

Movement of small mammals across divided highways with vegetated medians

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Abstract: Previous studies suggest the gap in forest cover generated by roads contributes to the barrier effect of roads on movement of forest-dwelling small mammals. However, it is not known if vegetated medians of divided highways affect movement of small mammals by reducing the effective highway width. The purpose of our study was to determine whether the type of vegetation cover in the median (treed or grassy) or median width affects small-mammal crossings of divided highways. At 11 study sites varying in median cover type and width, we live-trapped small mammals next to one side of the highway and translocated them to the opposite side of the highway using a standardized translocation distance. In total, 24% of translocated individuals were recaptured on the side of the highway of initial capture, i.e., they had moved across the entire highway. This was significantly lower than what would have been expected in the absence of the highway (58%). The overall probability of recapturing a translocated individual was not significantly related to median cover type or width. Our results suggest that efforts to mitigate the barrier effect of highways on small mammals cannot be accomplished by altering median vegetation type and width.

Résumé : Des études antérieures laissent croire que les trouées dans la couverture forestière formées par les routes contribuent à l'effet de barrière des routes sur les déplacements des petits mammifères forestiers. On ne sait pas, cependant, si des terre-pleins centraux de végétation dans les routes divisées affectent les déplacements des petits mammifères en réduisant la largeur effective des grandes routes. Le but de notre étude est de déterminer si le type de couverture végétale (arborescent ou herbeux) et la largeur du terre-plein central affectent la traversée des routes divisées par les petits mammifères. À 11 sites d'étude présentant une variété de types de couverture et de largeurs du terre-plein central, nous avons piégé des petits mammifères vivants près d'un côté de la grande route et les avons relocalisés sur le côté opposé à une distance standardisée de déplacement. En tout, 24 % des individus déplacés ont été recapturés du côté de leur capture originale, c.-à-d. qu'ils ont traversé toute la route. C'est un pourcentage significativement plus bas que celui attendu en l'absence de grande route (58 %). La probabilité globale de recapter un individu déplacé n'est pas reliée significativement au type de couverture, ni à la largeur du terre-plein central. Nos résultats font penser que les efforts de mitigation de l'effet de barrière des grandes routes sur les petits mammifères ne peuvent consister en une modification du type de végétation et de la largeur des terre-pleins centraux.

[Traduit par la Rédaction]

Introduction

Studies have shown that forest-dwelling small mammals are reluctant to cross roads. Particularly, the wider the road, the less likely small mammals are to cross it (Oxley et al. 1974; Kozel and Fleharty 1979; Mader 1984; Goosem 2001; Rondinini and Doncaster 2002; McDonald and St. Clair 2004; Rico et al. 2007a, 2007b; Ford and Fahrig 2008; McGregor et al. 2008). In the Czech Republic, for example, fewer translocated yellow-necked mice (*Apodemus flavicollis* (Melchior, 1834)) and bank voles (*Clethrionomys glareolus* (Schreber, 1780)) crossed a four-lane divided highway than a two-lane highway (Rico et al. 2007a). Similarly, in Kansas, fewer deer mice (*Peromyscus maniculatus* (Wagner, 1845))

crossed a four-lane divided highway than a two-lane road and roads <10 m wide (Kozel and Fleharty 1979). Furthermore, in the UK, road crossings by hedgehogs (*Erinaceus europaeus* L., 1758) were shown to decrease with increasing road width (Rondinini and Doncaster 2002).

These decreases in animal crossings may not necessarily be a direct response to increasing road width per se. Results of several studies suggest that the lack of forest cover (forest clearance) associated with roads, rather than the road itself, may be the key factor in the barrier effect of roads on small-mammal movement. Oxley et al. (1974), for example, found that white-footed mice (*Peromyscus leucopus* (Rafinesque, 1818)) and eastern chipmunks (*Tamias striatus* (L., 1758)) moved distances in forest that were similar to the widths of

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different roads and highways in their study area, yet only crossed roads with forest clearances of 30 m or less. Such results appear to be general, as they are observable for other temperate small-mammal species including the yellow-necked mouse, bank vole, common shrew (*Sorex araneus* L., 1758) (Rico et al. 2007b), and wood mouse (*Apodemus sylvaticus* (L., 1758)) (Richardson et al. 1997), as well as tropical rain-forest species (Goosem 2001). In addition, gaps in forest cover across powerline corridors can produce a similar deterrence to small-mammal crossings as found with roads, despite the absence of a road surface and associated traffic. In a study in Australia, small mammals travelled distances in the rainforest that were at least two times the width of a nearby powerline corridor, yet they were severely inhibited by the cleared corridor. However, crossings occurred in sections of the corridor that contained regrowth vegetation and canopy cover (Goosem and Marsh 1997). Although not all small mammals respond in a similar way to nonforested gaps (e.g., Bowman and Fahrig 2002), in general, areas of forest clearance affect movement by forest-dwelling small mammals.

While road width and traffic volume are typically correlated, studies have suggested that small mammals do not respond to the traffic volume, but to the road clearance itself. McGregor et al. (2008), using translocations of white-footed mice and eastern chipmunks across two-lane paved roads varying in traffic volume, found no significant effect of traffic on the probability of either species returning to its initial capture site. Ford and Fahrig (2008) further demonstrated that eastern chipmunks avoid roads independently of traffic volume, a result consistent with other small-mammal studies (e.g., Oxley et al. 1974; Goosem 2002; Rico et al. 2007b).

