road. Six of 12 (50%) radiotagged animals were located on both sides of the road on at least 1 occasion; however, >90% of all locations were on the same side as the original capture for all individuals. Roads were partial barriers to movements of rodents; however, when displaced, animals exhibited a greater likelihood of crossing a road. Although proportion of rodents crossing roads varied among the 3 studies, all techniques yielded consistent results.

RESUMEN—El paisaje del mundo se está fragmentado más cada año por caminos debido al crecimiento de la población humana. Numerosos estudios han documentado el impacto directo de las carreteras en la vida silvestre examinando la mortalidad causada por los vehículos, pero pocos han investigado el efecto indirecto de los caminos en los animales. Usamos captura-marca-recaptura (CMR), pigmentos fluorescentes, y técnicas de radiotelemetría para valorar la influencia de los caminos en los desplazamientos de los roedores. Durante CMR, sólo 5 de 53 (9.4%) individuos capturados más de una vez cruzaron los caminos espontáneamente, mientras que 21 de 51 (41.2%) de roedores que fueron llevados al otro lado de los caminos regresaron al lugar original de su captura. Sólo 1 de 54 (1.9%) de los roedores espolvoreados con pigmento fluorescente cruzó el camino cuando se les liberó en su lugar de captura. En contraste, 7 de 53 (13.2%) animales desplazados y espolvoreados cruzaron la carretera. Seis de 12 (50%) animales con radiotransmisores fueron localizados en ambos lados del camino al menos en 1 ocasión; sin embargo, >90% de todas las localizaciones fueron en el mismo lado de la captura original para todos los individuos. Los caminos fueron barreras parciales para los movimientos de los roedores; sin embargo, cuando fueron desplazados, los animales exhibieron una posibilidad mayor de cruzar el camino. A pesar de que la proporción de roedores que cruza los caminos varió en los 3 estudios, todas las técnicas produjeron resultados consistentes.

Fifteen to 20% of the land cover in the United States is influenced by roads (Forman and Alexander, 1998) and numerous researchers have documented mortality of mammals and other wildlife on highways (Scott, 1938; Dickerson, 1939; Davis, 1940; Huey, 1941; Haugan, 1944; McClure, 1951; Sargeant and Forbes, 1973). However, fewer studies have addressed indirect effects of roads on movements of animals (Kozel and Fleharty, 1979; Wilkins, 1982; Garland and Bradley, 1984; Swihart and Slade, 1984; Richardson et al., 1997). Roads are becoming more widespread throughout the world due to the increasing human population; therefore, a better understanding of the impact of these potential barriers to movements of small mammals is warranted.

Our objective was to use capture-mark-recapture (CMR), fluorescent pigments, and radiotelemetry techniques to assess the influence of roads on movements of small mammals. We tested the null hypothesis that similar proportions of small mammals would spontaneously move between 2 traplines separated by either a road or an equal width of homogenous grassland. We also assessed whether displaced animals would cross the road at a greater frequency than nondisplaced animals. Lastly, we tested for differences in sensitivity of the 3 techniques in detecting movements of animals across roads.

METHODS AND MATERIALS—*Study Site*—This study was conducted near the western edge of the city limits of Durant, Bryan Co., Oklahoma. We selected a blacktop road, an unimproved dirt road through a hayfield, and a hayfield as study sites. The 6-m wide blacktop road was oriented north-south (Fig. 1) and bordered by 3-m wide ditches that were about 1-m deep. Bordering each ditch was either a 3-stranded barbed-wire fence or remnants of a fence. A hayfield was contiguous with the west side of the blacktop road; a pasture bordered the east side. The 5-m wide dirt road was perpendicular to the blacktop road and extended west into the hayfield. The hayfield was mowed once per year in late June or early July; dominant vegetation included broomsedge bluestem (*Andropogon virginicus*), big bluestem (*A. gerardii*), and little bluestem (*A. scoparius*). In addition to the dominant plant species in the hayfield, roadside ditches also contained poison ivy (*Toxicodendron radicans*), small shrubs (*Ulmus, Cornus, Prunus,* and *Rhus*), ragweed (*Ambrosia*), sunflower (*Helianthus*), and sensitive briar (*Schrankia nuttalli*).

