MOVEMENT PATTERNS OF EASTERN CHIPMUNKS (*TAMIAS STRIATUS*) NEAR ROADS

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Previous studies suggest that eastern chipmunks (*Tamias striatus*) avoid roads, but it is unclear whether vehicle traffic plays a role in this avoidance. The purpose of this study was to determine whether road avoidance in chipmunks increases with traffic. We tracked the movements of 68 chipmunks released near roads with widely varying volumes of traffic. Our results suggest that chipmunks responded to changes in traffic volume only in the preliminary stages of their movement pathways. Apart from this initial response, we found that road avoidance was independent of traffic, with evidence that chipmunks avoided both the roadside verge and the road surface. Because avoidance of roads was independent of traffic, effects of roads on populations of chipmunks may be manifest more as population subdivision than as direct mortality.

Key words: acclimatization, barrier, edge, fragmentation, highway, pathway, traffic, translocation, vehicle

Road networks and traffic volumes are increasing in many jurisdictions, with concomitant increases in the negative effects of roads and traffic on persistence of wildlife populations (Forman et al. 2003). Traffic may affect wildlife populations directly through mortality from wildlife–vehicle collisions and indirectly through habitat fragmentation if individuals avoid crossing roads because of traffic (e.g., Dodd et al. 2004; Fahrig et al. 1995; Findlay and Bourdages 2000; Forman et al. 2003; Jaeger et al. 2005; Saeki and Macdonald 2004). Road avoidance can lead to genetic subdivision of populations or isolated subpopulations, which may, in turn, decrease population persistence (Fahrig 2003).

Several studies have examined the effects of roads on the movement of small mammals and found that many species exhibit some degree of road aversion (e.g., Burnett 1992; Clark et al. 2001; Conrey and Mills 2001; Mader 1984; McDonald and St. Clair 2004a; Rico et al. 2007; Rondinini and Doncaster 2002; Swihart and Slade 1984). We found only 3 studies that have directly examined the effect of traffic volume on movement of small mammals. Goosem (2002) found that road avoidance was the same at low-traffic sites (4 $\pm$ 1 *SE* vehicles/day) and high-traffic sites (264 $\pm$ 71 vehicles/day) for 3 species of tropical small mammals. Richardson et al. (1997) found that 2 species of vole had a significantly higher rate of road crossing at low traffic sites (<60 vehicles/h) than at high-traffic sites

(>250 vehicles/h). McGregor et al. (2007) found a weak negative effect of traffic volume on movement across roads by white-footed mice (*Peromyscus leucopus*). These studies suggest that traffic may play a role in road avoidance for some small mammal species.

There are 2 potential limitations with the design of many studies of road avoidance by small mammals: confounding road variables and use of capture–mark–recapture methods. Road variables, such as width, surface composition, and traffic volume are often confounded so it is difficult to determine the mechanism underlying aversive behavior to the road environment. For example, studies indicate that eastern chipmunks (*Tamias striatus*) may be less averse to small, dirt or gravel roads than to wider, paved roads (Conrey and Mills 2001; Getty 1981; McGregor et al. 2007; Oxley et al. 1974). Because small, dirt or gravel roads typically have less traffic than wider, paved roads, it is not clear whether the difference in road aversion is due to road type or traffic volume. Standardizing 1 or more road variables (e.g., width and surface composition) while testing for a response to the variable of interest (e.g., traffic) would help to clarify this issue.

Capture–mark–recapture techniques typically involve monitoring livetrapping grids on both sides of a road to record the movement of marked individuals at trap locations. Animal movement is either spontaneous (e.g., Goosem 2001) or induced through the translocation of animals across the road (e.g., Rico et al. 2007). Results of capture–mark–recapture studies are difficult to interpret when attempting to address questions of movement near roads for at least 3 reasons. First, capture–mark–recapture methods are based on a discrete, often categorical, representation of space. With this approach there is

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TABLE 1.—Traffic volume and road or forest configuration at release sites near Ottawa, Ontario, Canada.

Site	60-min traffic count, $\bar{X}$ (SD)	Categorical traffic volume[a]	Width of verge on release side of the road (m)[b]	Distance between forest edges across road (m)
A	1185 (590.38)	H	22	42
B	240 (92.69)	H	12	26
C	206 (68.94)	H	10	28
D	93 (65.78)	L	14	35
E	47 (12.06)	L	9	25
F	46 (12.97)	L	9	23

[a] H = high; L = low.
[b] Verge width = $\lambda - 4$ (see Fig. 1).

no way to determine how animals move between recaptures (Clark et al. 2001). For example, animals may move onto the road surface and then turn back toward roadside habitat as a vehicle approaches (Andrews and Gibbons 2005). This pattern of movement suggests that animals are avoiding individual vehicles. Other animals may avoid roads while traveling within roadside habitat in response to vehicle emissions such as noise or pollutants. In both cases, road avoidance increases with traffic volume but the 2 responses can have different effects on population persistence (Jaeger et al. 2005). Using the frequency of road crossings as a measure of avoidance would not distinguish these 2 responses in the capture–mark–recapture approach. Second, many capture–mark–recapture studies do not attempt to standardize the motivation to cross the road with respect to the road variables of interest (but see McDonald and St. Clair 2004a). For instance, dispersing individuals may be caught at the same location as territorial individuals and, after being translocated a short distance across the road, territorial individuals may have a stronger motivation to return to their home range than dispersing individuals (Kozel and Fleharty 1979). Third, some species of small mammals use roads to define the boundaries of their home range (Burnett 1992; Mader 1984; Swihart and Slade 1984). Capture–mark–recapture studies that depend on the spontaneous movement of individuals outside the home range can confound road avoidance behavior with avoidance of conspecific home ranges or territorial boundaries. Quantifying individual movement in novel terrain using tracking methods would help to alleviate some of these issues.