If forest clearance is the main reason small mammals are inhibited from crossing roads, then by extension, one can assume divided four-lane highways with wide, grassy medians should be greater barriers to small-mammal movement than those with narrow, treed medians. Trees between opposing lanes would reduce the forest clearance of a four-lane highway, possibly creating the illusion of a two-lane highway and a closer apparent forest edge for small mammals to orient towards (Lima and Zollner 1996; Zollner 2000). Additionally, highways with narrower medians typically have forest margins on either side of the highway that are closer together, creating a smaller total forest clearance.

There is almost no research that specifically measures impacts of median barrier characteristics on movement of small mammals (Kociolek and Clevenger 2007). Treed medians have been shown to be effective in facilitating highway crossings by arboreal species (e.g., the squirrel glider, *Petaurus norfolcensis* (Kerr, 1792); van der Ree et al. 2010), but the effect of vegetated medians on highway crossings of non- or semi-arboreal species is unknown. Small mammals in Banff National Park were able to cross two lanes of the four-lane Trans-Canada Highway, as well as the forested median; however, neither movement across the entire highway nor effects of the forested median were examined (McDonald and St. Clair 2004). Other studies that have investigated small-mammal crossings of four-lane highways either (i) do not give a description of the median (or even state whether one existed) (Oxley et al. 1974; Kozel and Fleharty 1979; Conrey and Mills 2001; Rico et al. 2007a) or (ii) describe the median, but do not address any potential role of the median it-

self in crossing rates (Wilkins 1982; Garland and Bradley 1984).

The purpose of our research was to test the predictions that (i) small mammals should be more likely to move across four-lane divided highways with treed medians than with grassy medians and (ii) small mammals should be more likely to move across four-lane divided highways with narrow medians than with wide medians. These predictions are based on the hypothesis that open-space inhibits highway crossings by forest-dwelling small mammals.

Materials and methods

Sites, small-mammal trapping, and translocations

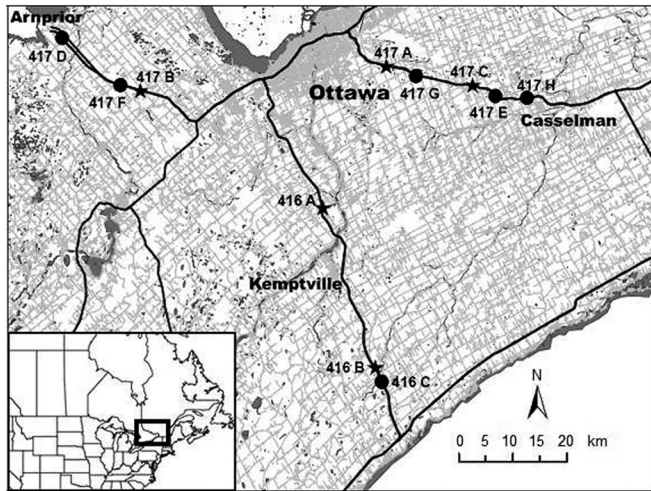
To test our predictions, we conducted a mark–translocate–recapture study of small mammals along 2, four-lane divided highways near Ottawa, Ontario, from May to September 2008. We selected 11 sites that varied in median width and contained either trees ($n = 6$) or grass ($n = 5$) in the median. Each site consisted of a 70 m length of four-lane highway that was absent of lights, guardrails, culverts, and concrete barriers. The paved lanes were ~3.75 m wide and had 1.5 m median shoulders (gravel shoulders adjacent to the median) and 3.0 m driving shoulders (gravel shoulders adjacent to the right paved lane). The width of the highway right-of-ways averaged 8.6 m and consisted of mowed grass and weedy vegetation. We selected sites with mixed deciduous forest on both sides of the highway. Common tree species included red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), eastern white cedar (*Thuja occidentalis* L.), and black ash (*Fraxinus nigra* Marsh.). We ensured that forest-patch size was similar on both sides of the highway for each study site. Annual average daily traffic (AADT) at the sites varied from 12 000 to 32 800 vehicles (Ontario Ministry of Transportation 2005). Each site was at least 3 km from the next nearest site (Fig. 1).

Sites were selected to allow estimation of the independent effects of median vegetation cover type (treed or grassy) and median width. We did this by first finding sites where the cover type in the central median could be clearly classified into one of the two vegetation categories. For each category, we then selected sites covering a range of median widths (grass: ~13 to 45 m; treed: ~18 to 50 m).

At each site, we trapped small mammals in the forest on one side of the highway using Sherman nonfolding aluminum live traps (7.5 cm × 9.0 cm × 23.0 cm; H.B. Sherman Traps Inc., Tallahassee, Florida, USA). Traps were arranged in an 8 × 8 grid, with 10 m spacing between traps. Each trap was baited with a mixture of rolled oats, sunflower seeds, peanut butter, and an apple slice. A fist-sized amount of synthetic cotton batten was also placed in the traps. Traps were set each evening between 1900 and 2000 and checked the following morning between 0800 and 0900. We trapped for 7 days at each site (day 1 was considered the first night traps were set), with the exception of two sites that had two trapping sessions, one at the beginning and the other at the end of the field season, owing to insufficient numbers of captures during the initial session. The 13 trapping sessions took place between 4 May and 12 September 2008 and the week each site was trapped was randomly selected.

Captured target species were weighed, sexed, assessed for

Fig. 1. Locations of 11 study sites along 2 four-lane divided highways (Hwy 416 and 417) in the Ottawa region. Symbols represent the type of vegetation in the median at each study site (★, grass median; ●, treed median).

