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Do small mammals avoid roads because of the traffic?

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Summary

1. Roads can act as barriers to animal movement, which may reduce population persistence by reducing recolonization of empty habitats and limiting immigration. Appropriate mitigation of this barrier effect (e.g. seasonal road closures, location and design of wildlife over- or underpasses) depends upon whether the animals avoid the road itself or the traffic on the road. Empirical studies of road avoidance to date do not generally differentiate between these.

2. We conducted short- and long-distance translocations and trapping studies of white-footed mice (*Peromyscus leucopus*) and eastern chipmunks (*Tamias striatus*) near two-lane paved roads, which differed widely in traffic amount, from 47 to 15 433 vehicles per day.

3. In the trapping study (13 sites) only five animals moved across a road, in comparison to 36 animals that moved the same distance without an intervening road ($P < 0{\cdot}0001$). In the short-distance translocations (15 sites), 51% of the small mammals that were translocated across roads returned, in comparison to a return rate of 77% of animals that were translocated a similar distance with no intervening road ($P = 0{\cdot}009$).

4. In the long-distance translocation study (24 sites) we found that each intervening road reduced the probability of successful return by about 50%.

5. We found no significant effects of traffic amount on return rates in either the short-distance or the long-distance translocations studies.

6. Small mammal densities were not lower near roads and we found no evidence for a decrease in density near roads with increasing traffic amount.

7. *Synthesis and applications.* Our results suggest that small mammals avoid the road itself, and not emissions such as noise from the traffic on the roads. Our results imply that the barrier effect of roads on these species cannot be mitigated by measures aimed at reducing traffic amount; other measures such as wildlife passages would be needed.

Key-words: animal movement, barrier, dispersal, habitat fragmentation, permeability, *Peromyscus leucopus*, road avoidance, *Tamias striatus*, traffic, translocation

Introduction

Roads are a large threat to some wildlife populations (Forman *et al.* 2003). Most studies of the effects of roads on wildlife focus upon animal–vehicle collisions (called 'traffic mortality'; reviewed in Forman *et al.* (2003: 114–122). However, it has also been suggested that roads act as complete or partial barriers to movement for some species (e.g. Oxley *et al.* 1974; Mader 1984; Swihart & Slade 1984; Brody & Pelton 1989; Burnett 1992; Rondinini & Doncaster 2002; Shine *et al.* 2004; Whittington *et al.* 2004). Such a barrier effect could fragment habitat and reduce population persistence by reducing recolonization of empty habitats and/or limiting immigration.

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That roads act as barriers to movement for some species implies that these species avoid roads (i.e. they are reluctant to cross them). Jaeger *et al.* (2005) discussed three types of possible road avoidance and argued that the type of avoidance largely determines the mechanism and strength of road effects on a population. The three types of avoidance behaviour are: (i) animals may avoid the road itself as it is a hostile environment onto which they will not venture (called 'road surface avoidance'); (ii) animals may avoid emissions from traffic such as fumes or noise, keeping them some distance away from the road [we call this 'general traffic avoidance'; Jaeger *et al.* (2005) call it 'noise avoidance']; or (iii) animals may avoid individual vehicles, waiting for a break in traffic before attempting to cross the road (called 'car avoidance'). In the case of road surface avoidance alone, all roads of similar type and size would have the same degree of barrier effect (i.e. the same permeability) to movement, irrespective of traffic amount. In the case of general traffic avoidance alone, the degree of barrier effect would be minimal for low-traffic roads, and would increase with increasing traffic amount. Car avoidance should reduce the degree of barrier effect for low- and medium-traffic roads, where breaks in traffic would be long enough for individual animals to cross successfully. When traffic is very high, such as on freeways, animals with car avoidance would never or rarely attempt to cross, so the barrier effect would be strong. These avoidance behaviours are not mutually exclusive; particular species could exhibit more than one (or none) of them.

Past empirical studies of road avoidance have not generally differentiated among types of road avoidance. Several studies were conducted on only one road (e.g. Swihart & Slade 1984; Burnett 1992; McDonald & St Clair 2004a; Shine *et al*. 2004), and studies conducted on more than one road (i.e. with different traffic amounts) confounded road type/width with traffic amount: dirt and gravel roads had lower traffic amounts than paved roads, and two-lane paved roads had lower traffic amounts than four-lane highways (e.g. Oxley *et al*. 1974; Mader 1984; Brody & Pelton 1989; Mader *et al*. 1990; Lovallo & Anderson 1996; Rondinini & Doncaster 2002; Whittington *et al*. 2004). Thus, the effects of traffic amount on road-crossing responses of animals cannot be distinguished from the effects of road type or width.