The purpose of this study was to test the hypothesis that the eastern chipmunk, a forest-dwelling small mammal, avoids roads independently of traffic volume by tracking movements of individuals translocated to novel terrain near roads of similar design but with varying volumes of traffic. We predicted 3 responses if chipmunks avoid roads because of traffic. First, the probability of crossing a road should decrease with increasing traffic. Second, the probability of chipmunks turning away from the road should increase, relative to the probability of them turning toward the road, with increasing traffic. Third, if chipmunks avoid the road because of traffic emissions such as noise, surface vibration, or pollutants, then animals should stay farther away from the road as traffic increases (Forman et al. 2003; Jaeger et al. 2005). Finally, we wanted to know whether road avoidance in chipmunks is caused by reluctance to move

out of forest habitat or an aversion to the road per se. If chipmunks avoid the road per se, then we would expect a much larger proportion of individuals to cross the forest edge than to cross the road.

MATERIALS AND METHODS

This study was conducted in the rural areas south and west of Ottawa, Ontario, Canada. This region is dominated by agricultural land use interspersed with small towns and remnant forest areas. Agricultural lands include hay, corn, soybean, and other crop fields and are often bordered by tree-lined fencerows. Forests in this area typically consist of an overstory of *Acer saccharum*, *Fraxinus americana*, *Tilia americana*, *Fagus grandifolia*, *Quercus macrocarpa*, *Tsuga canadensis*, *Pinus strobus*, and *Thuja*.

Six test sites were selected for this study based on the following criteria: a minimum of 300 m of forest edge along both sides of the road, with no driveways, adjoining roads, or housing; forest structure of mixed or deciduous dominant species with a closed canopy; 2-lane, straight, level, paved road sections; and absence of woody vegetation in roadside verges. Three of the test sites had low traffic volume and 3 had relatively high traffic volume (Table 1). The distance between forest edges on either side of the road ranged from 23 m to 42 m.

Chipmunks were trapped, translocated, and released from 10 May to 9 August 2005 from fencerows and forest patches using Sherman nonfolding aluminum live traps (7.5 × 9.0 × 23.0 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida) baited with a mixture of rolled oats, peanut butter, and shelled peanuts. A total of 7 sites were used for trapping, ranging in contribution from 1 to 26 individuals. Following Rizkalla and Swihart (2007) and Zollner (2000), all trapping sites were ≥5 km from the test sites to minimize the chances chipmunks were familiar with the area and to minimize directional bias caused by a homing response (Thibault and Bovet 1999). Furthermore, trapping locations were ≥1 km from the nearest road with regular traffic (i.e., >100 vehicles per day). Traps were opened in the morning (0700–1100 h) and checked and closed 4–6 h later. Once trapped, chipmunks were weighed and sex was determined. Adults were defined as weighing ≥90 g and juveniles were <90 g (Loew 1999). Sex was determined in adults by examination of external reproductive organs. All pregnant or lactating females and young weighing <60 g were

released at the point of capture. Chipmunks were held in a handling bag based on a design in Koprowski (2002) during processing and anesthesia was not used. All trapping and animal handling procedures described herein were approved by the Carleton University Animal Care Committee, in accordance with the Canadian Council on Animal Care, the Ontario Ministry of Natural Resources, and guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

Chipmunks were fitted with a 3.0- or 4.5-g tracking spool (Imperial Thread Inc., Northbrook, Illinois), for juveniles and adults, respectively, with approximately 110 m of string for spools attached to juveniles and 170 m of string for spools attached to adults. Weights of spools were <5% of the body mass of individuals for each age class. At each site approximately one-half of the trials were performed with adults and one-half with juveniles.

Spools were inserted into a dark-colored deflated balloon and glued to the back of the animal using VetBond surgical glue (3M Inc., St. Paul, Minnesota), based on the procedure described in Zollner (2000). Chipmunks were transferred to test sites in an opaque, wooden nest box (15.0 × 30.5 × 30.5 cm) herein referred to as the release device. Animals were held in this environment for 1–3 h before release. Only 1 animal was released at a given test site per day.

Each animal was released in the following manner: 1st, the release device containing the chipmunk was placed at the release point, which was at the same location at each site, 4 m from the forest-verge edge in the forest. Second, the loose end of the tracking string was tied to a marker stake, which was at the same location in each site, herein referred to as the starting point. Third, a 1.5-m-tall tripod was set up over the release device and 1 end of a 40-m rope was fed through a pulley at the top of the tripod and attached to the lid of the box. Last, 1 researcher walked parallel to the road for 40 m, alternating the direction from the release device for sequential releases at each site and, after waiting quietly for 5 min, the end of the 40-m rope was pulled, lifting the lid of the box directly upward. The release device contained a false roof to provide the animal with a sense of security after the lid was removed and was designed to allow the animal to exit in any direction.

One-half of all releases at each site were performed when a vehicle was passing by the site and one-half were performed when no vehicles were passing by the site as the release device was opened; however, at 1 site 10 of 13 releases were performed while a vehicle was passing because of an exceptionally high traffic volume (Table 1: site A). All releases were performed between 0800 and 1800 h during periods without precipitation.

A digital audio recorder (Panasonic RR-US360; Matsushita Electric Ltd., Kadoma, Japan) was placed along the side of the road in the grassy verge and recorded traffic for 60 min after the release. Volume signatures were used to estimate traffic volume using software included with the recorder. To validate this method, we conducted three 15-min tests at each of sites A and F. We simultaneously counted passing vehicles visually and with the audio recorder. Volume signature analyses match perfectly with visual counts at site F, but we missed some vehicle counts at site A when several vehicles passed by the

site close together during periods of exceptionally high traffic flow equivalent to >700 vehicles/h. Therefore, some of the highest traffic estimates reported here may be underestimates of the actual volume of traffic.

The morning after the release, we returned to the site and followed the string trail left by the chipmunk. Pathways were measured using a measuring tape and compass (Zollner 2000). The distance and bearing were recorded every 2 m along the pathway, and at additional points within the 2-m sections whenever the bearing deviated more than 20° from the previous bearing. These values were chosen to maximize efficiency of data collection in the field, minimize errors in data collection caused by missing more subtle changes in pathway bearings, and to provide a relatively high resolution of the movement path.