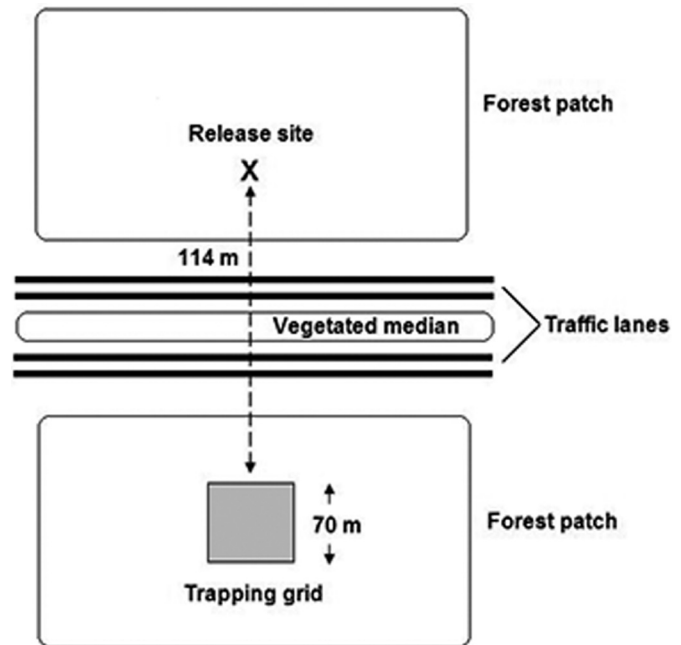


reproductive condition, and noted for any health-related characteristics (e.g., botfly parasites and cuts or wounds). In addition, we categorized each animal as either adult–subadult or juvenile based on mass and pelage colouration. Each animal was fitted with a 1 g Monel ear tag (National Band and Tag Co., Newport, Kentucky, USA), except pregnant or lactating females which were not used during this study.

Once tagged, individuals were translocated to the other side of the highway to the release location—directly opposite to the trapping grid (Fig. 2). Since it has been shown that translocation distance has a significant effect on return rates of translocated small mammals (Cooke and Terman 1977; McGregor et al. 2008), we ensured that the translocation distance was constant across all sites. We set the translocation distance for all sites based on the study site that contained the widest median (48.5 m). At this site, the edge of the trapping grid and the release location were both 5 m into the forest from the tree line along the highway. From this site, we measured the linear distance from the edge of the trapping grid on one side of the highway to the release location on the other side of the highway using aerial photographs. This distance, 114 m, was then used as the translocation distance for all of our study sites. It is well within the documented movement ranges of the species used in this study: southern red-backed voles (*Clethrionomys gapperi* (Vigors, 1830), 600 m; Bovet 1980), deer mice (3 220 m; Murie and Murie 1931), eastern chipmunks (550 m; Seidel 1961), and white-footed mice (>14 000 m; Maier 2002). Given that we used a constant translocation distance in our study, the distance between the point of release of tagged individuals and forest edge along the highway was variable between study sites owing to the different median widths. Nevertheless, a constant translocation distance ensured that we did not confound any possible effect of median cover type and (or) width.

At the designated point of release for each study site, tagged animals were individually released from a nondirectional release box. The lid of this box was attached to a rope and pulley that would lift up when pulled. Individuals were then free to leave the box in any direction (design details in

Fig. 2. Illustration of a study site showing trapping grid on one side of the highway and release location on the other side. Total linear translocation distance from edge of trapping grid to release site was 114 m for all 11 sites.



Ford and Fahrig 2008). Each animal was allowed to acclimate to the box for ~5 min to limit stress-based dashes out of the box when opened. Also, we stood ~5 to 10 m away from the release box when the lid was pulled open to avoid biases in movement of the tagged animals. Translocations were conducted from day 2 to 6 of each 7-day trapping session.

During each 7-day trapping session, we monitored daily for translocated animals on the trapping grid side of the highway. If such individuals were recaptured, we re-weighed them, recorded any visible changes in health, and noted the ear-tag number. They were then released on the spot. No animals were translocated more than once.

All of our methods for capture, translocation, and release of target species were approved by the Animal Care Committee at Carleton University.

Vegetation surveys

The purpose of conducting vegetation surveys was, first, to ensure that similar habitat existed on both sides of the highway for each site. Second, and more importantly, we wanted to ensure that there were no consistent associations between vegetation type on the translocation side of the sites and median cover type or width. If the vegetation type at the point of release affected the animals' behaviour, this could confound any effects of median cover type and (or) width. For example, if sites with treed medians had low-quality habitat on the translocation side of the highway (e.g., low tree density or low amounts of coarse woody debris), then translocated animals might be more motivated to move at these sites than at sites with grassy medians. This would produce an apparent effect of median vegetation that was actually caused by low quality of the release sites.

For each of the 11 sites, we sampled vegetation characteristics in four 10 m × 10 m plots, spaced 50 m apart in a square pattern, on both the trapping and translocation sides of the highways. Within each 10 m × 10 m plot, we measured the following: (i) cover of coarse woody debris using a 10 m transect; (ii) presence of nonwoody vegetation cover using 20 randomly selected points; (iii) density of coniferous and deciduous small trees, saplings, and shrubs using two 2 m × 2 m plots; and (iv) tree dispersion and fallen log dispersion using the point-centered quarter method (Waite 2000). In addition, we used an ocular tube (PVC pipe with cross hairs at one end) to determine canopy cover at each corner of the 10 m × 10 m plots by holding the tube above the head and perpendicular to the ground and noting whether the cross hairs intersected leaves or branches (1) or sky (0).

