The effect of traffic on the movement of eastern chipmunks (*Tamias striatus*)

By

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ABSTRACT

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 increasing traffic. We also tested whether chipmunks display anti-predator responses, such as tree climbing and use of coarse woody debris, in response to road traffic. We tracked the movements of 68 chipmunks released near roads with widely varying traffic amounts. Our results confirm that chipmunks avoid roads, but we found no evidence suggesting this response is caused by traffic. We also found no evidence suggesting that chipmunks display anti-predator responses to road traffic. Chipmunks need to disperse between remnant forest patches in order to maintain regional population persistence. Our results clearly show that roads inhibit chipmunk movement; therefore, we predict that the primary effect of roads on chipmunk populations is due to population subdivision.

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I came to Carleton University as a curious naturalist who wanted to learn more about the world around him; my goal was to leave with an ability to ask better questions and to provide clear responses when questions are asked of me. No one has been more instrumental in seeing me reach that goal than my supervisor, Lenore Fahrig. It has been a real pleasure to work under your guidance and I certainly could not have asked for a more productive and enjoyable two years than the time I spent in your research lab. Thank you for giving me this opportunity to grow as a person and into a scientist.

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DEDICATION

This thesis is dedicated to travelling individuals everywhere, especially the sciurid rodents of Ottawa. May you always find a way to cross the barriers in your path.

They ran on and crept through the hedge. Hazel looked down the road in astonishment. For a moment he thought that he was looking at another river – black, smooth and straight between its banks. Then he saw the gravel embedded in the tar and watched a spider running over the surface.

‘But that’s not natural,’ he said, sniffing the strange, strong smells of tar and oil. ‘What is it? How did it come there?’

‘It’s a [hu]man-thing,’ said Bigwig. “they put that stuff there and then the hrududil run on it – faster than we can; and what else can run faster than we?’

‘It’s dangerous then? They can catch us?’

‘No, that’s what’s so odd. They don’t take any notice of us at all. I’ll show you, if you like.’

Richard Adams
Watership Down p.58-59
Penguin Books Ltd,
Harmondsworth, England

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Introduction

Road network density and the number of vehicles on the road are increasing in many jurisdictions such that conservation efforts are becoming more involved with the interaction between roads and wildlife (Forman *et al.* 2003). The effect of roads on wildlife populations includes the loss and fragmentation of habitat as well as mortality associated with wildlife-vehicle collisions (e.g. Dodd *et al.* 2004; Findlay & Bourdages 2000; Fahrig *et al.* 1995; Forman *et al.* 2003; Saeki & McDonald 2004).

The magnitude of a road's effect on a given population depends on the species' response to road variables, such as road width and traffic amount (Mader 1984; Forman *et al.* 2003). Jaeger *et al.* (2005) modelled the effects of road size and traffic amount on population persistence and predicted that traffic amount has the greatest effect on the magnitude of the road impact. Traffic affects wildlife populations by increasing mortality (Caro *et al.* 2000; Clarke *et al.* 1998; Cleverger 2003; McClure 1951; Oxley *et al.* 1974) and road avoidance (Richardson *et al.* 1997). Road avoidance is any response by individual animals that reduces movement onto the road surface.

Jaeger *et al.* (2005) predict that the effect of traffic on mortality is negligible if animals avoid roads due to traffic or if they avoid the road surface *per se*. At the same time, as road avoidance increases the effect of the road on habitat fragmentation (causing resource inaccessibility and/or population subdivision) increases. If a species has a weak response to traffic and does not avoid the road surface then mortality increases with traffic amount (e.g. Carr & Fahrig 2001).

Several studies have examined the effect 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 & Mills 2001; Mader 1984; McDonald & St. Clair 2004a; Rondini & Doncaster 2002; Swihart & Slade 1984). It is unclear from these studies how traffic interacts with road avoidance because of the confounding effects of road width and traffic amount in these studies. To our knowledge only two studies have directly examined the effect of traffic amount on small mammal movement. Richardson *et al.* (1997) found that two species of vole had a significantly higher rate of road crossing at low traffic sites (<60 vehicles per hour) than at high traffic sites (>250 vehicles per hour). McGregor (2004) found a slight effect ($p=0.095$) of traffic amount on white-footed mouse (*Peromyscus leucopus*) movement across roads; she argued that small mammal road avoidance is primarily due to road surface avoidance.

Most studies on small mammal road avoidance, including Richardson *et al.* (1997) and McGregor (2004), use capture-mark-recapture (CMR) techniques with trapping grids on both sides of a road to monitor the movement of marked individuals. Movement is either spontaneous or induced through homing by translocating animals across the road. Road avoidance is defined in these studies as a significantly lower frequency of recaptures between grids on opposite sides of the road, relative to the frequency of recaptures of equivalent distance on one side of the road only.

Results of CMR studies are difficult to interpret when attempting to address questions of movement near roads for at least three reasons. First, CMR methods are based on a discrete, often categorical, representation of space. With this coarse-grained approach there is no way to determine how animals moved between recaptures (Clark *et al.* 2001). For instance, animals may move onto the road surface and then turn back towards roadside habitat as a vehicle approaches (Andrews & Gibbons 2005). This

pattern of movement would suggest that animals can avoid individual vehicles. Animals may also move away from the road while travelling within roadside habitat due to avoidance of vehicle emissions such as noise or pollutants. Both of these types of road avoidance would increase with traffic but have different predicted effects on population persistence (Jaeger *et al.* 2005); however, using the frequency of road crossings as a measure of avoidance would not distinguish these two responses in the CMR approach. Second, many translocation CMR studies do not attempt to standardize, across animals, the motivation to cross the road (but see McDonald & St. Clair 2004b). For instance, territorial individuals may have a stronger motivation to return to the initial capture location than dispersing individuals (Kozel & Fleharty 1979). Third, some species of small mammals use roads to define the boundaries of their home range (Burnett 1992; Mader 1984; Swihart & Slade 1984). CMR studies that depend on spontaneous movement of individuals outside the home range may confound road avoidance behaviour with avoidance of conspecific home ranges or territorial boundaries.