Pin flags were used to mark sequential points along the path. Pathway bearings were zeroed such that due north indicated movement directly toward the road from the release point. Once zeroed, each point along the pathway was converted to Cartesian coordinates using a customized script for ArcView GIS 3.2 (Environmental Systems Research Institute, Redlands, California). Note that the data are not corrected for potential accumulated spatial errors along the pathways (Turchin 1998).

Data analyses.—Thibault and Bovet (1999) showed that, under conditions of no structural avoidance, chipmunks disperse in a random direction after being translocated outside of their home range. In our study, if the chipmunks have been released sufficiently far from their home ranges, we expect to observe no tendency to move in the direction of their home ranges. This assumption carries through all 4 of our predictions. We verified this assumption by testing for an effect of trapping location on the straight-line bearing from the release point to where the pathway ended (Turchin 1998). We compared the actual bearing with an expected bearing if the animals were heading toward the trapping site, using a circular–circular correlation analysis.

For the 1st prediction, that the probability of crossing the road decreases with traffic volume, we used a binary (i.e., cross–no cross) logistic regression with traffic volume as the predictor.

For the 2nd prediction, we calculated the probability of chipmunks turning toward or away from the road by classifying each pathway segment as heading either toward (+) or away (−) from the road. Next, we classified pairs of moves as either (+,−), (+,+), (−,−), or (−,+), with the 1st sign indicating the direction of the 1st segment of the paired move and the 2nd sign representing the direction of the 2nd segment of the paired move. We calculated the probability of turning away from the road for each individual as $P_{away} = \sum(+,-)/[\sum(+,-) + \sum(+,+)]$ and the probability of turning toward the road as $P_{toward} = \sum(-,+)/[\sum(-,+) + \sum(-,-)]$. If chipmunks tend to turn away from the road then $P_{away} > P_{toward}$. We tested for an effect of road avoidance using a paired *t*-test comparing P_{away} with P_{toward}. Last, if traffic affects the direction of turning (directionality [*d*]), then the value $d = (P_{away} - P_{toward})/(P_{away} + P_{toward})$ should increase with traffic volume, with 1 representing a relatively large number of moves away from the road and a value of −1 representing a relatively large number of moves
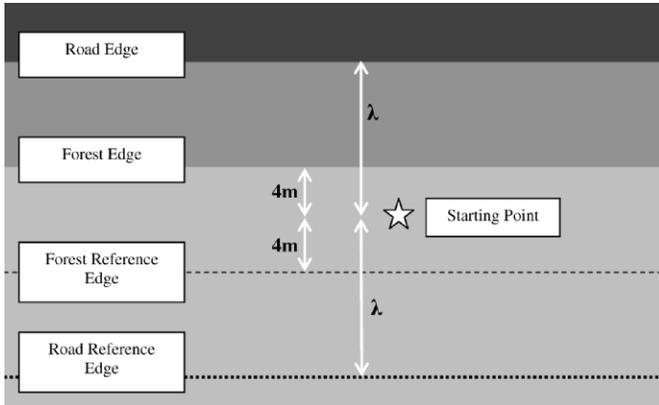
FIG. 1.—Design of edge crossing analysis, with the black area representing the road, the dark gray area representing the verge, and the light gray area representing the forest. The starting point is indicated by the white star. The distance, λ, varies among sites so we used the site-specific distance between the release point and the road to calculate the road reference edge (dotted line). The forest reference edge (dashed line) is 8 m from the actual forest edge at all sites and runs parallel to the road.

toward the road. We tested for an effect of traffic volume on directionality (*d*) with an analysis of covariance (ANCOVA) using directionality as the response variable and sex, age, sex × age, and traffic volume as predictor variables.

We also tested for an effect of a car passing at the time of release on the initial bearing of the chipmunk using a *V*-test, with a predicted bearing of 180° indicating movement directly away from the road. Significance ($P < 0.05$) in this test indicates that the mean bearing of the samples is not significantly different from the predicted bearing. To ensure adequate statistical power we pooled all ages and sexes for this analysis. Circular statistics were calculated using Oriana (Kovach Computing Services, Pentraeth, Isle of Anglesey, Wales, United Kingdom).

For the 3rd prediction, that distance from the road to the animal increases with traffic volume, we regressed the minimum distance from the road to each pathway on traffic volume. We included sex, age, and sex × age terms using a type I sums of squares in an ANCOVA with traffic volume entered last into the model. Data ($n = 10$) from 1 site (site A) were excluded from this analysis because this site had a verge width twice the typical verge width of the other sites (Table 1), which would greatly increase the distance from the road for any animals released at this site. This would give a spurious relationship with traffic volume because this site had the highest traffic volume. Because distance traveled increases the probability of encountering the road, we used the length of the shortest pathway recorded (i.e., 72 m) as the maximum length of all pathways in the analyses for the 2nd and 3rd predictions.

Chipmunks may be more or less sensitive to changes in traffic volume the longer they have traveled in a given test site. Changes in sensitivity to traffic may be due to an effect of translocation that wears off over the course of the movement path, acclimatization to the traffic stimuli during the movement path, or both. To address these potential effects, we divided each 72-m pathway into 2 equal lengths, and performed separate ANCOVAs on each half for the directionality and distance to the road analyses (i.e., the 2nd and 3rd predictions). The effect of traffic on these responses should be stronger within the 1st half of the pathways than in the 2nd half if chipmunks acclimatize to traffic; the effect of traffic should be weaker within the 1st half of the pathway if chipmunks are "recovering" from the translocation process and then respond to traffic later. If the responses of chipmunks to traffic are not affected by distance traveled since release and they do not avoid roads because of traffic, then there will be no significant effect of traffic in both portions of their pathways. Likewise, if chipmunks are as likely to respond to traffic within the 1st half of their pathway as the 2nd half, and they do respond to traffic, then there will be a positive effect of traffic in both the 1st and 2nd half of the pathways. In all analyses described above, the traffic variable we used was the log-transformed 60-min vehicle count after the release of the animal.