Statistical analyses

We used multiple logistic regression to test whether the probability of recapturing translocated small mammals was correlated with either median characteristic: cover type or width. Additionally, we tested for a possible interaction between cover type and width. We also included possible confounding variables: species, sex, age class, and days remaining in the trapping session (maximum possible = 5 days). We first analyzed the data with all the species together and then individually for white-footed mice and southern red-backed voles, the two most abundant species in the data set. We also tested whether median cover type or width affected the number of days it took to recapture translocated individuals after their release using a Student's *t* test for median cover type and a linear regression for median width.

To test for any dissimilarity in vegetation characteristics between the two sides of the highway (trapping versus translocation) for each site, we conducted a *Q*-mode ANOSIM (PRIMER-E 2009). Initially, all habitat variables were standardized to a common scale (mean = 0, standard deviation = 1). We then used Euclidean distance to determine the relative distance (similarity) between trapping and translocation sides of the highway for each site based on the 11 measured vegetation variables. For each site's pairing (trapping side versus translocation side), we ran an ANOSIM to test the null hypothesis of no difference.

Finally, we tested for associations between vegetation characteristics at the translocation side of the sites and median cover type and width, as well as for any associations between traffic volume at the sites and median cover type and width. We used Student's *t* tests to assess the relationships between the 11 vegetation variables and median cover type, and between traffic volume (AADT) and median cover type. We used regression analyses to test for any relationships between vegetation variables and median width and between traffic volume and median width.

We performed all statistical analyses using SPSS version 16.0 (SPSS Inc., Chicago, Illinois, USA), unless otherwise stated.

Results

Analyses of small-mammal translocation data

During 91 days of trapping, we captured and translocated 190 individuals (148 adults and 42 juveniles), of which 37%

were white-footed mice and 37% were southern red-backed voles. Other species translocated included eastern chipmunks ($n = 13$), woodland jumping mice (*Napaeozapus insignis* (Miller, 1891); $n = 27$), meadow jumping mice (*Zapus hudsonius* (Zimmermann, 1780); $n = 2$), and deer mice ($n = 6$). Nontarget species captured included flying squirrels (genus *Glaucomys* Thomas, 1908), red squirrels (*Tamiasciurus hudsonicus* (Erxleben, 1777)), masked shrews (*Sorex cinereus* Kerr, 1792), short-tailed shrews (*Blarina brevicauda* (Say, 1823)), and ermines (*Mustela erminea* L., 1758).

Of the 190 individuals translocated across the highways, 45 (23.7%) were recaptured on the side of the highway of initial capture within the 7-day trapping sessions. We tested to see if our recapture rate was significantly different than would be expected in the absence of roads using the multiple logistic regression model for translocated white-footed mice estimated by McGregor et al. (2008: Table 1). For our purposes, we set the number of roads and traffic volume in our model to zero and obtained an expected recapture rate for our translocation distance (114 m). Our observed recapture rate (~24%) was significantly lower than would be expected in the absence of roads (58%) based on the regression model for white-footed mice in McGregor et al. (2008) (for all species in our data set ($n = 190$): $\chi^2_{[1]} = 93.45$, $P < 0.0001$; white-footed mice only ($n = 71$): $\chi^2_{[1]} = 11.96$, $P < 0.001$). Therefore, our data support previous findings (see Introduction) that highways inhibit small-mammal movement.

When all species were included in the multiple logistic regression analysis, we found no significant relationship between the probability of a translocated individual being recaptured and the median cover type (Wald's $\chi^2_{[1]} = 0.052$, $n = 190$, $P = 0.819$; Fig. 3a), median width (Wald's $\chi^2_{[1]} = 0.176$, $n = 190$, $P = 0.675$; Fig. 3b), or their interaction (Wald's $\chi^2_{[1]} = 0.231$, $n = 190$, $P = 0.631$) when controlling for species, sex, age class, and days remaining in the trapping session. However, the probability of recapturing a translocated individual was significantly related to species (Wald's $\chi^2_{[5]} = 19.494$, $n = 190$, $P = 0.002$), age class (Wald's $\chi^2_{[1]} = 7.530$, $n = 190$, $P = 0.006$), and days remaining in the trapping session (Wald's $\chi^2_{[1]} = 12.629$, $n = 190$, $P < 0.001$). Using woodland jumping mice as the basis for comparison, the relative likelihood of recapturing deer mice, white-footed mice, eastern chipmunks, southern red-backed voles, and meadow jumping mice were 5.2, 3.4, 0.66, 0.35, and 7.0×10^{-9} times the likelihood of recapturing woodland jumping mice, respectively. The odds of recapture were 9.5 times higher for adults than juveniles and increased by a factor of 1.9 for every 1 day increase in days remaining in the trapping session. Neither sex (Wald's $\chi^2_{[1]} = 0.769$, $n = 190$, $P = 0.381$) nor its interaction with median width (Wald's $\chi^2_{[1]} = 0.929$, $n = 190$, $P = 0.335$) was a significant predictor of recapture. However, there was a significant interaction between median cover type and sex (Wald's $\chi^2_{[1]} = 4.709$, $n = 190$, $P = 0.030$). Specifically, females were 95% (odds ratio = 0.048) less likely to be recaptured at sites with grass medians relative to treed medians.