Several studies have suggested that chipmunks avoid roads. Oxley *et al.* (1974) found that chipmunks rarely crossed paved roads but frequently crossed low traffic, gravel roads. Conrey and Mills (2001) found that two species of chipmunks (*Tamias amoenus* and *T. ruficaudus*) were three times as likely to move adjacent to, rather than across, two-lane highways and never crossed four-lane highways. McGregor (2004) also found that fewer chipmunks crossed roads than was expected, although it is not clear from her study whether this result was caused by road aversion *per se*, a reluctance to move out of the forest onto the roadside verge or due to traffic mortality. Getty (1981) found that individual chipmunks included a low traffic road within their home range.

Together, these studies indicate that chipmunks most likely avoid roads, but they may be more averse to some roads than others. It is unclear from the literature how road variables, such as surface composition, width or traffic amount, affect road aversion.

The purpose of this study was to determine whether a forest dwelling small mammal species, the eastern chipmunk (*Tamias striatus*), avoids roads due to traffic. We did this by tracking movement paths of individual chipmunks released in unfamiliar terrain near roads with widely varying traffic amounts. We predicted three responses if chipmunks avoid roads because of traffic. First, the probability of crossing a road should decrease with increasing traffic amount. Second, the size of the turns in chipmunk pathways should increase with traffic amount. Third, if chipmunks avoid the road because of traffic emissions, such as noise or pollutants, then animals will stay farther away from the road as traffic increases (Forman *et al.* 2003).

Studies on amphibians (Mazerolle *et al.* 2005) and snakes (Andrews & Gibbons 2005) suggest that animals respond similarly to moving vehicles and predators, although this response may not necessarily direct the animal away from the road (Andrews & Gibbons 2005). Chipmunks have been known to flee up trees when pursued by predators in unfamiliar habitat (Clarke *et al.* 1993) and to increase their use of coarse woody debris for travel in poor quality habitat (Zollner & Crane 2003). We used two responses to test the hypothesis that chipmunks respond to vehicles as predators: the number of chipmunks that ascended trees and the use of coarse woody debris for travel by individuals. If chipmunks respond to vehicles as predators, we predicted that as traffic amount increases both the frequency of individuals that climb trees and the use of coarse woody debris should increase.

Life history of the eastern chipmunk

The eastern chipmunk was chosen for this study because they are numerous in the study area, easily live-trapped, and their behavioural ecology is well documented. They are also listed as Specially Protected Mammal under the Ontario Fish and Wildlife Conservation Act (1997) through the Ontario Ministry of Natural Resources. Unless otherwise noted, the summary of life history presented here is based on Snyder (1982).

The eastern chipmunk ranges west to Lake Manitoba, east to Nova Scotia and from the southern tip of James Bay to northern Florida State. Preferred habitat throughout this range includes remnant deciduous forest, although tree-lined fencerows (Henderson *et al.* 1985), brushy areas, rock walls and wooded urban areas are also used. Chipmunks are diurnal and considered semi-fossorial as they burrow and hibernate below ground. They prefer to forage on the forest floor although they may make use of arboreal habitats for foraging. Preferred diet includes hard mast and invertebrates.

Mating takes place twice per year, between February and April and again in late June or early July. Gestation lasts approximately 30 days and litter size averages 4 young per mother. Young emerge from the burrow after 5 weeks and reach adult size within 3 months of birth. Mothers typically become intolerant of young within a few days of emergence leading to juvenile dispersal. Adult body mass is typically greater than 90g and may reach more than 125g. Average life expectancy is 1.3 years with a maximum reported life span of 8 years.

Population densities have been reported up to 37.6 individuals/ha with recorded home ranges varying in size from 0.03 to 0.40ha. Chipmunks are central place foragers and respond more strongly to microhabitat as distance from the burrow increases (Bowers

1995; Clarke *et al.* 1993). Maximum recorded dispersal distance is 857m and Loew (1999) found that mean dispersal distance for males is 345m (maximum > 700m) and 85m (maximum 350m) for females. Chipmunks have returned from translocations up to 500m from their burrow.

Bowman and Fahrig (2002) found no effect of translocation distance on return rates of chipmunks translocated up to 250m across open habitat (Bowman & Fahrig 2002). Zollner (2000) found that chipmunks orient towards a forest edge from 120m away when placed in a crop field, suggesting that chipmunks can perceive habitat from at least this distance. Chipmunks are also considered neophilic towards objects although they may explore new areas visually from a fixed position rather than moving within the new area (Wolfe 1969).

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* sp.

Six test sites were selected for this study based on the following criteria: 1) a minimum 300m of forest edge along both sides of the road, with no driveways, adjoining roads or housing; 2) mixed or deciduous dominant forest with closed canopy; 3) two-lane paved road surface. Three of the test sites were estimated to have low traffic and three

were estimated to have high traffic (Table 1) based on preliminary surveys. The distance between forest edges on either side of the road ranged from 23 to 42m (Table 1).

Trapping and handling procedures described here have been approved by the Carleton University Animal Care Committee and the Ontario Ministry of Natural Resources. Chipmunks were trapped from May 10 to August 9, 2005 from fencerows and forest patches using Sherman™ non-folding aluminium live-traps (7.5cm x 9.0cm x 23.0cm) baited with a mixture of rolled oats, peanut butter and shelled peanuts. The trapping sites were located at least 5km from the release sites. We chose this distance to minimize the likelihood that the animals would be familiar with the test site or would be homing towards the capture site while being tracked. A total of 7 sites, located no more than a 30minute walk from the nearest road, were used for trapping with each site ranging in contribution from 1- 26 individuals. Traps were opened in the morning (i.e. 700-1100h) and checked and closed 4-6 hours later. Once trapped, chipmunks were sexed and weighed. Adults were defined as weighing more than 90g and juveniles were less than 90g (Loew 1999). Sex was determined in adults by examination of external reproductive organs. All pregnant or lactating females and young weighing less than 60g were released at the point of capture. Chipmunks were held in a handling bag based on Kaporowski (2002) during processing and anaesthesia was not used.