Capture-Mark-Recapture—During the first phase of our CMR study, we trapped small mammals for 6 consecutive nights (8–13 May 1995) using 3 pairs of parallel traplines; 1 pair in the hayfield, 1 pair on opposite sides of the dirt road, and 1 pair on opposite sides of the blacktop road (Fig. 1). Each trapline consisted of 20 large (7.6 by 8.9 by 22.9 cm) Sherman live traps set at 4-m intervals and baited with a peanut butter and oatmeal ball wrapped in weighing paper. We set pairs of traplines 8 m apart and parallel to each other. Traplines along the dirt road were about 30 m south of the southern most trap station for lines in the hayfield and along the blacktop road. Traplines in the hayfield paralleled those along the blacktop road and ca. 80 m separated the 2 sets of lines. We marked each rodent with a uniquely numbered ear tag. After recording species, sex, age, reproductive condition, mass, capture location, and tag number, we released the animal at its capture location.

During the second phase of our CMR study, we livetrapped small mammals for 12 consecutive days (27 October to 7 November 1994) along 3 pairs of traplines; each pair was separated by the blacktop road (Fig. 1). We used the same trapping protocols

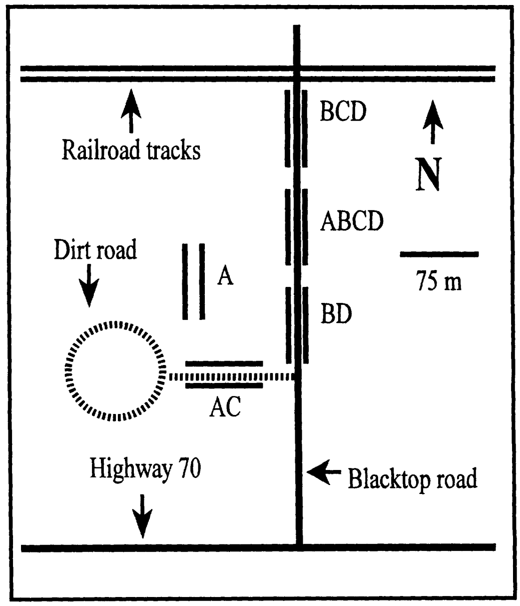

FIG. 1—Location of paired traplines used during the first (A) and second phase (B) of the capture-mark-recapture study, fluorescent pigment study (C), and radiotelemetry study (D).

as in the first aspect of the CMR study except for the following. On mornings 1 through 5, we ear tagged rodents and released them at their capture site. On the sixth morning, we released all individuals (both newly-marked individuals and recaptured animals) on the side of the road opposite of their capture. On mornings 7 through 12, we released all newly-marked animals on the opposite side of the road, whereas all recaptured animals were released at the capture site.

Fluorescent Pigments—On 2 and 8 November 1995, and 26, 28–29 February 1996, and 4–5 March 1996, we captured rodents using 2 sets of parallel traplines on opposite sides of the blacktop road (30 m separated the 2 pairs of lines) and 1 set of parallel traplines on opposite sides of an unimproved dirt road. Each morning, a maximum of 3 individuals from each pair of traplines was selected to be powdered with chartreuse, orange-red, or pink fluorescent pigment (Radiant Color, Richmond, California). We transported the rodents to the laboratory and housed them in cages with food and water *ad libitum* throughout the day. That evening, we returned individuals to their capture locations, powdered them, and released them at ca. 0.5 h after sunset. We followed powder trails left by the rodents the next morning before sunrise or the following evening after sunset. Instead of following individual powder trails through dense vegetation, we only searched along each side of the blacktop road and dirt road with a pocket black light (Zelco Ind., Inc., Mt. Vernon, New York) for evidence that an individual crossed the road. We powdered 54 mice of 4 species: house mouse (*Mus musculus;* 1 female and 3 males), deer mouse (*Peromyscus maniculatus*; 7 females and 5 males), hispid cotton rat (*Sigmodon hispidus*; 4 females and 9 males), and fulvous harvest mouse (*Reithrodontomys fulvescens*; 12 females and 13 males). We repeated this procedure from 11 to 22 March 1996 except all rodents were released on the side of road opposite to their capture location. We powdered 53 individual mice of 4 species: house mouse (2 males), deer mouse (12 females and 9 males), hispid cotton rat (1 female and 4 males), and fulvous harvest mouse (8 females and 17 males). No individual was used twice during the fluorescent pigment study. For both periods, traps were closed during evenings that we released powdered animals.