For white-footed mice specifically, we translocated 71 individuals and recaptured 27 (38%) (Fig. 4). There was no significant effect of median cover type (Wald's $\chi^2_{[1]} = 1.03 \times 10^{-4}$, $n = 71$, $P = 0.992$), median width (Wald's $\chi^2_{[1]} =$

Fig. 3. (a) Combined number of individuals of six small-mammal species recaptured ($n = 45$) and not recaptured ($n = 145$) after translocation across highways containing grass or treed central dividing medians during 7-day trapping sessions. The probability of recapturing translocated individuals was not significantly related to median cover type (Wald's $\chi^2 = 0.052$, $P = 0.819$). (b) Recaptured (1) or not recaptured (0) vs. median width (m). The probability of recapturing an individual was not significantly related to median width (Wald's $\chi^2 = 0.176$, $P = 0.675$).

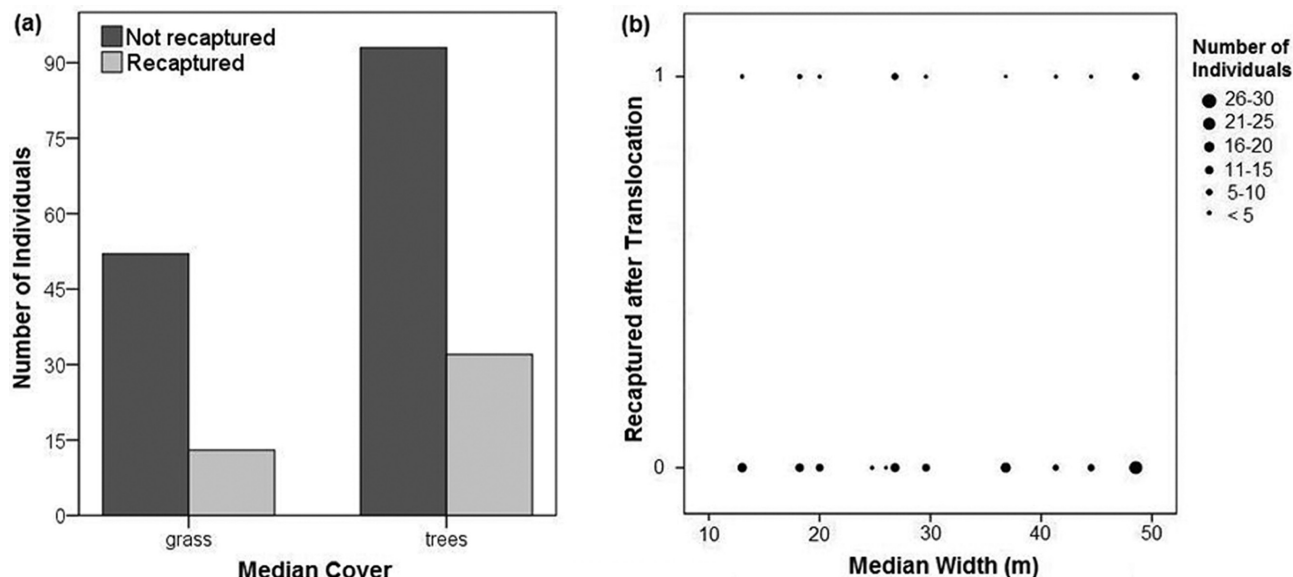
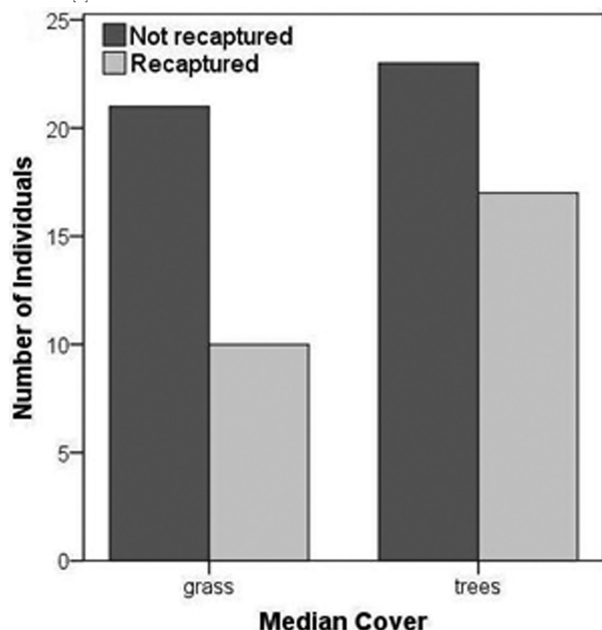


Fig. 4. Number of white-footed mice (*Peromyscus leucopus*) recaptured ($n = 27$) and not recaptured ($n = 44$) after translocation across highways containing grass or treed central dividing medians during 7-day trapping sessions. The probability of recapturing translocated individuals was not significantly related to median cover type (Wald's $\chi^2_{[1]} = 1.03 \times 10^{-4}$, $P = 0.992$).