Differentiation among these types of road avoidance is of practical importance for the mitigation of the barrier effect of roads. For example, if animals show general traffic avoidance, mitigation may be necessary only for high-traffic roads. An appropriate measure might be road closures during migration periods. If wildlife passages are built, they would need to be designed such that traffic noise and other emissions are reduced or eliminated on and near the passages (Reijnen *et al*. 1995; Clevenger *et al*. 2001). In contrast, if the animal avoids the road itself, irrespective of the amount of traffic on it, then road closures will not reduce the barrier effect of the road. Wildlife passages will be necessary. For such species, passages may be necessary even on roads with very low traffic if these roads bisect areas containing required resources.

The purpose of this study was to determine which type(s) of road avoidance are responsible for road avoidance by small mammals. We conducted short- and long-distance translocations and trapping studies at different road sites of similar road type and width, but which differed widely in their traffic amounts. This allowed us to differentiate between the influences of the road surface itself and the traffic on the road. If small mammals avoid the road surface but are insensitive to traffic noise or individual cars, we predicted that small mammals should reduce their movements across roads relative to their movements in continuous habitat, and there should be no effect of traffic amount on across-road movement rate. Also, in this case small mammal densities should not be reduced near the road. In contrast, if small mammals avoid traffic noise but not the road surface itself, we predicted that the frequency of small mammal movements across roads should decrease with increasing traffic amount. General traffic avoidance should also result in lower small mammal densities near roads than further from roads. Finally, if small mammals avoid individual cars, we predict reduced across-road movement at very high traffic amounts but, unlike general traffic avoidance, a decrease in small mammal densities near roads should not occur.

The two small-mammal species studied, white-footed mice (*Peromyscus leucopus*) and eastern chipmunks (*Tamias striatus*), are sufficiently abundant for the translocation study. They also represent two different time-periods of activity relative to the peaks of traffic on the roads in our area. In our area, traffic amounts are highest from 7.00 a.m. to 9.00 a.m. and from 4.00 p.m. to 6.00 p.m. We expected that traffic amount would have a larger effect on cross-road movement by the eastern chipmunk than by the white-footed mouse, because the former is diurnal while the latter is nocturnal.

Materials and methods

TRAPPING STUDY

A trapping study was undertaken to survey the densities of small mammals, and to quantify small mammal movement. The goal of the trapping study was to determine whether (i) small mammals show a lower tendency to spontaneously move across roads than a similar distance where no road intervenes; (ii) the tendency for small mammals to move across roads decreases with increasing traffic; (iii) small mammal densities are lower near roads than further from roads; and (iv) densities of small mammals near roads decrease with increasing traffic on the road.

We established 13 trapping sites. Each site included a 100 m length of two-lane paved road with shoulders and ditches but without approaches, driveways, culverts, streetlights or sidewalks. At each site there was forest on both sides of the road. We obtained traffic estimates (average number of vehicles per day) from the City of Ottawa (May–June counts) and selected road segments to cover a large range of traffic values, from 47 to 15 433 vehicles per day.

Each trapping site consisted of three square trapping grids containing 36 traps at 10 m spacing (Fig. 1). Two of the grids were

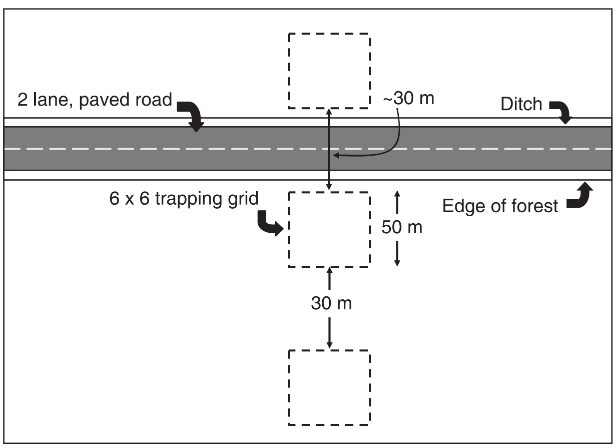

Fig. 1. Illustration of one trapping site for the trapping study (see Methods). Trapping was conducted at 13 similar sites, varying in traffic amount from 47 to 15 433 vehicles per day.