Chipmunks were fitted with a 3.0 or 4.5g tracking spool (Imperial Thread Inc, Northbrook, IL), for juveniles and adults, respectively, with approximately 110m of string for juvenile spools and 170m of string for adult spools. Spool weights are less than 5% of the body mass of individuals for each age class. At each site approximately half of the trials were performed with adults and half with juveniles.

Spools were inserted into a dark-coloured deflated balloon and glued to the back of the animal using VetBond™ surgical glue (3M Inc, St. Paul, MN), based on the procedure described in Zollner (2000). Chipmunks were transferred to test sites in an opaque, wooden box (15.0cm x 30.5cm x 30.5cm), which was placed in the back of a climate controlled research vehicle for no more than 1.5 hours (Figure 1). There was no talking in the research vehicle while animals were being transported to the test site. Only one animal was released at a given test site per day.

Each animal was released in the following manner: first, the box containing the chipmunk was placed at the release point, which was at the same location at each site, 4m from the forest/verge edge in the forest; second, the loose end of the tracking string was tied to a marker stake; third, a 1.5m tall tripod was set up over the release box and one end of a 40m string was fed through a pulley at the top of the tripod and attached to the lid of the box; lastly, one researcher walked parallel to the road for 40m, alternating the direction from the release box for sequential releases at each site and, after waiting quietly for 5minutes, the other end of the 40m string was pulled, lifting the lid of the box. The box 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 (Figure 1).

Half of all releases at each site were performed when a vehicle was passing by the release device and half were performed when no vehicle was passing by the site as the box was opened; however, at one site 10 of 13 releases were performed while a vehicle was passing due to an exceptionally high traffic amount (Table 1: Site A).

All releases were time stamped on a digital audio recorder (Panasonic RR-US360, Matsushita Electric, Japan) using hand-held radios (Cobra Electronics Corporation,

Chicago, IL). The audio recorder was placed along side the road in the grassy verge and recorded traffic amount for 60minutes following the release. Volume signatures were used to estimate traffic amount using software included with the recorder. Preliminary tests revealed that counting volume signatures using the software was as accurate as visual counting, except at very high traffic volumes (>700 vehicles per hour), where sounds from one vehicle start overlapping with sounds from other vehicles. Therefore, some traffic amounts reported here may underestimate actual traffic during the study.

After at least 60 minutes, we returned to the release point to gather the box and tripod but we did not gather the string used to open the box until the following day. Each entry to the site was made from directly in front of the release device and care was taken to be quiet and quick to minimize our impact on the animal. No chipmunks were observed or heard while we were gathering the equipment. 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 for each section of the pathway that deviated more than 20° from the previous bearing, when an animal climbed a tree or when the animal travelled along coarse woody debris. Tree climbs were defined as movement that was more than 0.5m off the ground located along or up a tree. Following Zollner and Crane (2003), travel along coarse woody debris (CWD) included sections of the pathway when the tracking string was directly over CWD and running lengthwise relative to the orientation of the CWD. Pin flags were used to mark sequential points along the path. Pathway bearings were zeroed such that due north indicated movement directly towards 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 CA). The origin of the coordinate grid coincides with the location of the release point.

Verge width was measured at each site by taking the distance from the road shoulder to the tree line (tree trunks) directly between the release site and the road. The point-centered quarter method was used to measure tree density. We measured the distance from the plot center to the nearest tree (>10cm diameter at breast height) in each quarter. This distance was converted to an area for each quarter:

$$D = \frac{p \cdot r^2}{4}$$

where r is the distance from the plot center to the nearest tree in the quarter in meters. The sum of D (4 quarters per plot x 10 plots) for each site was used to define tree density in m^2 . Five plots were located along the forest edge spaced 40m apart and five plots were located 50m into the forest interior at 40m intervals running parallel to the forest edge. Percent CWD cover was measured by summing the total length of CWD along 10 transects per site, each 10m long, and dividing this total by the total length of all transects (100 m). Transects were randomly oriented. CWD is defined as downed wood greater than 5cm in diameter at the intersection with the transect line, and longer than 10cm. The same plots used to measure tree density were used to measure CWD amount.

Statistical Analyses

For the first prediction, that the probability of crossing the road decreases with traffic amount, we used a binary (i.e. cross/ no cross) logistic regression controlling for total length of pathway with log normal traffic amount as the predictor.

For the second prediction, that the size of turns away from the road increases with increasing traffic amount, we analysed two responses: 1) the exit direction of each animal from the release device; 2) the mean size of the turning angle following movement segments when the animal was heading towards the road. To analyze the exit direction from the release device, releases were categorized based on a combination of the presence or absence of a vehicle passing by the site at the time of release and whether the release was performed at a high or low traffic site (Table 1), for a total of four groups. Each group was tested independently. Observed bearings were tested: 1) against a uniform distribution using Rao's Spacing Test; and 2), against an expected bearing of 180° (indicating movement directly away from the road) with a V-Test. Significance ($p < 0.05$) in the Rao's tests indicates that the bearings are not uniformly distributed. Significance ($p < 0.05$) in the V-Test indicates that bearings are concentrated near the specified mean. In the second analysis of this prediction we used turning angle size, defined as the mean turning angle between sequential pathway segments when the first segment was heading towards the road (i.e. $315-15^\circ$), as the response variable in a linear regression. We excluded any pathway segment found on the road surface from this analysis (see below). Log normal 60 minute traffic amount was used as the predictor. Analysis of circular data was performed using ORIANA v2.02c circular statistics program (Kovach Computing Services, Inc.).

For the third prediction, that the distance from the road to the animal increases with traffic amount, we performed two multiple regressions. For the first regression we used the minimum distance from the road for each movement path as the response variable and for the second regression we used median distance of the pathway from the

road as the response variable. Independent variables in both analyses were total amount of pathway traced and traffic amount. Total amount of pathway traced was included in the model because the likelihood of an animal getting closer to the road should increase the farther the animal is tracked. For traffic amount we used the log normal 60 minute vehicle count following the release of the animal. Data (n=10) from one 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 amount because this site had the highest traffic amount.