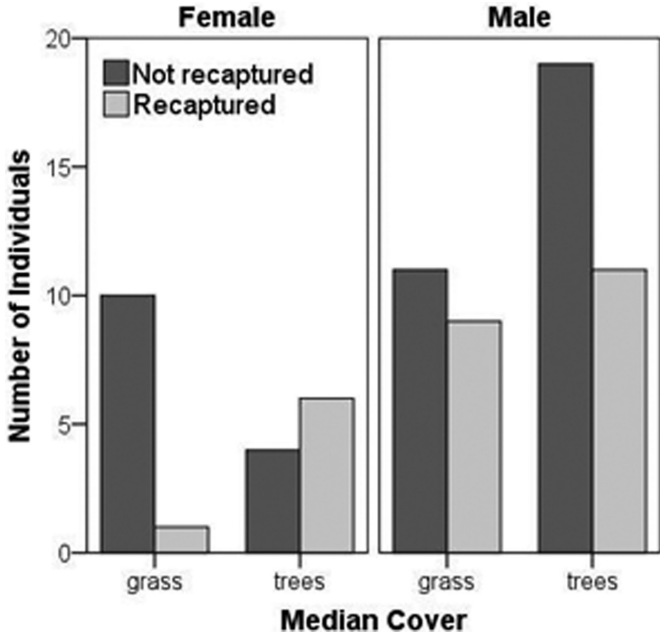
0.339, $n = 71$, $P = 0.561$), their interaction (Wald's $\chi^2_{[1]} = 0.018$, $n = 71$, $P = 0.895$), or sex (Wald's $\chi^2_{[1]} = 0.426$, $n = 71$, $P = 0.514$) on the probability of recapturing a translocated white-footed mouse. The significant interaction found between median cover type and sex when all species were included in the analysis was driven by white-footed mice, which also showed this significant interaction (Wald's $\chi^2_{[1]} =$

5.394, $n = 71$, $P = 0.020$): translocated females were 99% (odds ratio = 0.009) less likely to be recaptured at sites with grass medians relative to treed medians (Fig. 5). The interaction between median width and sex was marginally significant (Wald's $\chi^2_{[1]} = 3.008$, $n = 71$, $P = 0.083$) for white-footed mice: the odds of females being recaptured were 1.14 times the odds for males for every 1 m increase in median width. Age class (Wald's $\chi^2_{[1]} = 6.923$, $n = 71$, $P = 0.009$) and the number of days remaining in the trapping session (Wald's $\chi^2_{[1]} = 6.266$, $n = 71$, $P = 0.012$) were significant: the odds of a recapture were 25.5 times higher for adults than juveniles and increased by a factor of 1.9 for every 1 day increase in days remaining in the trapping session.

For southern red-backed voles, we translocated 71 individuals and recaptured only 8 (11.3%) (Fig. 6). With 8 recaptures, we could not fit a full multiple logistic regression including possible confounding variables. Therefore, we only included median cover type, width, and their interaction in the model. The probability of recapturing a translocated red-backed vole was not significantly related to median cover type (Wald's $\chi^2_{[1]} = 0.499$, $n = 71$, $P = 0.480$), median width (Wald's $\chi^2_{[1]} = 0.384$, $n = 71$, $P = 0.536$), or the interaction between median cover type and width (Wald's $\chi^2_{[1]} = 0.706$, $n = 71$, $P = 0.401$).

We could not statistically analyze the data for the remaining species individually because of low sample sizes and an inadequate number of study sites where captures occurred. Woodland jumping mice were trapped at 4 out of 11 study sites, all of which had wide medians (>30 m). In addition, approximately 70% of woodland jumping mice were trapped at one treed median site and all those that were recaptured ($n = 5$) occurred at this same site. Eastern chipmunks were trapped at 4 out of 11 study sites, 3 of which had narrow medians (<30 m). Only one adult female eastern chipmunk was recaptured.

Fig. 5. Number of translocated female ($n = 21$) and male ($n = 50$) white-footed mice (*Peromyscus leucopus*) that were recaptured and not recaptured. The interaction effect between sex and median cover type was significant (Wald's $\chi^2 = 5.394$, $P = 0.020$): the probability of recapturing females at highway sites with grass medians was significantly lower than at sites with treed medians.



All returned individuals were recaptured within 4 days of being released and 87% within 2 days. It took significantly fewer days to recapture individuals at sites with grass medians (mean = 1.15 days) than at treed median sites (mean = 1.75 days) (Student's t test with correction for unequal variance: $t_{[32.127]} = 2.848$, $n = 45$, $P = 0.008$). There was no significant relationship between median width and number of days it took to recapture individuals ($F_{[1,43]} = 1.064$, $n = 45$, $P = 0.308$).

Analyses of vegetation and traffic volume data

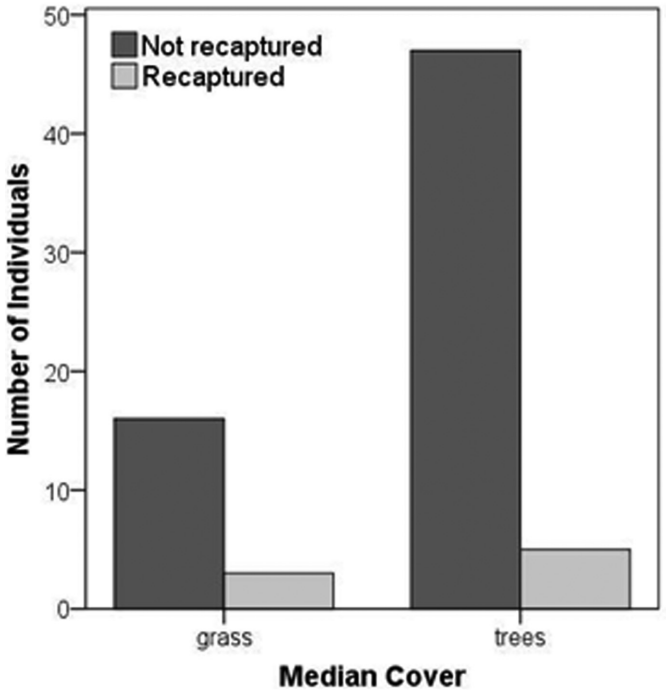
Of the 11 study sites, only 1 site showed a significant difference in the habitat structure between the two sides of the road (ANOSIM site 417G, $R = 0.708$, $P = 0.029$). Using the SIMPER function (PRIMER-E 2009), we identified differences in percentage of coarse woody debris between the trapping and the translocation sides of the highway for this one site contributed most (33%) to the within-site difference, with the trapping side containing more woody debris than the translocation side. For the remaining 10 sites, no significant differences in habitat structure were found (ANOSIM, all sites $P > 0.05$).