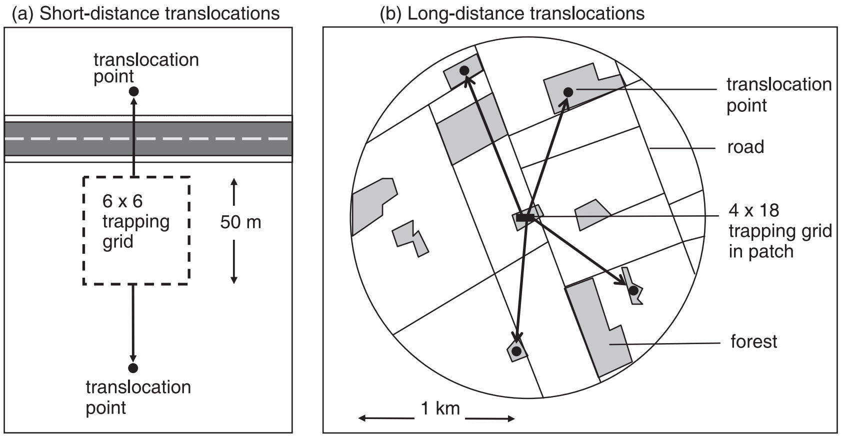

Fig. 2. Illustration of translocation experiments. (a) Short-distance translocations: animals were trapped and translocated 35 m from the edge of the trapping grid, either across the road or further into the forest. Fifteen sites were used, ranging in traffic amount from 47 to 15 433 vehicles per day. (b) Animals were trapped and translocated to another forest patch within 1.25 km of the trapping site. Twenty-four sites were used, with animals translocated across zero to four roads, with total traffic amounts of zero to 15 433 vehicles per day.

on either side of the road ('roadside grids') beginning 10 m from the road edge, so that all traps were in forest. The third grid ('interior grid') was further into the forest on one side of the road, with 30 m between the roadside grid and the interior grid, to match the distance approximately between the two roadside grids. We used Sherman™ non-folding aluminium traps baited with peanut butter and sunflower seeds to trap white-footed mice and eastern chipmunks. We trapped each site for 6 consecutive days, and checked traps each morning (8–10 a.m.) and late afternoon (4–5 p.m.). Captured animals were ear-tagged and released at point of capture.

A movement was recorded when an individual that was trapped and tagged at one grid was trapped later in another grid. We used a χ^2 contingency test to compare the number of small mammals that moved between the two roadside trapping grids (i.e. crossed the road) relative to the number that moved between the nearest roadside grid and the interior grid (i.e. moved a similar distance without an intervening road). We compared the number of animals trapped (index of density) near the road vs. numbers trapped further into the forest using a pairwise *t*-test, comparing the mean number of animals trapped at the two roadside grids to the number trapped at the forest interior grid for each site (Fig. 1). To determine whether traffic decreased the number of animals near roads, we performed a simple linear regression comparing the number of individual animals found in the roadside grids at each site to the traffic amount, for both species combined and for each species separately.

TRANSLOCATION STUDIES

From the trapping study (above), we determined that small mammals are unlikely to cross roads during their regular movements. However, even if small mammals are unlikely to cross roads during their regular movements, their motivation and tendency to cross roads may increase during particular movement events, e.g. during dispersal. To simulate such high-motivation situations, we performed translocation experiments in which we moved animals across roads and determined the probability that they returned to the point of capture. We performed these translocations in both the immediate neighbourhood of the road ('short-distance translocations'), to evaluate the effects of varying traffic amount while holding road type and size approximately constant, and over much longer distances ('long-distance translocations') to simulate dispersal movements more accurately. The translocation studies provided information on whether (i) small mammals translocated across a road are less likely to return than animals translocated a similar distance without an intervening road; (ii) the probability of animals returning across a road decreases with increasing traffic amount on the road; and (iii) the probability of small mammals returning following long-distance translocations decreases with increasing number of intervening roads and/or increasing traffic amount on the intervening road(s).