Multiple regression analysis was used to test the prediction that the proportion of chipmunks at a site that climbed trees increased with traffic amount, measured as the mean log normal 60 minute traffic amount for the site. We controlled for the probability of encountering trees by including tree density as a predictor variable. Multiple regression was also used to test the prediction that use of CWD increased with traffic amount. The use of CWD by individuals at each site was calculated by summing the length of string that ran along CWD and dividing by the total length of the pathway for each individual. The response variable was the mean CWD used (across individuals) at each site. The amount of CWD at each site was included as predictor variable to control for the probability of encountering CWD. Five pathways ended prematurely because the tracking spool fell off the animal, which usually occurred shortly after release (<50m of pathway) and one other pathway we recorded was later found to contain measurement error and was subsequently removed. These pathways were excluded from all regression analyses. Multiple regressions were performed with the General Linear Model feature on

SPSS v12.0.2 (SPSS Inc.).

We conducted a preliminary test to determine the durability of the tracking string when placed across a high traffic road. We laid five 30m segments of tracking string from five different spools across the road at Site B for 20 hours starting at 1300h. This duration and time of day approximates the actual exposure of the string to traffic during the animal tracking component of this study. We found that two of five string segments laid across the road at Site B were severed. In both cases the breakage occurred >2m away from the paved surface boundary on the road surface itself. Thus, if an animal were to cross the road during our study but the string was severed by traffic by the time we returned to trace the pathway, then we would still likely find string on the road surface.

We conducted another preliminary test to determine how the position of the string is affected by passing vehicles. We manually played out five separate sections of string approximately 10m in length starting in the roadside verge, arcing onto the road surface and then ending on the same side of the road as the start of the pathway about 2m away from the starting point for each section. This pattern would simulate the pathway of a chipmunk that had moved onto the road surface and then turned back towards the forest, thereby mimicking road avoidance. We chose this pattern because we wanted to know if a potential absence of animal pathways on the road surface could be caused by passing vehicles blowing the string off the road, as opposed to actual road avoidance by chipmunks. We made direct observations of the string as vehicles drove near or over the simulated pathways and ended the observation period when the string appeared to stop moving as additional vehicles passed by. We found that portions of all five simulated pathways blew off the road surface due to wind and/or passing vehicles, although these

segments never moved farther than the boundary between the pavement and the adjacent gravel shoulder of the road. Therefore, we will consider pathway segments found within 0.5m of the paved road surface as movement on the road. Furthermore, we will exclude any pathway segments found on the road surface from analysis of the mean size of the turning angle.

Results

Figure 3 shows the pathways of each individual with respect to the forest and road edges, excluding those from Site A. Site A was excluded from this figure because the verge width at site A was about twice the verge width at the other sites (Table 1), making it impossible to plot the pathways for Site A on the same figure as the pathways for the other sites. Among all sites, 25 individuals moved at least 2m beyond the forest edge into the roadside verge and two of these pathways moved within 0.5m of the road surface.

Only one animal was confirmed to have crossed a road during this study. One 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. Therefore, an analysis of the effect of traffic amount on the probability of crossing the road could not be performed

We analysed the exit bearings of 68 chipmunks. The Rao's spacing test indicated a significantly non-uniform distribution of exit bearings at low traffic sites when a vehicle was passing by the site (Table 2; Figure 4c). Exit direction bearings at high traffic sites and at low traffic sites when no vehicle was passing by the site were not significantly different from random (Table 2). The results of the V-test indicate a

significant clustering of exit direction bearings at 180° (i.e. movement away from the road) for the releases at the low traffic sites when a vehicle was passing by the site (Figure 4c, Table 2) There also was a marginally significant clustering of exit direction bearings at 180° for the low traffic releases when no vehicle was passing by the site and for high traffic releases when a vehicle was passing through the site (Figure 4a and d, Table 2).

Contrary to our prediction, the size of the mean turning angle when chipmunks were moving towards the road decreased, rather than increased, with traffic amount (Table 3; Figure 5). Although the effect of traffic on turning angle size was statistically significant ($p=0.013$) the amount of variation explained by traffic was low ($R^2=0.08$).

Traffic amount did not significantly affect the minimum (Table 4; Figure 6) or median (Table 5; Figure 7) distance from the road. Results of a power analysis suggested that we had a sample size large enough to detect an $R^2=0.17$ (i.e. effect size [f^2] = 0.2) with a power of 0.8 for both analyses.

There was a slight negative effect of traffic on the proportion of chipmunks that climbed trees when tree density was controlled for (Table 6; Figure 8). The use of CWD decreased significantly as traffic increased when amount of CWD was controlled for (Table 7; Figure 9). Both of these results are opposite our predictions; however due to a low number of degrees of freedom these two results should be interpreted with caution.

Discussion and conclusion

Our results confirm that chipmunks avoid roads (Figure 3), as has been found in previous studies (McGregor 2004; Oxley *et al.* 1974). Our results do not support the

hypothesis that chipmunks avoid roads because of traffic; none of our three predictions was supported. Below we review these results and discuss the likely mechanisms through which chipmunks avoid roads. In addition, we made two predictions based on the hypothesis that chipmunks respond to vehicles in the same way that they respond to large predators. Again, our results did not support these predictions. Following our discussion of road avoidance, we review the results on predator response and suggest a possible explanation. Finally, we summarize the implications of our findings.

Our first prediction was that if chipmunks avoid roads due to traffic then the probability of an animal crossing the road would decrease as traffic increases. Implicit in this prediction was the assumption that at least a few chipmunks would cross the road, particularly at low-traffic release sites. Only one of 62 pathways crossed the road. This result did not allow us to analyze the effect of traffic on the frequency of road crossing. It is also consistent with the notion that chipmunks avoid roads independently of traffic (McGregor 2004; Oxley *et al.* 1974), and in contrast to Richardson *et al.* (1997) who found that road avoidance increased with traffic amount for two vole species.

Second, we predicted that the size of turning angles should increase with traffic amount. We found very little effect of traffic on turning angle size in two analyses, and what effect we did find was opposite to our prediction: the clustering of exit bearings was near 180° (i.e., away from the road) only at low traffic sites when a vehicle was passing by the site; and the mean size of the turning angle when chipmunks were heading towards the road decreased with increasing traffic volume. A possible explanation for the first result is that perhaps the individuals released at high traffic sites became acclimatized to traffic noise during the 5 minutes before the box lid was lifted. In the low

traffic sites few vehicles would have passed during that time, so the animals responded when a vehicle was passing as the box lid was lifted. This suggests that chipmunks likely acclimatize very quickly to traffic noise.