Radiotelemetry—We captured 6 deer mice (3 females and 3 males) and 6 fulvous harvest mice (3 females and 3 males) along the blacktop road between 6 and 8 May 1996 and attached a MD2C radio transmitter (Holohil Systems, Ontario, Canada) to each individual. One person held the rodent while another slipped the pre-assembled collar over the animal's head; the entire process took <1.5 min. We maintained rodents in laboratory cages with food and water *ad libitum* for 12 h after tagging to allow them to calm down and ensure that the collar fit properly; radiotagged animals were then released after sunset at their capture location. We used a TRX-1000S receiver and 3-element Yagi antenna (Wildlife Materials, Carbondale, Illinois) to determine the locations of animals (same or opposite side of the road as the original capture) each evening after sunset and morning after sunrise through 9 June 1996. We walked along the road until all animals were located with the receiver, or until we were confident that the animal would not be located with further effort (0.5 to 1.0 h of searching).

Statistical Analysis—We used Fisher's exact test to assess for differences in proportion of individuals that were captured on both traplines in grassland habitat and on both traplines separated by a road. We also used Fisher's exact test to determine if a greater proportion of displaced than nondisplaced individuals moved across the road during studies using CMR and fluorescent pigments. We assessed for differences among techniques by making pairwise comparisons of the proportion of animals that spontaneously crossed the road with Fisher's exact test.

RESULTS—*Capture-Mark-Recapture*—Four species of rodents were represented in the 64 individuals and 155 captures during the first phase of the CMR study: hispid cotton rat (n = 49), fulvous harvest mouse (6), marsh rice rat (*Oryzomys palustris*; 5), and deer mouse (4). We pooled data for animals captured on traplines near the dirt road and blacktop road as no significant differences were noted in proportions of animals using traplines on both sides of either road ($P > 0.10$). Of 28 hispid cotton rats captured more than once, a greater proportion were captured on both traplines in the hayfield (10 of 16; 0.625) than those near roads (0 of 12; 0.000; $P < 0.001$); no difference was noted between females and males ($P > 0.10$). Insufficient numbers of the other 3 species were captured more than once to test (n = 3, 2, and 3 for fulvous harvest mice, marsh rice rats, and deer mice, respectively). For all rodents captured more than once, we captured a significantly greater proportion of animals on both traplines in the hayfield (12 of 18; 0.667) than along roads (4 of 18; 0.222; $P < 0.01$).

We captured 6 species of rodents and 2 species of shrews in the 163 individuals and 418 captures during the second phase of the CMR study (Table 1). We pooled data for both sexes because there were no significant differences in patterns of capture exhibited by females and males ($P > 0.05$). After displacing individuals, proportions of hispid cotton rats captured on one side or both sides of the road did not differ between displaced and nondisplaced individuals (Table 1). In contrast, a significantly greater proportion of displaced than nondisplaced fulvous harvest mice and deer mice crossed the road at least once after being displaced (Table 1). When all rodents captured more than once were considered, a significantly greater proportion of displaced animals (0.412) were capture on both sides of the road than nondisplaced individuals (0.094; Table 1).

Fluorescent Pigments—Only 1 deer mouse of 54 rodents powdered with flourescent pigment spontaneously moved across the blacktop road after being released, whereas 7 of 53 displaced animals moved back to the side on which they were trapped (Table 2). For displaced animals, we pooled data for the 2 types of roads because we found no difference ($P > 0.30$) in the proportion of animals crossing the dirt (2 of 15; 0.125) or blacktop (5 of 30; 0.167) road. We did not test for differences among species, or between males and females, because of the limited number of individuals crossing the road. A significantly greater proportion of displaced

TABLE 1—Numbers of unique individuals captured on only 1 side or both sides of a blacktop road in southeastern Oklahoma when released at their capture location (Nondisplaced) or released on the opposite side of the road (Displaced). Fisher's exact test was used to assess for differences between nondisplaced and displaced animals for proportions captured on one or both sides of the road (nt = not tested).

