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Positive effects of roads on small mammals: a test of the predation release hypothesis

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Abstract Some authors have hypothesized that observed increases in small mammal populations with increasing road density (after controlling for habitat effects) are due to predation release. Predation could be reduced in areas with high road density because of negative effects of roads on predator numbers and/or hunting activity. However, there are no studies testing the relationship between road density and predation rate on small mammals. Based on the predation release hypothesis, we predicted that white-footed mouse (*Peromyscus leucopus*) individuals placed in sites with higher surrounding paved road density and/or closer to a paved road would experience fewer predation attempts than *P. leucopus* individuals placed in sites with lower surrounding paved road density and/or farther from a paved road. We recorded predation attempts on *P. leucopus* placed in wire mesh enclosures, using motion-triggered cameras, at 28 sites ranging widely in surrounding road density. There was no overall decline in predation attempts with increasing paved road density, or increase in predation attempts with increasing distance to the nearest paved roads. However, we cannot rule out the predation release hypothesis for larger mammalian predators, as they were not well sampled in our study. For predatory birds, we found weak evidence in support of the predation release hypothesis, but this conclusion is very tentative, as we only recorded three predation attempts by birds. We suggest that the predation release hypothesis for positive road effects on small mammals merits further investigation, using methods tailored to the particular predators most likely to impact small mammal populations.

Keywords Landscape fragmentation · Predator–prey · Raptor · Road mortality · Traffic disturbance

Introduction

Most studies of the effect of roads on animal population abundance and distribution show negative effects (~59 %) (Fahrig and Rytwinski 2009). These negative effects are thought to result from increased road mortality, population fragmentation, and traffic disturbance resulting in reduced habitat amount and quality (Forman and Alexander 1998; Trombulak and Frissel 2000; Forman et al. 2003). Species that are most negatively affected by roads include amphibians and reptiles, more mobile birds, and mid- to large-sized mammals, mainly carnivores, with low reproductive rates and large home ranges (Rytwinski and Fahrig 2011, 2012, 2015).

Although the majority of population-level responses to roads are negative, Fahrig and Rytwinski (2009) found that around 29 % of populations are unaffected and ~12 % of populations are positively affected by roads. Following the addition of unpublished data and several recent studies, the estimated proportion of positive road effects increased to about 24 % (Rytwinski and Fahrig 2012). There are several possible explanations for neutral and positive effects of roads on wildlife populations. Populations of species that avoid going onto roads but are not disturbed by road traffic, have small territory sizes, and have high reproductive rates should show weak or no effect of roads (Rytwinski and Fahrig 2013). For such species, traffic mortality should be low and viable populations should be able to exist within areas bounded by roads. This combination of conditions has been suggested as an explanation for observed lack of effect or weak effects of roads on some small mammals (Garland and Bradley 1984; McGregor et al. 2008). Positive effects of roads are more difficult to explain. In some cases the road may provide a resource such as food (Knight and Kawashima 1993; Meunier et al. 2000; Lambertucci et al. 2009), nesting sites

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(Haxton 2000; Steen et al. 2006) or basking sites (Rosen and Lowe 1994). As long as the species is able to avoid oncoming vehicles, provision of these resources could, at least in theory, lead to a positive effect on abundance near roads (but see Rytwinski and Fahrig 2013). Alternatively, the delineation of small habitat patches by roads might cause high small mammal densities in areas with high road densities, because small mammal densities are often higher in smaller patches (Yahner 1992; Nupp and Swihart 1996, 2000; Schmid-Holmes and Drickamer 2001; Anderson et al. 2003), likely due to positive kin-based behaviours that increase fitness (Wolff et al. 1997; reviewed in Banks et al. 2007). However, counter to this suggestion, Rytwinski and Fahrig (2007) found a positive road effect on the white-footed mouse (*Peromyscus leucopus*), but no effect of patch size on *P. leucopus* population density. An alternative explanation for positive effects of roads on animal populations is that roads may indirectly cause increases in abundances of animals whose predators are negatively affected by roads, the predation release hypothesis (Johnson and Collinge 2004; Rytwinski and Fahrig 2007; Fahrig and Rytwinski 2009; Rytwinski and Fahrig 2013).