Third, we predicted that if chipmunks avoid roads because of traffic emissions then they would venture closer to the road as traffic decreased. We found no effect of traffic amount on either the minimum distance from the road (Table 4) or the median distance from the road (Table 5). This finding is consistent with McGregor (2004) who found that densities of chipmunks and white-footed mice (*Peromyscus leucopus*) in roadside habitats were not affected by traffic amount. Note, however, that emissions aversion has been documented in other fauna such as songbirds (Forman *et al.* 2002; Reijnen *et al.* 1996).

These three results support the notion that chipmunks avoid the road itself and that road avoidance is independent of traffic amount. Furthermore, road aversion is not simply due to an unwillingness to move out of the forest into the open verge. Of the 62 pathways we traced, 25 (40%) moved onto the roadside verge. Thus, important components of road avoidance occur while animals are moving within the roadside verge. Two possible explanations for this occurrence is a response by chipmunks to changes in verge vegetation structure or proximity to the road surface *per se*. Previous studies have found that the frequency of road crossing in forest-dwelling small mammals increased when vegetation complexity in road verges was artificially supplemented (Goosem 2001; McDonald & St.Clair 2004b). Chipmunks are known to respond to microhabitat structure, especially when displaced beyond their home range (Bowers 1995). Thus, the structure and composition of verge vegetation may affect chipmunk movement. At the

same time, chipmunks may be avoiding roads due to environmental gradients associated with the road surface *per se* such as changes to light, temperature, texture or odour. Support for this prediction is suggested by the fact that chipmunks may respond to different types of road surface composition (e.g. gravel, paved), since the structure of these environmental gradients change with road surface composition. For instance, Oxley *et al.* (1974) found that chipmunks crossed gravel roads more often than paved roads, although road surface composition and traffic amount were confounded in their study. Others have found that some small mammals respond to the composition of the road surface by altering their movement patterns even though these individuals did not avoid the road (Brock & Kelt 2004; McDonald & St. Clair 2004a). In our study, changes in verge vegetation structure and distance to the road surface are confounded so we cannot isolate these potential effects on chipmunk movement. Further research is needed to determine if changes in vegetation near roads or surface composition affect road aversion in chipmunks.

Our results did not support our predictions from the hypothesis that chipmunks would respond to traffic in a similar way that they respond to large predators. First, we predicted that more individuals would climb trees as traffic amount increases. This prediction was based on a study by Clarke *et al.* (1993), who found that chipmunks tend to climb trees when pursued by humans in unfamiliar habitat. Second, if chipmunks respond to vehicles as predators we expected their use of CWD for travel to increase with traffic amount. This prediction was based on Zollner and Crane's (2003) study in which chipmunks were observed using CWD more frequently than expected in less hospitable environments. We found that both the number of chipmunks that climbed trees and the

use of CWD decreased with traffic amount (Table 6 & Table 7). These results may again indicate that chipmunks become acclimatized to traffic noise quickly, particularly when traffic flow is constant (high traffic sites). At low traffic sites the noise of infrequent individual vehicles may cause a response similar to predator avoidance. Such avoidance of individual vehicles may reduce the mortality rate of chipmunks when crossing roads at low traffic sites. For example, Oxley *et al.* (1974) found that chipmunks comprised 42% of individual mammals observed crossing roads but only 11% of the mammalian roadkill detected within their study area.

Our results suggest that paved roads, irrespective of the traffic on them, reduce landscape connectivity (*sensu* Taylor *et al.* 1993) for chipmunks. It is often suggested that higher landscape connectivity is associated with higher population persistence because it reduces local extinction probabilities and increases recolonization of local extinctions (Fahrig & Merriam 1985; Franken & Hik 2004). Indeed, small mammal species are known to suffer from local extinctions in the study area (Henderson *et al.* 1985; Wegner & Merriam 1979) and the recolonization of formerly occupied habitat may require dispersing individuals to cross roads. Thus, it seems reasonable to predict that roads reduce persistence of chipmunk populations. On the other hand, it has been suggested that population persistence may actually increase with increasing habitat fragmentation (see Fahrig 2003 for possible reasons). For example, some insect populations are more abundant near low-permeable edges and have higher population persistence in patches with such edges (Haynes & Cronin 2006). Interestingly, McGregor (2004) found that chipmunks were more numerous in forest sites near roads than in forest interior sites, and Rtywinski (unpubl. data) found that white-footed mouse population densities increased

with road density. Together these results suggest that roads might actually increase chipmunk population persistence. Determining which of these contrasting possibilities is correct will require a future study evaluating the effect of road density on chipmunk population abundance and distribution.

Although roads inhibit the movement of chipmunks, the amount of road crossing may still be enough to maintain genetic exchange across the region. Merriam *et al.* (1989) found that 8% of 115 white-footed mice living near roads crossed the road. They were unable to genetically identify sub-populations on the basis of the road boundary and attributed this to the movement across the road. We found that 1 in 62 ($\approx 2\%$) chipmunks crossed the roads in our study. This is likely an underestimate, as some individuals may have crossed after the tracking spool had expired. Oxley *et al.* (1974) found that approximately 3% of 179 chipmunks crossed roads during two years of trapping and McGregor (2004) found that 6% of 63 chipmunks living near roads crossed during her two-year study. Conrey and Mills (2001) found that 4% of 234 individuals from two species of chipmunks (*T. amoenus* and *T. ruficaudus*) crossed two-lane highways and 0% crossed four-lane highways. With the exception of the four-lane highway, the observed road crossing frequency in chipmunk populations, between 2% and 6% of marked individuals, is slightly less than the observed rate of crossing in Merriam *et al.* (1989), but it exceeds the theoretical minimum of one migrant per generation needed to maintain a panmictic population (Wright 1969).