Species	Nondisplaced		Displaced		P
	One	Both	One	Both	
Sigmodon hispidus	20	4	17	7	0.16
Reithrodontomys fulvescens	9	0	1	5	<0.01
Peromyscus maniculatus	11	0	7	4	<0.05
Mus musculus	3	0	1	3	nt
Oryzomys palustris	4	0	3	1	nt
Peromyscus leucopus	1	1	1	1	nt
Total	48	5	30	21	<0.001

(0.132) than nondisplaced (0.019) rodents crossed the road after release when all individuals were pooled (Table 2).

Radiotelemetry—We detected no obvious differences in locations of animals between males and females, or between the deer mice and fulvous harvest mice; therefore, data for all individuals were pooled. We found 6 rodents on both sides of the road on at least one occasion; 6 rodents only were found on the side of the road of their original capture and release (Table 3). This pattern was similar for both morning (7 of 12 animals located only on the side of original capture) and evening (6 of 12 animals on side of original capture) observation periods (Table 3). Overall, >90% of all locations of animals were on the same side of the road as their original capture. One deer mouse (M094) typically was located on the same side as the original capture each morning (27 of 29 days); however, it was on the opposite side of the road most evenings (24 of 31 nights). One harvest mouse (F940) was located on the side of the road of its original capture for 3 days and 4 nights; it was then located on the opposite side of the road for 4 days and 4 nights after which it was never located again.

Comparison of Techniques—A significantly greater proportion ($P < 0.01$) of small mammals were detected spontaneously crossing roads when radiotelemetry was used (0.50 located on both sides) than either flourescent pigments (<0.02) or CMR (0.12 and 0.10 during the 2 different phases). Regardless of which technique was used, a smaller proportion of animals crossed roads than moved between 2 traplines set a similar distance apart in a hayfield (0.61). A greater proportion of animals crossed a road after being displaced than spontaneously crossed for both the CMR (displaced = 0.41, spontaneous = 0.09) and flourescent pigment (displaced = 0.13, spontaneous = 0.02) studies.

TABLE 2—Numbers of unique individuals that crossed a road after being powdered with fluorescent pigment when released at their capture location (Nondisplaced) or released on the opposite side of the road (Displaced). Fisher's exact test was used to assess for differences between proportions of displaced and nondisplaced animals that crossed the road (nt = not tested).

Species	Nondisplaced		Displaced		P
	Remained	Crossed	Remained	Crossed	
Sigmodon hispidus	13	0	3	2	0.07
Reithrodontomys fulvescens	25	0	22	3	0.12
Peromyscus maniculatus	11	1	19	2	0.46
Mus musculus	4	0	2	0	nt
Total	53	1	46	7	0.03

TABLE 3—Number of days an individual was located on the opposite side of the road of original capture as determined by radiotelemetry.

			Morning		Evening	
Species	Sex	Number	Days	Opposite	Days	Opposite
Peromyscus maniculatus	F	033	30	0	31	0
	F	053	27	0	30	0
	F	070	30	0	31	0
	M	094	29	2	31	24
	M	962	28	0	29	0
	M	979	29	3	30	1
Reithrodontomys fulvescens	F	013	28	0	29	0
	F	873	29	1	30	1
	F	940	7	4	8	4
	M	839	28	2	29	1
	M	851	3	0	6	0
	M	919	29	0	30	1
Total			297	12	314	32