To examine the effect of the forest edge on movement of chipmunks we calculated the number of individuals that moved out of the forest and into the grassy verge. To provide a comparison for the potential effect of the forest edge on movement of chipmunks, we analyzed movement across a reference "edge." The reference edge is a line running parallel to the actual forest edge on the forest interior side of the starting point. Both the actual and reference forest edges are equidistant from the starting point (Fig. 1). The number of chipmunks crossing the actual and reference edges should be similar if chipmunks do not perceive the forest edge as a barrier. We compared movement across the reference edge to movement across the actual forest edge using a chi-square test. To ensure adequate replication we combined both sexes and ages.

We then wanted to know if chipmunks that crossed the forest edge are deterred from crossing the road; however, fewer animals will cross the road edge than the forest edge simply because the road edge is farther away from the starting point. To separate the confounding effects of distance and road avoidance on movement toward the road, we compared 2 proportions: the number of chipmunks that crossed the reference road edge (Fig. 1) divided by the total number of individuals that crossed the reference forest edge; and the number of animals that crossed the actual road edge divided by the total number of animals that crossed the actual forest edge. Again, the reference road edge is the same distance from the release point as the actual road edge, which is a site-specific measure (Table 1). These 2 proportions should be similar if chipmunks do not perceive the road as a barrier. We used a binomial test, using the proportion of movement across the reference road edge as the expected value for proportion of movement across the actual road edge. Unless otherwise noted, all statistical analyses were performed with SPSS version 12.0.2 (SPSS Inc., Chicago, Illinois).

RESULTS

We tracked 68 individuals for a total distance of 8,132 m (Table 2). Only 1 animal was confirmed to have crossed a road

during this study. An additional pathway terminated on the road surface, but we were unable to detect tracking string on the far side of the road so we could not determine whether the animal actually crossed (Fig. 2). Bearings at the release site were not oriented toward the trapping sites ($r = -0.049$), indicating that the chipmunks were not homing.

Chipmunks tended to move away from the road at the time of release (Fig. 3). The results of the *V*-test indicate a significant ($n = 37$, $V = 0.25$, $P = 0.015$) clustering of exit bearings at 180° for releases performed as a vehicle was passing by the site. We did not detect a significant orientation away from the road when there were no vehicles passing by the site at the time of release ($n = 25$, $V = 0.154$, $P = 0.139$).

We excluded the pathways of 6 individuals from the analysis of directionality, distance to the road, and probability of crossing the forest edge analyses because the tracking string broke on these individuals prematurely (10–40 m from the release point). The probability of chipmunks turning away from the road was greater than the probability of them turning toward the road for both the first and second 36-m stretches of pathway as well as the entire 72-m pathway length (Table 3). Traffic volume, sex, age, or sex × age did not explain a significant ($P > 0.05$) amount of variation in directionality in any stretch of pathway examined (Table 4).

Traffic significantly affected the minimum distance from the road during the 1st half of the pathways only (Fig. 4), although the amount of variation explained by the overall model was low. Age, sex, and age × sex did not significantly affect minimum distance to the road (Table 4).

Among all 6 test sites, 35 (56%) of 62 individuals crossed the actual forest edge, which was significantly fewer than the number of chipmunks that crossed the reference forest edge (57 [92%] of 62; $\chi^2 = 20.386$, $d.f. = 1$, $P < 0.0001$). The proportion of animals that crossed the reference forest edge and then crossed the reference road edge (34 [60%] of 57) was significantly greater ($P < 0.0001$) than the proportion of animals that crossed the actual forest edge and ventured onto the road surface (2 [6%] of 35).

DISCUSSION

Our results confirm that chipmunks avoid roads (Fig. 2), as has been found in previous studies (McGregor et al. 2007; Oxley et al. 1974). Our results suggest that road avoidance in chipmunks is primarily caused by a response to the road, roadside verge, or both, although we did detect subtle responses to traffic in the initial portion of their pathways. Our 1st prediction was that if chipmunks avoid roads because of traffic then the probability of an animal crossing the road would decrease as traffic increases. Based on Thibault and Bovet (1999), who showed that chipmunks disperse in a random direction after translocation and release, we assumed that nearly one-half of the chipmunks would venture onto the road if they did not exhibit road avoidance behavior. Of the animals that ventured onto the road, we expected at least a few of them to cross, particularly at low-traffic release sites (Oxley et al. 1974). In our study, only 1 (2%) of 62 pathways crossed the

**TABLE 2.**—Demographic characteristics of translocated chipmunks (*Tamias striatus*) by release site.

Site	Adult males	Adult females	Juvenile males	Juvenile females	Total
A	7	0	1	2	10
B	2	2	5	3	12
C	3	1	6	1	11
D	3	2	2	3	10
E	3	3	2	2	10
F	5	1	3	3	12

road. This result did not allow us to analyze the effect of traffic on the frequency of road crossing; however, it is comparable to chipmunk road avoidance patterns in other studies that used capture–mark–recapture methods. Oxley et al. (1974) found that approximately 3% of 179 chipmunks crossed roads during 2 years of trapping and McGregor et al. (2007) found that 6% of 63 chipmunks living near roads crossed them. Conrey and Mills (2001) found that 4% of 234 individuals from 2 other species of chipmunks (*Tamias amoenus* and *T. ruficaudus*) crossed 2-lane highways and 0% crossed 4-lane highways.

Our results support the notion that chipmunks may acclimatize to traffic. We found that during the initial portion of the pathway, chipmunks stayed farther away from the road as traffic increased. Furthermore, we found that chipmunks were more likely to move directly away from the road if a vehicle was passing by the site at the time of release than if no vehicle was passing by the site at the time of release. Over the 2nd half of the pathway we detected no effect of traffic on the minimum distance of the pathway to the road. That the effect of traffic on chipmunk movement is stronger during the 1st half of the pathway compared to the 2nd half is consistent with an acclimatization response to traffic. McGregor et al. (2007) found that traffic volume had no negative effect on chipmunk population density in roadside habitat, which also suggests that they acclimatize quickly to the presence of traffic. This differs from other species, such as songbirds, in which traffic has been shown to negatively affect population densities up to 930 m from roads (reviewed in Forman et al. 2003).