In conclusion, our results suggest that chipmunks avoid crossing roads, but we found no compelling evidence that chipmunks avoid roads because of traffic emissions. We detected a small but statistically significant response of chipmunks to vehicles at low-

traffic sites only, possibly indicating that chipmunks become quickly acclimatized to traffic noise and other emissions at high traffic sites. Chipmunk populations are likely not strongly affected by mortality from traffic. Rather, we predict that the effect of roads on chipmunk population persistence is mainly due to population subdivision. Such subdivision could result in either an increase or a decrease in population persistence; future research is needed to determine the population-level effects of roads on chipmunks.

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Table 1. Site data.

Site	Mean 60 minute traffic count (standard deviation)	Categorical traffic amount (High/Low)	Verge width on release side of the road (m)	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

Table 2. Summary statistics for the exit direction analysis. *Vehicle* refers to releases performed when a vehicle was passing through the site.

	High traffic		Low traffic	
	Vehicle	No vehicle	Vehicle	No vehicle
Number of observations	22	14	16	16
Mean vector (μ)	135°	226°	137°	193°
Length of mean vector (r)	0.278	0.172	0.402	0.267
Rao's spacing test U (p)	121 (>0.50)	143 (>0.10)	168 (<0.05)	134 (>0.10)
V test (V; expected mean 180.00°)	0.196	0.119	0.293	0.261
V test u (p)	1.299 (0.098)	0.631 (0.266)	1.657 (0.049)	1.474 (0.071)

Table 3. ANOVA table for the effect of traffic on the mean turning angle when chipmunks were moving towards the road.

Source	Type III sum of squares	df	Mean square error	F	p	Estimate	Standard error
Corrected model	1143.193	1	1143.193	6.572	0.013		
Intercept	277760.623	1	277760.623	1596.683	<0.001	85.515	7.440
Log (60min. traffic)	1143.193	1	1143.193	6.572	0.013	-8.619	3.362
Error	10437.660	60	173.961				
Total	289341.475	62					
Corrected total	11580.852	61					

Table 4. ANOVA table for minimum distance from the road. Data (n=10) from one 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].

Source	Type III sum of squares	df	Mean square error	F	p	Estimate	Standard error
Corrected Model	23.827	2	11.913	0.561	0.574		
Intercept	22.859	1	22.859	1.076	0.305	5.545	5.346
Log (60min. traffic)	22.438	1	22.438	1.056	0.309	1.988	1.934
Length of pathway	0.046	1	0.046	0.002	0.963	-0.001	0.024
Error	1041.014	49	21.245				
Total	5619.417	52					
Corrected total	1064.841	51					

Table 5. ANOVA table for median distance from the road. Data (n=10) from one 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].

Source	Type III sum of squares	df	Mean square error	F	p	Estimate	Standard error
Corrected model	237.427	2	118.714	1.202	0.309		
Intercept	14.214	1	14.214	0.144	0.706	4.373	11.524
Log (60min. traffic)	136.380	1	136.380	1.381	0.246	4.901	4.170
Length of pathway	148.174	1	148.174	1.501	0.226	0.064	0.052
Error	4838.119	49	98.737				
Total	30167.264	52					
Corrected Total	5075.546	51					

Table 6. ANOVA table for proportion of chipmunks that climbed trees at each site. Mean traffic is the mean of the log normal 60 minute traffic count from each release at a given site

	Type III sum of squares	df	Mean square error	F	p	Estimate	Standard error
Corrected model	0.077	2	0.038	3.160	0.183		
Intercept	0.086	1	0.086	7.098	0.076	1.124	0.422
Tree density	0.001	1	0.001	0.052	0.834	-1.032	4.519
Mean traffic	0.076	1	0.076	6.254	0.088	-0.240	0.096
Error	0.036	3	0.012				
Total	1.820	6					
Corrected Total	0.113	5					

Table 7. ANOVA table for the mean use of coarse woody debris by chipmunks. Mean traffic is the mean of the log normal 60 minute traffic count from each release at a given site.

	Type III sum of squares	df	Mean square error	F	p	Estimate	Standard error
Corrected model	0.051	2	0.025	20.018	0.018		
Intercept	0.009	1	0.009	6.863	0.079	0.200	0.077
Coarse woody debris amount	0.029	1	0.029	22.610	0.018	0.001	<0.001
Mean traffic	0.022	1	0.022	17.699	0.025	-0.128	0.030
Error	0.004	3	0.001				
Total	0.118	6					
Corrected total	0.055	5

Figure 1. Mechanism for releasing individual chipmunks. The left photo shows the tripod and release device as it appeared prior to release of an animal. The right photo shows the false roof after the outer box has been removed.

Figure 2. Graphical representation of all pathways greater than 40m in length. Solid lines are pathways at low traffic sites and the double-dashed line are pathways from high traffic sites. The dark gray area represents the verge, the light gray area is the forest and the black area is the road surface. The approximate location of the release point is indicated by the black star. Each grid cell represents 2m^2 . The mean verge width of Sites B-F was used for this figure. Site A was excluded because its verge width was almost twice as large as the verge width of the other sites.

Figure 3. Histograms of exit direction bearings. Bars represent a width of 12° , concentric rings indicate a frequency of 2 pathways. Numbers outside of the circle are the bearings of the cardinal directions with 0° indicating movement directly towards the road. The black vector is the mean direction and the arc outside of the circle is the 95% confidence interval. *Vehicle* refers to releases performed when there was a vehicle passing through the site.

Figure 4. Effect of traffic amount on the mean turning angle when chipmunks were heading towards the road (315° to 45°). Adjusted $R^2 = 0.084$ for the model.

Figure 5. Effect of traffic amount on minimum distance from the road. Site A was excluded from this analysis; see text for explanation. Adjusted $R^2 < 0.01$ for the model.

Figure 6. Effect of traffic amount on median distance from the road. Site A was excluded from this analysis; see text for explanation. Adjusted $R^2 < 0.01$ for the model.

Figure 7. Relationship between use of trees by chipmunks and traffic amount at six test sites. Residuals from the percent of chipmunks climbing trees regressed on tree density were plotted against traffic amount, to illustrate the effect of traffic amount when tree dispersion is controlled for. Adjusted $R^2=0.464$ for the model.