SHORT-DISTANCE TRANSLOCATIONS

We established 15 sites for the short-distance translocations. These sites were selected using the same criteria as in the trapping study, and they varied in traffic amount from 47 to 15 433 vehicles per day. With three exceptions, the short-distance translocation study sites were on the same road segments as in the trapping study, but displaced by about 200 m along the road. Each site consisted of one trapping grid of 36 traps (Fig. 2a). Captured white-footed mice and eastern chipmunks were ear-tagged and translocated in mesh bags 35 m from the edges of the grid, either across the road or further away from the road into the forest (Fig. 2a). At the two release points, the releaser stood between the released animals and the trapping grid from which they were removed. After releasing the animals, the releaser returned directly to the trapping grid. We trapped and conducted translocations at each site for 6 consecutive days, each morning (8–10 a.m.) and late afternoon (4–5 p.m.). Marked animals that were recaptured within the trapping session for each site were recorded as returned successfully.

We compared the returns of small mammals translocated across the road to those translocated on the same side of the road using a *G*-test of independence. We determined whether the probability of an animal returning from across the road decreased with increasing traffic amount using logistic regression analysis with traffic amount and species as predictor variables.

LONG-DISTANCE TRANSLOCATIONS

For the long-distance translocations, we trapped animals in 24 forest patches around the Ottawa region. In each patch, we used a rectangular grid of four transects at 10 m spacing, each containing 18 traps, with 5 m spacing between traps within transects. Each patch was trapped for 6 consecutive days. On initial capture, all white-footed mice and eastern chipmunks were marked with an ear tag and then translocated to another forest patch within 1·25 km of the trapping site (Fig. 2b). Tagged mice or chipmunks that returned within the trapping session were recorded as returning successfully.

We determined whether the probability of return of each species decreased with number of intervening roads (between the capture site and the translocation site) and total traffic amount on those roads, using stepwise multiple logistic regression analyses. We included distance between capture and release sites as a covariate in the analysis to control for the negative effect of translocation distance on small mammal return rates (Bender & Fahrig 2005).

Results

Although the roads and associated forest sites selected were as similar as possible (with the exception of traffic amount), it was not possible to control completely for variation in road width, canopy cover, canopy type and ground cover type. Road widths varied from 6·8 to 14·4 m for the pavement width only, and from 6·8 to 17·8 m for the pavement plus gravel shoulders. Mean canopy cover ranged from 20 to 55%. In six sites the dominant canopy trees were mainly coniferous, in five sites they were mainly deciduous and in five sites they were mixed. In eight of the sites the ground cover was mainly herbaceous vegetation, while in the other eight sites litter was the dominant ground cover.

However, these differences among sites were not correlated with traffic amount. The correlation between traffic amount and pavement width was $r = 0{\cdot}17$ ($P = 0{\cdot}53$, $n = 16$), between traffic amount and the width of pavement plus gravel shoulders was $r = 0{\cdot}37$ ($P = 0{\cdot}15$, $n = 16$) and between traffic amount and mean canopy cover was $r = -0{\cdot}23$ ($P = 0{\cdot}39$, $n = 16$). There was no significant relationship between traffic amount and dominant canopy tree composition [analysis of variance (ANOVA) $R^2 = 0{\cdot}04$, $P = 0{\cdot}75$, d.f. = 2,13], or between traffic volume and dominant ground cover (ANOVA $R^2 = 0{\cdot}002$, $P = 0{\cdot}86$, d.f. = 1,14). Because there was no association between site characteristics and traffic amount, site characteristics are unlikely to have confounded our results (below).

TRAPPING STUDY

We captured 136 white-footed mice and 104 eastern chipmunks in 8424 trap nights. Sixty-eight mice and 54 chipmunks were recaptured at least once after their initial capture (50% and 52% recaptured, respectively). Forty-one small mammals moved among grids; 36 (17 mice and 19 chipmunks) moved between roadside and forest interior grids, whereas only five (four chipmunks and one mouse) moved between roadside grids. This difference was statistically significant ($\chi^2 = 24{\cdot}4$, $n = 41$, $P < 0{\cdot}0001$). Due to the small number of animals crossing roads, we could not evaluate the effect of traffic amount on the probability of across-road movement.