All the chipmunks in our study were captured >1 km from the nearest road with regular traffic (i.e., >100 vehicles/day), so it is unlikely that any of the animals used in our study were already acclimatized to traffic when we released them. Acclimatization is normally defined as a period of time in which a response weakens to a lower level than it was after the initial exposure to the stimulus. Unfortunately, we did not have a time frame associated with the movement parameters we measured in the field. Rather, distance traveled serves as a proxy for time in our study under the assumption that chipmunk velocity was independent of traffic volume or distance from the road, or both. Further work is needed to more accurately assess the temporal components of road avoidance behavior and potential acclimatization to traffic in small mammals.

At least 3 lines of evidence support the notion that chipmunks avoid roads independently of traffic (after an initial acclimatization), at least for the traffic densities common to the 2-lane, paved roads in our study area: 1st, few chipmunks
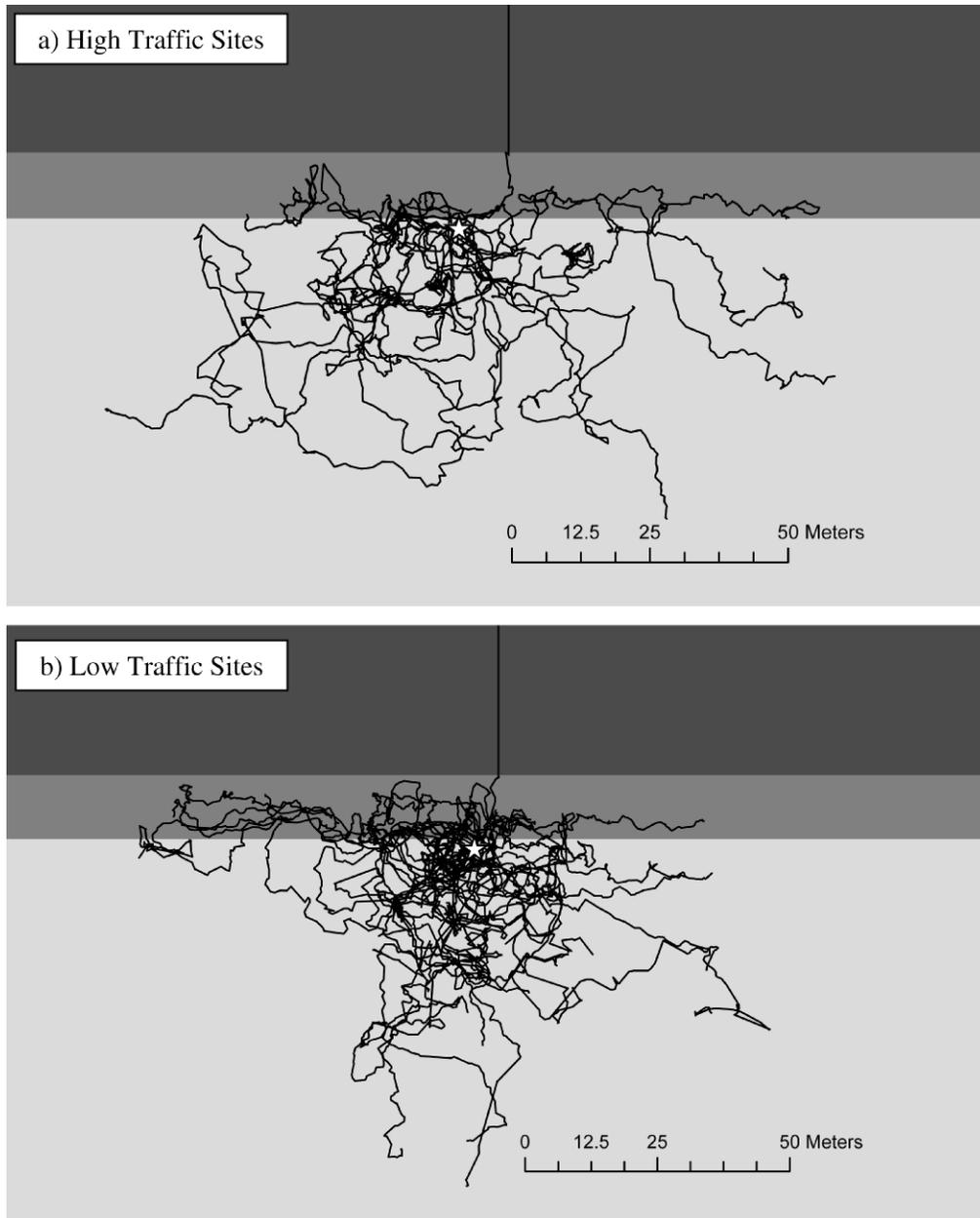
FIG. 2.—Graphical representation of all pathways that were ≥72 m in length for high-traffic sites (top) and low-traffic sites (bottom). The dark gray area represents the verge, the light gray area is the forest, and the black area is the road surface. The location of the starting point is indicated by the star. The mean verge width of sites B–F (i.e., ≈10 m) was used for this figure. Releases performed at site A were excluded from Fig. 2a because width of its verge was almost twice as large as the width of the verge of the other sites (see Table 2).

crossed roads in our study despite their being exposed to 3 orders of magnitude difference in traffic volume; 2nd, the probability of chipmunks turning away from the road was greater than the probability of them turning toward the road and traffic did not affect the difference between these 2 values; and 3rd, traffic only affected the distance chipmunks came toward the road during the 1st half of their pathways.

Road avoidance, if not caused by traffic, may be related to avoidance of the forest edge, roadside verge, or road surface itself. As forest-dwelling habitat specialists (Bender and Fahrig 2005), it is not surprising that many chipmunks were reluctant to cross the forest edge; however, that 51% of individuals moved into the roadside verge, many on more than 1 occasion ($\bar{X} = 1.6 \pm 0.25$ *SE* crossings/individual, $n = 68$, range 0–7), suggests that the forest edge was highly permeable to chipmunks during this study. Other studies also have found that chipmunks were willing to cross forest edges, even across gaps in the forest canopy up to 250 m wide, an order of magnitude wider than several of the right-of-way distances in our study (Bowman and Fahrig 2002; McGregor et al. 2007).