Figure 8. Relationship between use of coarse woody debris and traffic amount at six test sites. Residuals from CWD amount at each site regressed on the mean proportion of each pathway that ran along CWD, to illustrate the effect of traffic amount when CWD amount is controlled for.. Adjusted $R^2=0.884$ for the model.

Appendix A. Number of chipmunks contributed by each trapping site to each release site and distances between all pairs of sites.

Trapping Site	Release Site											
	A		B		C		D		E		F	
	Distance (m)	n	Distance (m)	n	Distance (m)	n	Distance (m)	n	Distance (m)	n	Distance (m)	n
1	1210	0	23346	9	28216	3	32931	4	44510	5	19471	5
2	6869	3	17643	0	22739	2	27201	0	38582	0	15217	1
3	20861	3	9426	0	11050	1	16856	2	32084	0	240	0
4	23985	5	831	0	5682	2	10070	3	23920	4	8780	2
5	25749	2	2188	0	5901	4	8423	3	21101	1	11797	3
6	52139	0	30906	1	29584	0	23985	0	8002	0	40197	0
Total		13		10		12		12		10		11
												68

Appendix B. Coordinates of trapping sites, given in MTM Zone 9 Projection.

Site	Easting(m)	Northing(m)
1	339804	5002097
2	345739	5001976
3	355195	4989868
4	361725	4995457
5	364073	4997351
6	388753	5002647
7	390832	5007993

Appendix C. Coordinates of release sites, given in MTM Zone 9 Projection.

Site	Easting (m)	Northing(m)
A	338938	5002941
B	362343	4996012
C	366074	4991800
D	371627	4993625
E	384296	5003376
G	354954	4989867

Appendix D. Summary data of chipmunks used in this study. All references to dates occurred during 2004. Shaded rows indicate data excluded from regression analyses. Data are available in Appendix F. *Car* refers to the passing of a vehicle in the site when the animal was released with *Y* indicating the presence of a vehicle. The mean turning angle is only calculated for sequential pathway segments when the first segment was heading towards the road and the second segment deviated more than 20° from the previous bearing.

Animal ID	Release Site	Date	Time Released	Trap Site	Mass (g)	Age (a/j)	Sex (m/f)	Car (y/n)	60 Minute Traffic Count	Total Path Length (m)	% of path along CWD	Exit Bearing (°)	Tree Climbs	Mean Turning Angle (°)	Min. Distance From Road (m)	Med. Distance From Road (m)
1	A	Jul-06	1311	4	88	J	M	Y	822	39.47	*	27	0	*	*	*
2	A	Jul-08	1640	4	114	A	M	Y	2211	176.19	0.89%	325	2	50.13	11.78	21.20
3	A	Jul-13	1001	4	98	A	M	Y	714	178.67	1.86%	143	1	39.29	9.45	34.79
4	A	Jul-18	1459	3	102	A	M	Y	1380	168.27	0.00%	205	0	60.53	19.90	25.93
5	A	Jul-19	1153	2	118	A	M	Y	612	164.86	1.83%	189	5	62.62	15.29	19.68
6	A	Jul-21	1454	2	92	A	F	Y	1044	115.47	1.81%	183	0	80.1	25.89	43.11
7	A	Jul-25	1154	2	102	A	M	Y	752	177.65	6.05%	135	0	72.67	13.74	32.61
8	A	Jul-26	1354	3	92	A	M	Y	1650	20.28	*	75	0	*	*	*
9	A	Jul-27	1351	3	112	A	M	Y	887	174.42	3.80%	125	1	59.54	25.24	43.64
10	A	Jun-08	1655	4	115	A	M	Y	1080	18.39	*	27	0	*	*	*
11	A	Jun-10	1600	4	120	A	M	N	1311	170.87	10.65%	189	0	64.89	6.51	24.47
12	A	Jun-27	1705	5	80	J	F	N	2185	107.59	3.10%	339	3	57.23	19.77	24.80
13	A	Jun-29	1358	5	80	J	M	N	756	116.97	0.46%	123	0	67.73	25.48	31.98
14	B	Jul-05	1438	1	70	J	M	N	56	95.25	5.15%	296	1	68.17	7.33	10.04
15	B	Jul-13	1311	1	98	A	M	Y	46	169.73	9.70%	138	2	65.67	12.96	33.90
16	B	Jul-19	1354	1	110	A	F	N	39	102.82	6.08%	228	1	70.57	8.86	16.34
17	B	Jul-11	1350	1	110	A	F	Y	51	165.84	22.45%	176	0	91.89	11.07	22.15
18	B	Jun-10	1317	1	105	J	F	N	38	111.35	10.54%	164	0	92.25	8.76	11.58
19	B	Jun-20	1625	1	70	J	F	Y	76	105.13	8.78%	34	2	65.52	3.52	13.84
20	B	Jun-28	0900	1	105	A	F	Y	37	101.63	13.03%	280	3	50.67	8.78	16.26
21	B	Jun-30	1107	1	72	J	M	Y	37	110.02	14.98%	170	0	78.67	13.08	37.26
***22	B	May-10	1445	6	100	A	M	N	52	100.39	0.00%	220	2	74.07	<0.00	9.52
		May-18														26.01
23	B		1628	1	110	A	M	N	45	166.54	40.19%	246	2	74.43	9.39	
24	C	Jul-04	1654	5	128	A	M	N	33	145.91	29.46%	144	1	63.14	13.55	32.59