There was no significant difference between the number of mice captured in roadside and interior grids (Fig. 3; paired-$t = 0{\cdot}24$, d.f. = 12, $P = 0{\cdot}82$). Roadside grids had significantly more chipmunks than interior grids (Fig. 3; paired-$t = 2{\cdot}9$, d.f. = 12, $P = 0{\cdot}014$). There was no significant effect of traffic amount on the number of animals trapped in the sites (Fig. 4; for mice: $F = 0{\cdot}02$, d.f. = 1,11, $P = 0{\cdot}88$; for chipmunks: $F = 2{\cdot}2$, d.f. = 1,11, $P = 0{\cdot}17$).

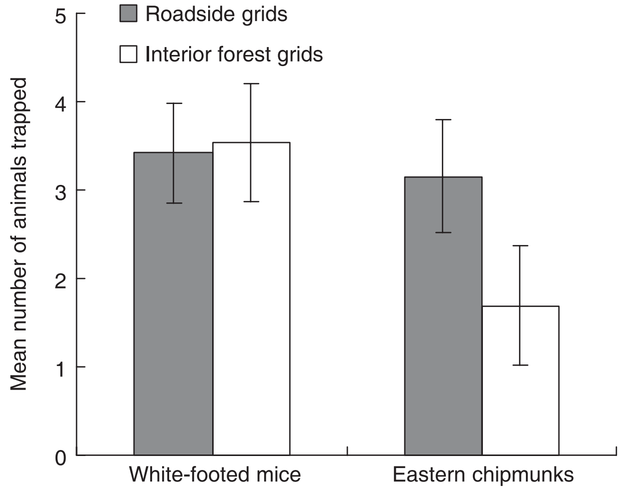

Fig. 3. Mean numbers (± SE) of white-footed mice and eastern chipmunks trapped in roadside trapping grids and interior forest trapping grids. There was no significant difference for white-footed mice (paired-$t = 0.24$, d.f. = 12, $P = 0.82$); the number of chipmunks trapped in roadside grids was significantly higher than the number trapped in interior forest grids (paired-$t = 2.9$, d.f. = 12, $P = 0.014$).

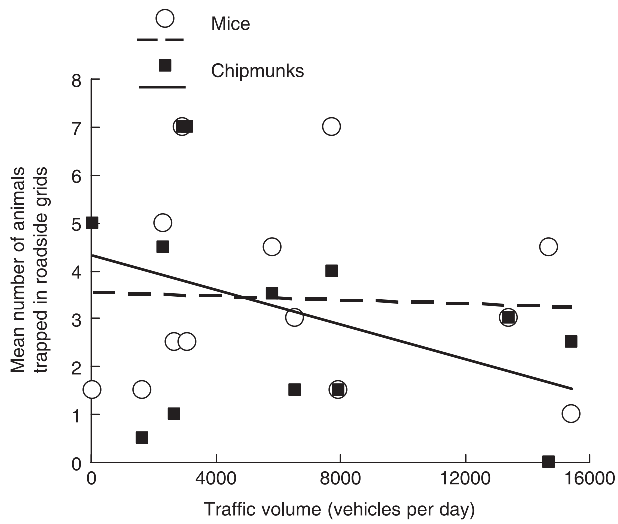

Fig. 4. Mean number of animals trapped in roadside grids vs. traffic amount; means were calculated for the two roadside grids at each site. Linear regression lines are shown, although both are non-significant at $\alpha = 0.05$ (white-footed mice: $F = 0.02$, $P = 0.88$; eastern chipmunks: $F = 2.2$, $P = 0.17$).

TRANSLOCATION STUDIES

Of the 91 small mammals translocated during the short-distance translocation study, 58 were recaptured. Of the 47 animals (22 white-footed mice, 25 eastern chipmunks) translocated across roads, 24 returned (13 mice, 11 chipmunks). Of the 44 small mammals (25 mice, 19 chipmunks) that were translocated on the same side of the road, 34 returned (18 mice, 16 chipmunks). Significantly more of the animals translocated on the same side of the road returned than for animals translocated across the road (Fig. 5; $G = 6{\cdot}9$, $n = 91$, $P = 0{\cdot}009$). Analysed separately, this result was due mainly to a significant reluctance of