A possible example of predation release occurs in the white-footed mouse. Rytwinski and Fahrig (2007) found larger populations of white-footed mice in forest sites in landscapes with higher road densities than in forest sites in landscapes with lower road densities. They tested various possible explanations involving habitat and food availability, for this unexpected result. None was sufficiently supported by their data and they suggested that the positive effect of roads on mice might be explained by predation release, as small mammals may be less susceptible to road effects than their predators, resulting in lower predation in sites surrounded by more roads. Predation in such sites could be reduced through a decrease in predator abundance due to road mortality and/or through a reduction in hunting activity if predators are disturbed by traffic. The predation release hypothesis has been proposed several times as a possible explanation for the positive effects of roads on small mammal species (Johnson and Collinge 2004; Rytwinski and Fahrig 2007; Fahrig and Rytwinski 2009), as well as the White-tailed Deer (*Odocoileus virginianus*) (Munro et al. 2012), but it has never been directly tested.

While the predation release hypothesis has not been directly tested, it seems to be supported in studies demonstrating weaker negative effects of roads on small mammals than on large mammals (Rytwinski and Fahrig 2011, 2012), which can be predators on smaller species. Furthermore, recent theoretical work supports the predation release hypothesis for positive road effects on prey (both small- and large-bodied prey) (Rytwinski and Fahrig 2013). Strong negative effects of roads on predatory birds (e.g., Newton et al. 1991; Trombulak and Frissel 2000; Bautista et al. 2004; Zabala et al. 2006) also provide indirect support for the predation release hypothesis for the positive effect of roads on small

mammals (but see Knight and Kawashima 1993; Meunier et al. 2000).

The objective of this study was to test the predation release hypothesis for the positive effect of road density on population abundance of the white-footed mouse (Rytwinski and Fahrig 2007), by comparing predation rates on white-footed mice in forest sites in landscapes with higher road densities to forest sites in landscapes with lower road densities. We placed individual white-footed mice in wire mesh enclosures within forest patches selected to represent a range of road densities in the surrounding landscapes. We recorded predation attempts on white-footed mice in the enclosures using motion triggered cameras. We predicted a decrease in predation attempts with increasing road density and an increase in predation attempts with increasing distance from the nearest road, if the predation release hypothesis explains the positive effect of roads on white-footed mice abundance.

Materials and methods

Site selection

The study was conducted in eastern Ontario, Canada, between 8 May and 18 August 2012, using a random subset of 28 of the 36 focal forest patches surveyed for white-footed mice abundance by Rytwinski and Fahrig (2007, 2011). Focal patches were all larger than 2 ha and of similar forest type (deciduous or mixed deciduous). The focal patches were located within rural landscapes that varied widely in paved road density [range 0.27–1.69 km/km²; mean 0.83 ± 0.08 (SE)]. Each landscape was defined as the area within a 2-km radius from the center of each focal patch. This size of landscape was based on reported movement ranges of *Peromyscus* sp. of more than 1 km in under a month (Murie and Murie 1931; Howard 1960; Bowman et al. 1999; Maier 2002). Selected landscapes contained ~18–38 % forest, no rivers or lakes, and no railways. Landscapes with lower and higher paved road densities were distributed across eastern Ontario as much as possible to avoid any effects of regional trends (overall size of study area = 8543 km²) (Fig. 1).

We calculated paved road density as the total length of paved roads within each 2-km radius landscape, divided by the total area of the landscape (km/km²), using data from the Ontario Road Network dataset (Ontario Ministry of Natural Resources 2012a). We also calculated total road density (including paved, gravel and dirt roads), but we report results for paved road density only since results using total road density were qualitatively identical to the results for paved road density. In addition, we measured the distance from the experimental sites within the focal patches (i.e., the center of the area where the four wire mesh enclosures were placed—see ‘Predation attempts’ below) to the nearest paved road