Animal ID	Release Site	Date	Time Released	Trap Site	Mass (g)	Age (a/j)	Sex (m/f)	Car (y/n)	60 Minute Traffic Count	Total Path Length (m)	% of path along CWD	Exit Bearing (°)	Tree Climbs	Mean Turning Angle (°)	Min. Distance From Road (m)	Med. Distance From Road (m)
25	C	Jul-06	1538	1	106	A	M	Y	62	168.9	57.16%	136	2	87.67	13.43	33.03
26	C	Jul-11	1412	1	84	J	F	N	22	40.99	*	232	*	*	*	*
27	C	Jul-18	1718	1	82	J	F	Y	45	73.32	**	160	**	**	**	**
28	C	Jul-20	1345	2	90	J	F	N	38	121.17	5.77%	12	1	72.89	6.28	14.02
29	C	Jul-26	1124	2	98	A	M	Y	49	113.11	1.17%	74	2	75.42	3.38	7.49
30	C	Jun-03	0835	4	130	A	M	N	35	174.33	43.48%	114	6	87.79	11.45	33.60
31	C	Jun-13	1622	5	120	A	M	N	60	94.82	42.96%	144	4	42	13.37	27.11
32	C	Jun-20	1505	5	70	J	M	Y	41	115.16	25.06%	168	0	71.11	1.51	17.38
33	C	Jun-22	1544	4	110	A	M	Y	65	167.95	36.35%	168	4	64.4	10.26	19.02
34	C	Jun-29 May-	1311	5	80	J	M	Y	29	109.47	32.58%	342	3	87.41	5.37	13.35
35	C	27	1835	3	100	A	M	N	51	151.93	25.68%	356	2	82.31	4.88	16.80
36	D	Aug-09	1538	3	94	A	M	Y	140	136.62	7.99%	137	1	53.07	15.95	33.41
37	D	Jul-04	1633	5	112	A	M	Y	290	163.54	14.24%	1	3	62.07	6.10	19.83
38	D	Jul-07	1411	1	70	J	M	N	210	103.53	1.00%	267	1	69.45	11.96	37.03
39	D	Jul-12	1356	1	88	J	M	N	186	106.61	2.95%	5	2	29.33	13.25	40.19
40	D	Jul-14	1418	1	78	J	F	Y	217	106.87	7.52%	229	2	73.8	16.11	45.80
41	D	Jul-15	1538	3	82	J	F	Y	417	117.34	0.00%	171	1	51.12	10.96	20.20
42	D	Jun-13	1715	5	105	A	M	Y	324	123.14	0.00%	115	0	59.68	7.20	9.98
43	D	Jun-16	1625	4	67	J	M	Y	63	108.62	1.64%	299	0	41.33	11.29	29.19
44	D	Jun-21	1624	5	80	J	M	N	303	82.62	0.00%	3	5	54.33	7.23	10.69
45	D	Jun-23	1409	4	68	J	F	N	194	111.98	0.00%	287	0	76.27	11.70	25.46
46	D	Jun-24	1436	4	110	A	F	Y	276	72.67	1.16%	15	4	56.91	8.99	13.50
47	D	Jun-28	1451	1	90	J	F	N	264	95.25	2.97%	263	4	52.95	7.16	24.23
48	E	Jul-07	1452	1	116	A	F	N	64	114.64	2.11%	142	2	65.19	4.07	17.79
49	E	Jul-12	1437	1	92	A	F	N	60	107.18	13.57%	206	1	91.33	14.43	29.43
50	E	Jul-14	1502	1	88	J	M	Y	65	86.95	1.05%	76	2	50.33	12.80	16.67
51	E	Jul-15	1618	4	90	J	F	Y	98	111.48	0.66%	270	0	65.23	13.30	19.32
52	E	Jul-18	1750	1	110	A	M	N	65	143	0.00%	262	2	57.65	1.07	9.94
53	E	Jun-15	1742	5	70	J	F	N	59	110.49	0.00%	104	5	67.45	13.72	18.61

Animal ID	Release Site	Date	Time Released	Trap Site	Mass (g)	Age (a/j)	Sex (m/f)	Car (y/n)	60 Minute Traffic Count	Total Path Length (m)	% of path along CWD	Exit Bearing (°)	Tree Climbs	Mean Turning Angle (°)	Min. Distance From Road (m)	Med. Distance From Road (m)
54	E	Jun-16	1715	4	65	J	F	Y	275	95.01	6.90%	188	2	81.09	16.67	33.21
55	E	Jun-24	1710	4	70	J	M	Y	105	116.23	1.52%	78	4	60.25	5.01	10.62
56	E	Jun-30	1146	1	105	A	M	N	70	144.9	0.81%	22	5	73.47	1.90	8.61
57	E	May-30	1500	4	120	A	M	Y	72	154.33	6.33%	92	1	78.11	7.70	15.19
58	F	Jul-05	1413	1	76	J	M	N	190	115.54	11.36%	114	1	71.33	14.19	18.81
59	F	Jul-06	1508	1	72	J	F	Y	174	92.85	5.15%	102	1	92	9.43	23.40
60	F	Jul-08	1601	4	90	J	M	N	373	99.94	12.11%	244	0	68	12.18	26.73
61	F	Jul-13	1249	1	90	J	M	Y	156	99.77	17.14%	178	3	70.55	15.43	33.53
62	F	Jul-20	1321	2	92	A	M	N	167	129.12	9.13%	258	0	47.86	6.17	19.00
63	F	Jun-02	1645	1	108	A	M	N	276	21.88	*	140	0	*	*	*
64	F	Jun-14	1802	5	115	A	F	N	143	126.55	7.45%	172	9	78.36	15.16	25.60
65	F	Jun-21	1554	5	70	J	M	Y	227	111.26	8.84%	172	2	67.08	0.00	14.25
66	F	Jun-27	1635	5	105	A	M	Y	245	167	10.97%	82	1	81.27	2.10	10.35
67	F	May-11	1422	1	102	A	M	N	151	156.14	1.05%	112	3	65.9	12.42	44.96
68	F	May-30	1716	4	110	A	M	Y	231	164.09	8.09%	282	5	56.29	13.09	25.50

*not calculated because pathway ended prematurely

**not calculated because of measurement error while tracing pathway

***individual that crossed the road

Appendix E. Pathway maps from each release. The italicized number to the right of the figure corresponds to the Animal ID in Appendix D. The light grey area represents the forest, the dark grey area represents the roadside verge and the black area represents a portion of the road edge starting at the verge/road edge. The entire width of the road surface is not represented in these maps. The grid cells are 2m². Pathways are represented by the irregular black line, unless the pathway ventured onto the road surface in which case the pathway is white. The release location is at the same coordinate at each site, 4m from the forest/verge edge.

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