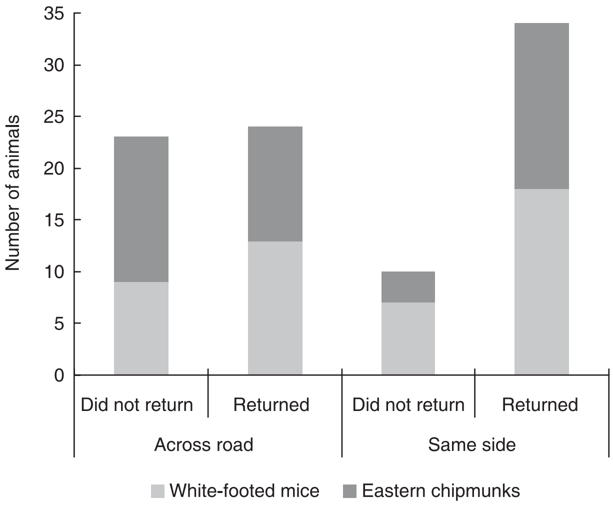

Fig. 5. Number of white-footed mice and eastern chipmunks returning to their capture sites after being translocated either across a road or the same distance further into the forest on the same side of the road as the capture site (see Fig. 2a). Fifteen sites were used, ranging in traffic amount from 47 to 15 433 vehicles per day. There was a significantly higher rate of return for animals translocated on the same side of the road than for animals translocated across the road ($G = 6.9$, $P = 0.009$), which was due mainly to a response by chipmunks (mice: $G = 0.87$, $P = 0.35$; chipmunks: $G = 7.8$, $P = 0.005$).

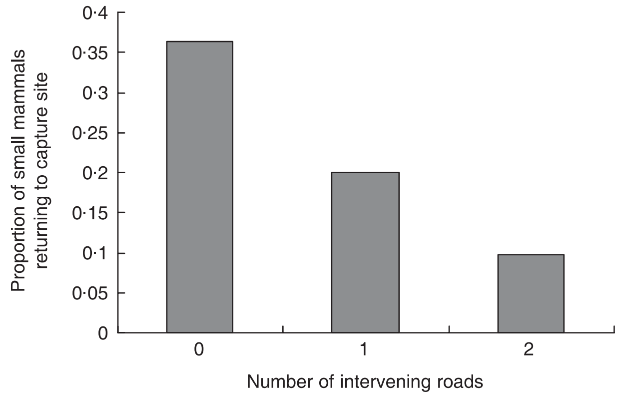

Fig. 6. Proportion of small mammals returning from long-distance translocations (see Methods), when translocated across zero, one or two roads (Table 1: Wald $\chi^2 = 16.1$, $P < 0.0001$). The number of animals translocated was 77, 170 and 62, respectively. In addition, two animals were translocated across three roads, and one animal was translocated across four roads; none of these three animals returned to its capture site.

chipmunks to return across the road (mice: $G = 0{\cdot}87$, $n = 47$, $P = 0{\cdot}35$; chipmunks: $G = 7{\cdot}8$, $n = 44$, $P = 0{\cdot}005$). For the 47 animals translocated across the roads, we found no significant effects of traffic amount (Wald $\chi^2 = 1{\cdot}5$, $P = 0{\cdot}22$), species (Wald $\chi^2 = 1{\cdot}7$, $P = 0{\cdot}2$) or the interaction between species and traffic amount (Wald $\chi^2 = 0{\cdot}63$, $P = 0{\cdot}43$) on the probability of small mammals returning to their initial capture site following translocation across roads.

In the long-distance translocation study, we marked and translocated 312 individuals (197 white-footed mice and 115 eastern chipmunks) from 24 patches over 10 368 trap nights. After controlling for a strong negative effect of distance between capture and translocation sites, we found that the number of intervening roads significantly negatively affected the probability of return of both white-footed mice (Wald $\chi^2 = 9{\cdot}1$, $n = 197$, $P = 0{\cdot}0025$; Table 1a) and eastern chipmunks (Wald $\chi^2 = 7{\cdot}2$, $n = 115$, $P = 0{\cdot}0072$; Table 1b). The probability of return decreased by about 50% with the addition of each intervening road (Fig. 6). The probability of return of white-footed mice was marginally significantly negatively affected by total traffic amount on the intervening roads ($\chi^2 = 2{\cdot}8$, $P = 0{\cdot}095$; Table 1a).