If chipmunks are willing to leave the forest, but do not cross the road, then where does avoidance take place? The 6% of
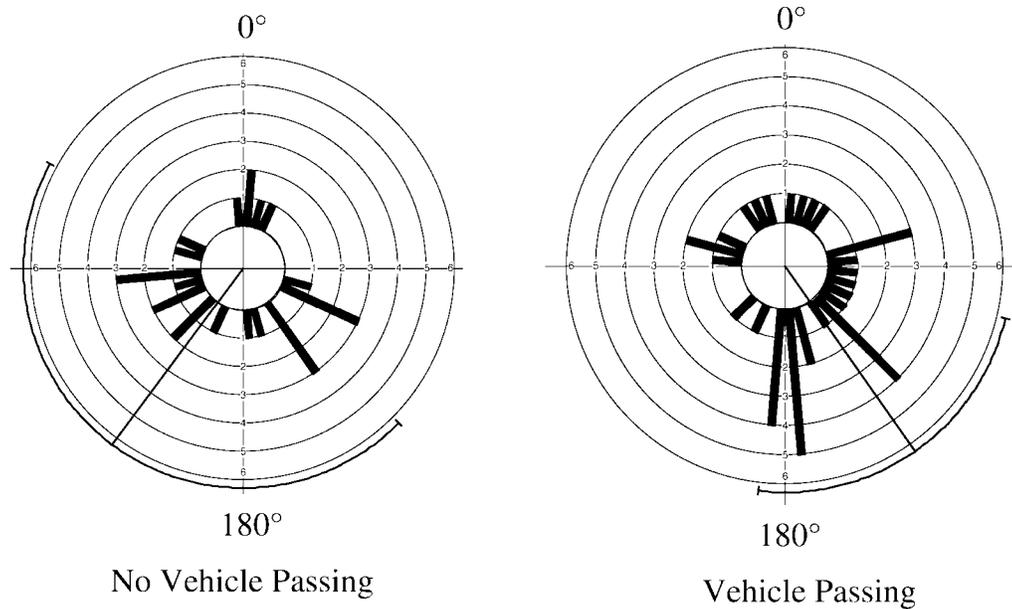
FIG. 3.—Circular histograms for the initial bearings of animals released when a vehicle was passing (right panel) and was not passing (left panel) by the site at the time of release. The radii represent a count of 1 individual, grouped in bins of 10° (bars). The vector represents the mean bearing and the arc outside the circle is the 95% confidence interval for the mean bearing. The top of the circle, or 0°, represents movement directly toward the road.

chipmunks that reached the road edge was far lower than the 60% of chipmunks that crossed the reference road edge, suggesting that the structural elements of the roadside verge (McDonald and St Clair 2004b) or road surface composition (Oxley et al. 1974) are important to road aversion. A further study comparing small mammal movement near forest edges with and without adjacent roads is needed to determine how the interaction between road surface (e.g., gravel or asphalt) and verge characteristics (e.g., slope and vegetation type) affects movement of small mammals near roads.

A potential criticism of our study is that long-distance translocation may affect an animal's stress level and affect its response, or lack thereof, to traffic or roads compared to more natural conditions, thus limiting the relevance of our findings to broader ecological patterns. Four lines of evidence support the assertion that our results are consistent with reported dispersal patterns of chipmunks (Bennett et al. 1994; Henderson et al. 1985; Thibault and Bovet 1999). First, we attempted to minimize stress on chipmunks by holding them in a secure, quiet, and stable environment for 1–3 h before release. Other studies involving the tracking of movement by small mammals held animals in traps, nest boxes, or handling cones for an unspecified amount of time (Stapp and Van Horne 1997; Stapp et al. 1994; Zollner and Crane 2003), 5–20 min (Key and Woods 1996; Steinwald et al. 2006.), overnight (Zollner 2000), or up to 3 days (Rizkalla and Swihart 2007). The purpose of holding animals for some time before release is to reduce the impact of handling and translocation on stress levels (Koprowski 2002). Second, chipmunks were able to leave the release device on their own accord and while researchers were >40 m away. Zollner (2000) found that chipmunks stayed in a release device (of a different design) for at least an hour after the door had

been opened. Thus, it is unlikely that chipmunks in our study were fleeing from researchers upon release. Third, if chipmunks were so stressed that they did not respond to traffic at all then our conclusions would be suspect; however, the diminished effect of traffic on distance from the highway over the course of the pathway suggests that chipmunks rapidly acclimatize to traffic or they quickly recover from the translocation process, or both. Lastly, it is also likely that animals dispersing under natural conditions experience a stress response brought about by travel through novel terrain (Scantlebury et al. 2006). The notion that chipmunks are overwhelmed by their new surroundings and unable to respond to traffic is not supported by our results and is unlikely to occur under conditions of natural dispersal (Loew 1999). Despite our attempts to standardize motivation to cross the road through translocation, it is still possible that some individuals varied in their response to the road because of other factors such as previous experience or physiological condition.

Given the effects of roads on movements by chipmunks observed in this study, we hypothesize that dispersing chipmunks are probably more responsive to traffic than chipmunks

TABLE 3.—Results of the paired t-test comparing the probability of turning away from the road versus the probability of turning toward the road (n = 62).

Cumulative distance traveled (m)	Probability of turning toward road, $\bar{X}$ (SE)	Probability of turning away from road, $\bar{X}$ (SE)	t	P
72	0.2351 (0.011)	0.5160 (0.023)	10.660	< 0.001
0.00–36.00	0.2250 (0.012)	0.3767 (0.026)	4.749	< 0.001
36.01–72.00	0.2705 (0.021)	0.3526 (0.023)	2.389	0.020

TABLE 4.—Summary table of ANCOVAs on the effect of traffic on both directionality and the minimum distance from the pathway taken by chipmunks (*Tamias striatus*) to the road.