We found no significant relationships between any of the vegetation characteristics on the translocation side of the highway or traffic volume and median cover type or median width (Table 1).

Discussion

Neither median cover type nor width were significant main predictors of the probability of translocated small mammals returning across four-lane divided highways. There have

Fig. 6. Number of southern red-backed voles (*Clethrionomys gapperi*) that were recaptured ($n = 8$) and not recaptured ($n = 63$) after translocation across highways containing grass or treed central dividing medians during 7-day trapping sessions. The probability of recapturing translocated individuals was not significantly related to median cover type (Wald's $\chi^2 = 0.499$, $P = 0.480$).



been numerous studies on the movement of small mammals in relation to roads, but with the exception of the study by van der Ree et al. (2010) on squirrel gliders, this study is the first to examine the effects of vegetated median features on movement across divided highways. Contrary to our predictions, reducing the forest clearance created by a four-lane divided highway by having trees in the median or a narrower median does not provide a significant advantage for small-mammal movement over highway sections with grassy or wide medians. For treed medians, it is possible that some individuals may have started to cross the highway, but then chose to remain in the median. Adams (1984), for example, found small mammals inhabiting forested highway medians. Therefore, the effect of individuals choosing to remain in the median may have counteracted any predicted increase in cross-highway movement owing to reduced clearance provided by treed medians. Alternatively, it is possible that an effect of median cover type or width may have gone undetected given our small number of study sites. Nevertheless, if an effect exists, it almost certainly is small or else it would have been detected even with the relatively small sample size.

Our study design limited, to the extent possible, potential confounding effects. We can eliminate traffic volume as a possible confounding factor in our study. Individuals were recaptured across our range of study sites, which varied in average daily traffic from 12 000 to 32 800 vehicles (Ontario Ministry of Transportation 2005). In addition, previous work on small-mammal movements near and across roads indicates that the aversion of roads by small mammals is independent of traffic volume (Ford and Fahrig 2008; McGregor et al.

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Table 1. Comparisons of median cover type and width to annual average daily traffic (AADT) and 11 vegetation characteristics on the translocation side of the 11 study sites.

Response	Median cover		Median width			
	<i>t</i>	<i>P</i>	Standardized β	<i>F</i>	df	<i>P</i>
Traffic variable						
AADT	−0.355	0.731	−0.272	0.719	1, 9	0.418
Vegetation variables						
Tree dispersion	−0.618	0.552	−0.266	0.686	1, 9	0.429
Fallen log dispersion	0.436	0.673	−0.240	0.548	1, 9	0.478
Proportion canopy cover	−0.584	0.580	−0.063	0.036	1, 9	0.853
Proportion vegetation cover	0.836	0.425	0.330	1.097	1, 9	0.322
Percent coarse woody debris	−1.278	0.233	−0.333	1.125	1, 9	0.316
Coniferous shrub density	−1.000	0.363	0.538	3.674	1, 9	0.087
Deciduous shrub density	1.933	0.085	−0.194	0.354	1, 9	0.567
Coniferous sapling density	−0.742	0.477	−0.166	0.254	1, 9	0.626
Deciduous sapling density	−0.138	0.894	0.100	0.091	1, 9	0.770
Coniferous small tree density	−1.329	0.238	−0.025	0.006	1, 9	0.942
Deciduous small tree density	0.564	0.587	0.540	3.696	1, 9	0.087

Note: Student's *t* tests were performed to test for relationships with median cover type and regression analyses for relationships with median width. Negative *t* values represent a lower value of the variable at sites with grass medians relative to sites with treed medians. Positive *t* values represent a higher value of the variable at sites with grass medians relative to sites with treed medians.

2008). Furthermore, there were no correlations between traffic volume and median cover type or width in our study design.

Although our main predictors (median cover type and width) did not significantly affect the probability of recapturing translocated small mammals, we did find some interesting ancillary results. Specifically, the interaction between median cover type and sex was found to be a significant predictor of the probability of white-footed mice returning across the highway. Female white-footed mice were less likely to be recaptured when the median consisted of grassy vegetation, a result which may be explained by the behavioural ecology of small mammals. Females must select habitat that provides safe nesting areas, whereas males, who provide little parental care, are able to seek habitats based on resource availability and mates (Morris 1984). The predominant role of females as caregivers to their young likely guides them to be more vigilant and selective in their movements through the landscape and they may have perceived crossing highways with grass medians as more risky than crossing highways with treed medians. Males may be more willing to move through suboptimal, open spaces because of their drive for mating opportunities and resources.