Table 1. Multiple logistic regression analysis results of the probability of small mammals returning to the site where they were captured following long-distance translocations on translocation distance, traffic amount, and number of intervening roads (see Methods; n = 197 white-footed mice and 115 eastern chipmunks)

Parameter	Estimate	Wald χ^2	*P*
(a) *Peromyscus leucopus* (white-footed mouse)			
Intercept	0·71	3·3	0·069
Translocation distance	–0·0033	16·7	< 0·0001
Number of roads	–0·85	9·1	0·0025
Traffic	–0·00011	2·8	0·095
(b) *Tamias striatus* (eastern chipmunk)			
Intercept	1·02	2·6	0·11
Translocation distance	–0·0046	9·3	0·0023
Number of roads	–1·4	7·2	0·0072
Traffic	–0·00006	0·45	0·50

Discussion

Taken together, our results suggest that small mammals avoid the road surface itself rather than traffic noise or other emissions. There are three lines of evidence that support this conclusion. First, we predicted that if small mammals avoid the road surface, they should show reduced movement across roads relative to movements on the same side of the roads. Both the trapping study and the translocation studies supported this prediction. Very few animals moved across roads in the trapping study. In the short-distance translocations, 51% of the small mammals that were translocated across roads returned, in comparison to 77% of the animals that were translocated a similar distance within the forest. Kozel & Fleharty (1979) also found that over half of all rodents (including *P. maniculatus*, a close relative of *P. leucopus*) translocated across roads did not return. Bakowski & Kozakiewicz (1988) found that bank voles translocated into continuous forest returned to the trapping grid faster and in greater numbers than those translocated to the other side of a road. Our long-distance translocation study was consistent with the short-distance translocation results; each intervening road reduced the probability of successful return by about 50%. Of course, the fate of the animals that did not return is unknown. We do not know whether they avoided the roads or were killed on them. However, if it was mortality, the return rate should have decreased with increasing intervening traffic amount, which it did not.

Secondly, we predicted that if small mammals only avoid the road surface and not traffic noise or other emissions, the probability of movement across roads should not change with increasing traffic amount. On the other hand, if they are repelled strongly by traffic noise (or suffer from direct traffic mortality), the probability of movement across roads should decrease with increasing traffic amount. We found no significant effects of traffic amount on return rates in either the short-distance or the long-distance translocation studies, even though our study sites varied widely in traffic amounts. Note that these results do not preclude the possibility that small mammals show a weak negative response to traffic. There are several possible sources of noise in the data, including variations in habitat type, between-individual capturability and possible tag losses, which could obscure a weak response to traffic.

Thirdly, we predicted that if small mammals only avoid the road surface, their densities should not be reduced near roads. In contrast, if they avoid traffic noise, the densities should be lower near roads, and the densities near roads should decrease with increasing traffic amount. Small mammal densities were not reduced near roads; in fact, densities of eastern chipmunks were actually higher near the roads. This increase may have resulted from the combined effects of the road acting as a barrier to movement and the habitat edge along the road funnelling movement along it (e.g. Doncaster *et al*. 2001). Garland & Bradley (1984) found no relationship between proximity to a road and home range size or life span of desert rodents. We also found no evidence for a decrease in density near roads with increasing traffic amount (with the same caveat as above). These results suggest that small mammals mainly avoid the road surface itself, rather than emissions such as noise from the traffic on the roads.

Our results are equivocal on the issue of whether small mammals avoid individual cars, waiting for a break in traffic before attempting to cross a road (car avoidance). For car avoidance we predicted that across-road movements would decrease with very high traffic amounts, with no decrease in small mammal density near roads. We found a small, marginally significant decrease in return rates with increasing traffic amount for white-footed mice in the long-distance translocation experiment. For car avoidance, one might not expect a strong statistical effect, because even on busy roads there are time-periods when traffic is lighter and when car-avoiding animals might find sufficient breaks in traffic to cross the road. We found no decrease in small mammal density near roads, even high-traffic roads, which is consistent with car avoidance. Although we did not search systematically for carcasses, we did not observe any dead mice or chipmunks in over 600 h of field work. Therefore, we cannot rule out the possibility that mice and chipmunks avoid individual cars. Further research is needed to test this conclusively.