DISCUSSION—Both blacktop and dirt roads were at least partial barriers to movements of small mammals in our study, consistent with previously reported results in the literature. Swihart and Slade (1984) documented that few hispid cotton rats (10%) and prairie voles (*Microtus ochrogaster*, 3%) crossed a 3–3.6-m wide road during their 9-year study in Kansas. Similarly, Kozel and Fleharty (1979) captured only 6 individuals, 5 thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) and 1 deer mouse, on both sides of various types of roads (gravel, 2-lane state highway, and a divided, 4-lane interstate highway) in western Kansas. Only 1 of 387 recaptured rodents crossed a divided, 4-lane state highway in the Mojave Desert in southern Nevada (Garland and Bradley, 1984). In Texas, <6% of the hispid cotton rats, <2% of the northern pygmy mouse (*Baiomys taylori*), and 1% of fulvous harvest mice crossed a 4-lane divided highway or a 2-lane highway; no individual for 7 other species of rodent was captured on both sides of these roads (Wilkins, 1982). Lastly, only 3 of 94 small mammals spontaneously crossed roads in Great Britain (Richardson et al., 1997). Animal movement across roads was undoubtedly influenced by distance between habitats on opposite sides of a road (Oxley et al., 1974). Regardless of road type, a 3-m wide dirt path to a divided, 4-lane highway, movements of animals were impeded by the presence of a road.

In contrast, red-backed voles (*Clethrionomys gapperi*) in Manitoba had home ranges that included a road and used both sides (Buckner, 1957). High numbers of rodents killed on highways in California (Huey, 1941), Iowa (Scott, 1938), and Michigan (McClure, 1951) suggest that at least certain species of rodents may cross roads at a greater rate than indicated by capture-mark-recapture data. We did not find carcasses of small mammals on the road during any aspect of this study.

We documented a greater proportion of rodents crossing roads after displacement than spontaneously crossing. Similarly, Kozel and Fleharty (1979) documented that 5 of 7 species of rodents returned to their original capture location after being translocated across a road; only 2 of 7 species crossed roads on their own. Griffo (1961) found that cotton mice (*Peromyscus gossypinus*) would return to home ranges after being displaced across a road. Richardson et al. (1997) also found a greater proportion of displaced small mammals returning to the side of their original capture during a study in Great Britain.

Many of the CMR studies cited above involved longer periods of time than our study. Proportion of animals crossing roads may have increased if our study was extended; however, the proportion of animals we observed crossing roads spontaneously was similar to that reported for similar species elsewhere (even those with longer trapping periods). Trapping methods we used precluded us from determining what proportion of animals had home ranges that included both sides of the road. Some animals in our study may have had home ranges that included a road. These individuals may have been more likely to spontaneously cross the road than those animals with their entire home range on only 1 side of the road. Similarly, animals with home ranges only on a single side of the road probably are more likely to return to their home range by crossing a road when displaced.

We expected that the 3 techniques used in our study would vary in sensitivity of detecting movements of animals across roads and that radiotelemetry would be the most sensitive, followed by CMR, and fluorescent pigments. Differences among techniques may have accounted for, at least in part, the greater proportion animals crossing roads during the telemetry portion of our study. The greater frequency of spontaneous crossing of roads by radio-tagged animals also may be due to the minimal disturbance to individuals after attachment of the transmitter compared to the other techniques. Radiotagged animals could be detected over greater areas than covered by our traplines (>0.8 km from our traplines). Furthermore, we followed several radio-tagged animals for 34 days, much longer than the 6 or 12 days of trapping during the CMR studies or the single night for an animal powdered with fluorescent pigment. Animals may have been attracted to the traps or bait during the CMR and fluorescent pigment studies; however, traps and bait were removed after the 12 animals were captured for the radiotelemetry study. CMR would be intermediate in sensitivity because of multiple opportunities that individuals could be captured during a trapping period. However, movements of animals may be influenced by presence of baited traps or capture. We had a limited opportunity to document a rodent crossing the road when using fluorescent pigments. Powder trails could only be followed a short distance and each animal was used only once.

The network of roads found throughout the world is fragmenting and encroaching on greater expanses of land each year. Furthermore, roads are becoming wider to meet demands of an evergrowing volume of traffic. Further study is necessary to better document both direct and indirect effects of roads on activities of mammals and other wildlife. Long-term studies concerning population ecology of different species inhabiting areas near roads may be better able to address questions concerning the effect of inclusion of a road in home ranges of an individual, seasonality of crossing events, or differences among sexes, ages, and species. Impact of roads may be species specific and we would encourage future research to concentrate on these potential differences. For example, grassland species may be less influenced by road clearance (distance between habitats on opposite sides of the road) than woodland or fossorial species. Lastly, the genetic consequences of population fragmentation should be investigated, especially for those species that rarely, if ever, cross certain types of roads.

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