Additionally, there was a significant effect of median cover type on the return time of translocated individuals. Small mammals translocated across highway sites with grass medians took significantly fewer days to return to their point of initial capture than individuals translocated across highway sites with treed medians. The habitat preferences of forest-dwelling small mammals and risk of predation in open spaces may make individuals feel vulnerable in areas that lack trees. Consequently, individuals crossing a divided highway containing a grass median, which may result in upwards of 80–90 m of total forest clearance, may do so quickly to reduce possible predation risk. On the other hand, treed medians offer protective cover and habitat for forest-dwelling small

mammals. Small mammals have been found in forested highway medians in similar densities to forests adjacent to divided highways (Adams 1984). Therefore, individuals that returned across highway sections containing treed medians may have spent time in the median, perhaps foraging, which could have resulted in longer recapture times for these individuals. Note, however, that all returning individuals were recaptured within 4 days of their translocation, 87% of them within 2 days. Therefore, the slightly longer return time of animals translocated across treed median sites did not confound our main result (above).

Over 95% of recaptured individuals were adults, relative to 78% of translocated individuals that were adults. The higher return rate for adults compared with juveniles could be due to the accumulation of an individual's experience in its surroundings with age. Kozel and Fleharty (1979) described two types of ranges for small mammals: home range, or the region containing the individual's basic activities, and life range, or the region that contains explorations outside of the home-range area. Mature small mammals will have made more exploratory excursions than juveniles, and hence, have larger life ranges. In our study, such explorations may have included previous successful crossings of the highways that we studied, and therefore, the adults were less likely to be disoriented after translocation. In addition, juveniles may have lower motivation to return across the highway, because they likely have not established territories at the site of their initial capture and are being stimulated to disperse by resident individuals (Gaines and McClenaghan 1980). The limited recapture of juveniles in our study is consistent with findings from other translocation studies (e.g., Kozel and Fleharty 1979; Bowman and Fahrig 2002).

We translocated equal numbers of southern red-backed voles and white-footed mice (71 of each species), but fewer southern red-backed voles were recaptured. This may suggest a species-specific response to four-lane divided highways.

This trend may be explained by differences in habitat preferences and dispersal abilities. A more generalist species, such as the white-footed mouse, will likely be less inhibited by the contrast between a forest and highway corridor compared with the red-backed vole, a forest specialist (Adams and Geis 1983; McDonald and St. Clair 2004). Furthermore, Witt and Huntly (2001) found that densities of red-backed voles in isolated forest patches were negatively correlated with distance from other forest areas, whereas deer mice, a closely related species to the white-footed mouse, showed no such effect. We expect that the difference in recapture rates between red-backed voles and white-footed mice in our study was the result of the stronger habitat specificity and smaller movement ranges of red-backed voles compared with white-footed mice.

It can be argued that movement of translocated individuals may not necessarily reflect movement under natural conditions. However, it is next to impossible to study the factors affecting cross-road movements of nontranslocated small mammals, because small mammals rarely cross roads during their everyday movements (Kozel and Fleharty 1979; Garland and Bradley 1984; Swihart and Slade 1984; Richardson et al. 1997; Goosem 2001; Clark et al. 2001; Rico et al. 2007a; Ford and Fahrig 2008; McGregor et al. 2008). This leaves cross-road translocations as the only alternative for studying factors affecting road crossing by small mammals. We, along with others who have conducted cross-road translocations (Kozel and Fleharty 1979; Richardson et al. 1997; Clark et al. 2001; McDonald and St. Clair 2004; Rico et al. 2007a; McGregor et al. 2008) implicitly assume that the results from such studies apply to small mammals crossing roads during exploratory or dispersal movements. Cross-road translocations are, therefore, essentially a way of determining whether small mammals could, in fact, cross roads, if they ever wanted or needed to in natural situations.

Although we did not find an effect of median vegetation type and width on small mammal cross-highway movements, we should not overlook the fact that some individuals were able to cross the entire highway. It is possible that other types of medians, particularly those containing physical barriers, such as concrete "Jersey barriers" or "Texas barriers" may not be as permeable and could affect small-mammal populations by significantly limiting movement across highways (Barnum 2003; Kociolek and Clevenger 2007). Empirical studies of the effects of these and other median barriers are lacking. Nevertheless, it is not clear that encouraging animals to attempt to cross multiple lanes of traffic by maintaining vegetation in medians would be most beneficial to the population, as it may increase wildlife mortality. For example, Cain et al. (2003) found that maintaining the preferred habitat of bobcats (*Lynx rufus* (Schreber, 1777)) in the median and along the verges of a four-lane divided highway in Texas increased the likelihood of crossings, but they also found that more bobcats were killed in these sections of the highway relative to other sections with less preferable cover types. Similarly, higher mortalities of white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) have been found where the highway median and verges provided areas for grazing (Bellis and Graves 1971). The net effect of divided highways with vegetated medians at the population level is likely a combination of the barrier and mortality effects (Jaeger and

Fahrig 2004; Jaeger et al. 2005). We found that small mammals were able to cross highways with vegetated medians and we did not detect any road-killed individuals at our study sites, suggesting that the benefit of vegetated medians (connectivity between fragmented habitat patches) may outweigh the cost (road mortality) for some species.

Our results suggest that four-lane highway crossings by small mammals are not strongly affected by vegetation type or width of the central median. Although previous studies have suggested that forest clearance is a central factor contributing to the barrier effect of roads on movement by forest-dwelling small mammals, our findings suggest that efforts to mitigate such an effect cannot be accomplished by altering the characteristics of a vegetated median, such as its vegetation type and width. The mere presence of a more natural median, rather than one containing structures such as concrete barriers, may be what is relevant for wildlife movement across divided highways. Further research on highway medians is needed to determine which designs will not only increase the willingness of animals to cross roads, but also increase their likelihood of a safe crossing.

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