Response	Cumulative distance traveled (m)	Adjusted R^2_{model}	F_{model}	n	F_{sex}	F_{age}	$F_{age \times sex}$	$F_{traffic}$
Directionality	72	< 0.01	0.858	62	1.170	0.273	0.118	1.873
	0.00−36.00	< 0.01	0.582	62	0.008	0.707	1.379	0.232
	36.01−72.00	0.06	1.953	62	0.973	0.886	2.690	3.263*
Minimum distance to the road	72	0.04	1.495	52	2.461	0.530	0.019	2.971*
	0.00−36.00	0.06	1.760	52	0.836	0.004	0.928	5.274**
	36.01−72.00	< 0.01	0.686	52	< 0.001	1.556	< 0.001	1.187

* $P < 0.10$; ** $P < 0.05$.

whose home ranges are near roads, but this effect likely subsides as dispersing individuals acclimatize to traffic. Because chipmunks avoid roads per se, more so than the traffic on them, we hypothesize that the strongest effect of roads on chipmunk populations is likely to be population subdivision (Jaeger et al. 2005) rather than direct mortality from vehicle collisions.

The distribution of populations of chipmunks is likely to be affected by road density and road network configuration at both the landscape and within-patch scales. At the landscape scale we expect that as road density increases the population density of occupied patches and the number of extirpated patches should increase. If road avoidance limits emigration from subpopulations living near roads, then fewer animals will leave the patch, which in turn would increase the population densities in those subpopulations (Rytwinski and Fahrig 2007; Schooley and Wiens 2004; Stamps et al. 1987). At the same time, reductions in movement between patches could limit recolonization of nearby extinct patches. This in turn would create a landscape with a larger number of extirpated patches than expected for a particular landscape configuration and composition (Bender and Fahrig 2005; Reunanen and Grubb 2005). At the within-patch scale, chipmunks may have higher densities near roads than in the patch interior, that is, the ''home-

range-pile-up'' phenomenon (Riley et al. 2006; Strasburg 2006). Indeed, McGregor et al. (2007) found higher densities of chipmunks near roads than in the forest interior, although they did not compare these densities to nonroad habitat edges. At both landscape and within-patch scales, movement patterns of chipmunks in roaded landscapes could be modeled as a biased (away from roads) correlated random walk (Turchin 1998), which could then be used to generate hypotheses for population distribution and persistence within specific landscapes. Further research is needed to explicitly link individual movement of small mammals near roads with the viability of their populations.

ACKNOWLEDGMENTS

LITERATURE CITED

ANDREWS, K. M., AND J. W. GIBBONS. 2005. How do highways influence snake movement? Behavioral responses to roads and vehicles. Copeia 4: 772–782.

BENDER, D., AND L. FAHRIG. 2005. Matrix structure obscures the relationship between interpatch movement and patch size and isolation. Ecology 86:1023–1033.

BENNETT, A., K. HENEIN, AND G. MERRIAM. 1994. Corridor use and the elements of corridor quality: chipmunks and fencerows in a farmland mosaic. Biological Conservation 68:155–165.

BOWMAN, J., AND L. FAHRIG. 2002. Gap crossing by chipmunks: an experimental test of landscape connectivity. Canadian Journal of Zoology 80:1556–1561.

BURNETT, S. 1992. Effects of a rainforest road on movements of small mammals: mechanisms and implications. Wildlife Research 19: 95–104.

CLARK, B. K., B. S. CLARK, L. A. JOHNSON, AND M. T. HAYNIE. 2001. Influence of roads on movements of small mammals. Southwestern Naturalist 46:338–344.

CONREY R., AND L. S. MILLS. 2001. Do highways fragment small mammal populations? Pp. 448–457 in Proceedings of the International Conference on Ecology and Transportation, Key-
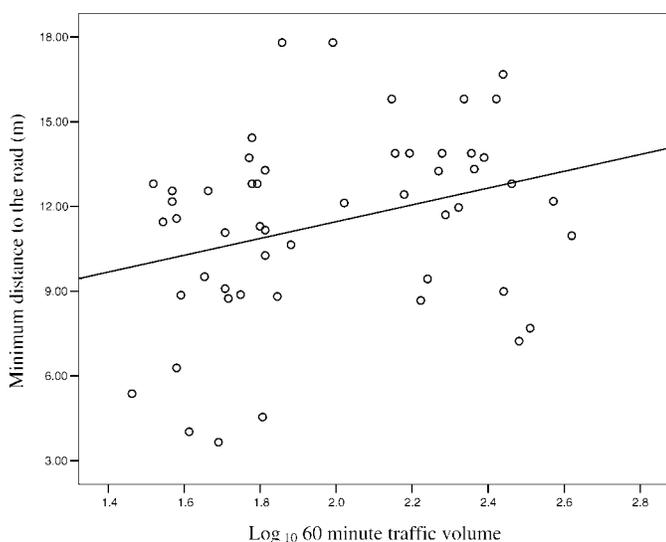
FIG. 4.—Effect of traffic volume on the minimum distance to the road within the first 36 m of travel.

stone, Colorado, September 24–28, 2001 (C. L. Irwin, P. Garrett, and K. P. McDermott, eds.). Center for Transportation and the Environment, North Carolina State University (March 2002), Raleigh.

DODD, C. K., W. J. BARICHIVICH, AND L. L. SMITH. 2004. Effectiveness of a barrier wall and culverts in reducing wildlife mortality on a heavily traveled highway in Florida. Biological Conservation 118:619–631.

FAHRIG, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution and Systematics 34: 487–515.

FAHRIG, L., J. H. PEDLAR, S. E. POPE, P. D. TAYLOR, AND J. F. WEGNER. 1995. Effect of road traffic on amphibian density. Biological Conservation 73:177–182.

FINDLAY, C. S., AND J. BOURDAGES. 2000. Response time of wetland biodiversity to road construction on adjacent lands. Conservation Biology 14:86–94.