We had expected a stronger effect of traffic on eastern chipmunks than on white-footed mice, because eastern chipmunks are diurnal and therefore more exposed to traffic than white-footed mice, which are nocturnal. Although our results suggest that eastern chipmunks may avoid roads more strongly than white-footed mice (Fig. 5), there was no evidence to suggest a difference between the two species in their responses to traffic amount. The fact that we did not find a stronger effect of traffic amount on eastern chipmunks than on white-footed mice further supports our conclusion that small mammals avoid the road itself rather than the traffic on it. A road is present and creating a barrier to movement at all times, whether the animal approaches it during the day (eastern chipmunks) or night (white-footed mice), and whether or not there is traffic on it.

Our results were not confounded by associations between traffic and site characteristics. Dominant canopy type (coniferous, deciduous or mixed), percentage of canopy cover and dominant ground cover type (litter or vegetated) were not related to traffic. The roads were selected purposefully to be as similar in width as possible. Unavoidably, there was a weak (although not statistically significant) positive correlation between total road width (pavement plus gravel shoulder) and traffic ($r = 0{\cdot}37$, $P = 0{\cdot}15$, $n = 16$). We might have expected this weak correlation to result in a spurious negative effect of traffic amount on movement across roads. As we did not find a relationship between traffic amount and movement across roads, our conclusion that small mammals avoid the road surface itself rather than traffic noise or other emissions is robust.

This study is the first to show, over a wide range of traffic amounts, that traffic amount plays little or no role in road avoidance by white-footed mice and eastern chipmunks. Goosem (2002) studied the effect of traffic amount on road crossing by small mammals on narrow, dirt, rainforest roads that ranged in traffic amounts. As in our study, she found little or no effect of traffic amount on small mammal road-crossing. However, the traffic amounts on the roads in Goosem (2002) were all very low (less than a few hundred cars per day). Our study extends this by showing that small mammals do not respond to a very large range in traffic amount, from less than 50 to over 15 000 vehicles per day.

Jaeger *et al*. (2005) argue that the type of avoidance, i.e. avoidance of the road itself or the traffic on the road, is critical for predicting the probable effects of roads on population persistence. Small mammals in the Ottawa area are known to suffer frequent local extinctions (about 5–15%) due to high overwintering mortality (Merriam & Wegner 1992). If roads create partial barriers to movement, this could reduce the likelihood and/or the speed of recolonization of empty forest patches in the spring and summer. According to the model proposed by Jaeger *et al*. (2005), animals that show road surface avoidance should be highly vulnerable to these effects. Therefore, our results imply that small mammal population sizes should be lower in landscapes with higher road densities. On the other hand, if small mammals do avoid cars, as hinted at by our data, the predicted effect of road density on small mammal populations would be lessened (Jaeger *et al*. 2005). We are not aware of any data available to evaluate the effect of road density on small mammal populations; this will require further research.

Although our results and those of Goosem (2002) suggest that small mammals do not show general traffic avoidance, there is some evidence that larger animals may avoid traffic.

Results of radiotelemetry studies on black bears (Brody & Pelton 1989; Beringer *et al*. 1990) and bobcats (Lovallo & Anderson 1996) have been interpreted as evidence of traffic avoidance, although a radiotelemetry study of grizzly bears indicated that road avoidance was independent of traffic amount (McLellan & Shackleton 1988). Seiler (2005) found that the traffic mortality of moose in Sweden increased with increasing traffic amount up to about 5000 vehicles per day, but then decreased at higher traffic amounts. He interpreted this to mean that moose avoid high-traffic roads. Similarly, an analysis of badger traffic mortality in Britain showed that badger deaths increased asymptotically with traffic amount; again the authors interpreted this to mean that badgers showed avoidance of high traffic roads (Clarke *et al*. 1998). In these studies, traffic amount was confounded with road size and/or type, so the conclusions regarding traffic amount are not definitive. A recent study of elk response to off-road all-terrain vehicles provides the strongest evidence of animals moving to avoid vehicles (Preisler *et al*. 2006).

Finally, our study has implications for the effectiveness of different possible mitigation strategies aimed at reducing the barrier effect of roads on small mammal movement. Measures aimed at reducing traffic amount or traffic speed or altering the timing of traffic seasonally or daily would not mitigate effectively the effects of roads on small mammal movement. More effective measures might be construction of suitable wildlife passages (Clevenger *et al*. 2001; McDonald & St. Clair 2004b), reduction of the width of the road and/or the road right-of-way, and in extreme cases (e.g. mitigation for endangered species), removal of the road itself. Our results also support the suggestion that conservation of large roadless areas should be a priority (Crist *et al*. 2005).

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