FORMAN, R. T. T., ET AL. 2003. Road ecology: science and solutions. Island Press, Washington, D.C.

GANNON, W. L., R. S. SIKES, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 88: 809–823.

GETTY, T. 1981. Territorial behavior of eastern chipmunks (Tamias striatus): encounter avoidance and spatial time sharing. Ecology 62:915–921.

GOOSEM, M. 2001. Effects of tropical rainforest roads on small mammals: inhibition of crossing movements. Wildlife Research 28:351–364.

GOOSEM, M. 2002. Effects of tropical rainforest roads on small mammals: fragmentation, edge effects and traffic disturbance. Wildlife Research 29:277–289.

HENDERSON, M., G. MERRIAM, AND J. WEGNER 1985. Patchy environments and species survival: chipmunks in an agricultural mosaic. Biological Conservation 31:95–105.

JAEGER, J. A., ET AL. 2005. Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. Ecological Modelling 185:329–348.

KEY, G., AND R. WOODS. 1996. Spool-and-line studies on the behavioural ecology of rats (Rattus spp.) in the Galapagos Islands. Canadian Journal of Zoology 74:733–737.

KOPROWSKI, J. 2002. Handling tree squirrels with a safe and efficient restraint. Wildlife Society Bulletin 30:101–103.

KOZEL, R., AND E. FLEHARTY. 1979. Movements of rodents across roads. Southwestern Naturalist 24:239–248.

LOEW, S. S. 1999. Sex-biased dispersal in eastern chipmunks, Tamias striatus. Evolutionary Ecology 13:557–577.

MADER, H. J. 1984. Animal habitat isolation by roads and agricultural fields. Biological Conservation 29:81–96.

MCDONALD, W. R., AND C. C. ST. CLAIR. 2004a. The effects of artificial and natural barriers on the movement of small mammals in Banff National Park, Canada. Oikos 105:397–407.

MCDONALD, W., AND C. C. ST CLAIR. 2004b. Elements that promote highway crossing structure use by small mammals in Banff National Park. Journal of Applied Ecology 41:82–93.

MCGREGOR, R., D. J. BENDER AND L. FAHRIG. 2007. Do small mammals avoid roads because of the traffic? Journal of Applied Ecology (OnlineEarly Articles), DOI:10.1111/j.1365-2664.2007.01403.x.

OXLEY, D. J., M. B. FENTON, AND G. R. CARMODY. 1974. The effect of roads on populations of small mammals. Journal of Applied Ecology 11:51–59.

REUNANEN, P., AND T. GRUBB. 2005. Densities of eastern chipmunks (Tamias striatus) in farmland woodlots decline with increasing area and isolation. American Midland Naturalist 154:433–441.

RICHARDSON, J., R. SHORE, J. TREWEEK, AND S. LARKIN. 1997. Are major roads a barrier to small mammals? Journal of Zoology (London) 243:840–846.

RICO, A., P. KINDLMANN, AND F. SEDLACEK. 2007. Road crossing in bank voles and yellow-necked mice. Acta Theriologica 52:85–94.

RILEY, S., ET AL. 2006. A southern California freeway is a physical and social barrier to gene flow in carnivores. Molecular Ecology 15:1733–1741.

RIZKALLA, C., AND R. SWIHART. 2007. Explaining movement decisions of forest rodents in fragmented landscapes. Biological Conservation 140:339–348.

RONDININI C., AND C. P. DONCASTER. 2002. Roads as barriers to movement for hedgehogs. Functional Ecology 16:504–509.

RYTWINSKI, T., AND L. FAHRIG. 2007. Effect of road density on abundance of white-footed mice. Landscape Ecology 22:1501–1512.

SAEKI, M., AND D. W. MACDONALD. 2004. The effects of traffic on the raccoon dog (Nyctereutes procyonoides viverrinus) and other mammals in Japan. Biological Conservation 118:559–571.

SCANTLEBURY, M., J. SPEAKMAN, M. OOSTHUIZEN, T. ROPER, AND N. BENNETT. 2006. Energetics reveals physiologically distinct castes in a eusocial mammal. Nature 440:795–797.

SCHOOLEY, R. L., AND J. WIENS. 2004. Movements of cactus bugs: patch transfer, matrix resistance and edge permeability. Landscape Ecology 19:801–810.

STAMPS, J., M. BUECHNER, AND V. V. KRISHNAN. 1987. The effects of edge permeability and habitat geometry on emigration from patches of habitat. American Naturalist 129:533–552.

STAPP, P., AND B. VAN HORNE. 1997. Response of deer mice (Peromyscus maniculatus) to shrubs in shortgrass prairie: linking small-scale movements and the distribution of individuals. Functional Ecology 11:644–651.

STAPP, P., J. YOUNG, S. VANDEWOUDE, AND B. VAN HORNE. 1994. An evaluation of the pathological effects of flourescent powder on deer mice. Journal of Mammalogy 75:704–709.

STEINWALD, M., B. SWANSON, AND P. WASER. 2006. Effects of spool-and-line tracking on small desert mammals. Journal of Mammalogy 51:71–78.

STRASBURG, J. 2006. Roads and genetic connectivity. Nature 440: 875–876.

SWIHART, R. K., AND N. A. SLADE. 1984. Road crossing in Sigmodon hispidus and Microtus ochrogaster. Journal of Mammalogy 65:357–360.

THIBAULT, A., AND J. BOVET. 1999. Homing strategy of the eastern chipmunk, Tamias striatus (Mammalia: Rodentia): validation of the critical distance model. Ethology 105:73–82.

TURCHIN, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.

ZOLLNER, P. 2000. Comparing the landscape level perceptual abilities of forest sciurids in fragmented agricultural landscapes. Landscape Ecology 15:523–533.

ZOLLNER, P. A., AND K. J. CRANE. 2003. Influence of canopy closure and shrub coverage on travel along coarse woody debris by eastern chipmunks (Tamias striatus). American Midland Naturalist 150:151–157.