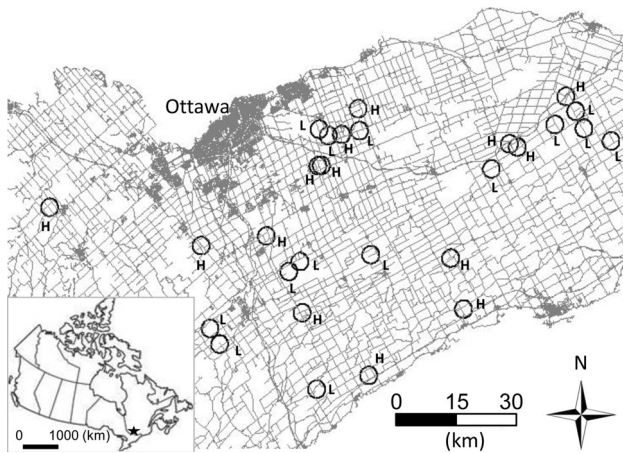


Fig. 1 Distribution of study landscapes ($n = 28$) across eastern Ontario, Canada. Circles represent 2-km radius landscapes and letters correspond to landscape type (*L* low paved road density (≤ 0.75 km/km²) and *H* high paved road density (≥ 0.85 km/km²)). Excluded from this map is the amount of forest. All landscapes were in rural areas

[range 0.11–1.28 km; mean 0.44 ± 0.06 (SE)]. As expected, there was a significant negative correlation between paved road density in the surrounding 2-km radius landscapes and the distance to the nearest paved road ($r = -0.381$, $P = 0.04$). ArcView 10.0 (ESRI, Redlands, California) was used to analyse all geographic information systems data.

Mouse trapping

The white-footed mouse individuals used in the predation experiment (see below) within a given focal patch were obtained by trapping mice in that patch immediately before the experimental 2-day period for that patch. Traps were placed in the focal patch the night prior to the experimental period and checked within 24 h. Since three mice were needed for each experimental period, if three mice were not obtained within 24 h, the trapping continued for a second night and the start of the experimental period was delayed by 1 day. In this situation, any mouse trapped the first night was placed into separate enclosures and kept on site until the experimental period began the next day. Following the second night of trapping, enclosures containing a mouse were cleaned and vegetation, cotton, and food were replaced (see ‘Predation attempts’ below). We used 30 ($20.32 \times 7.62 \times 10.16$ cm) Sherman live traps (H. B. Sherman Traps, Inc., Tallahassee, Florida), randomly placed against fallen logs or stumps. Traps were baited with peanut butter and an apple slice. Cotton batting was also added for warmth and shelter. Trapped mice that were pregnant or lactating were not used in the experiment. Trapping procedures followed guidelines from the Canadian Council on Animal Care (CCAC) and the protocol for the full study was ap-

proved by the Carleton University Animal Care Committee (Protocol #: B12-4).

Predation attempts

To estimate the number of predation attempts at each site we placed each of the three trapped mice (above) from the site in one of three wire mesh enclosures. A fourth enclosure was included as a control to ensure that predators were attracted to the mouse rather than the enclosure itself. The four enclosures were placed in the focal patch a minimum of 40 m and a maximum of 200 m from each other and from the edge of the forest (Fig. 2). Mice were left in the enclosures for 48 h while two video cameras recorded predation attempts. Given that we used 28 sites to ensure adequate replication and a gradient in road density, we were only able to sample predation attempts for one 48-hour period at each site. Therefore, to avoid any potential correlation between road density and seasonal trends in predation attempts, we randomized the order in which sites were visited. After the experimental 48 h period, the mice were released at their location of capture.

The enclosures were built to allow predators to detect the mouse by sight, sound, or smell. The enclosures were $38.1 \times 30.48 \times 30.48$ cm, mounted on a 1.22×1.22 m piece of plywood (Fig. 3a). The top and sides were covered with 12.7 mm steel mesh. The top was hinged at the halfway point to allow insertion of the mouse, and food and new bedding as needed. All metal, with the exclusion of the steel mesh, was painted black using an odorless outdoor paint (BEHR Premium Plus; Behr Process Corp., Calgary, Alberta) to limit light reflection. Inside each enclosure we covered the floor with substrate from the surrounding forest including leaves, twigs and grasses, and we added a fist sized ball of cotton batting. 125 ml of black oil sunflower seeds were added for food. Enclosures were checked daily for structural damage and to provide the mouse with additional seeds, vegetation and cotton as needed. The control enclosure was treated identically to experimental enclosures, except for the absence of a mouse. The enclosure used as the control was rotated through the field season, such that each enclosure served as the control at seven of the 28 sites.

To monitor predation attempts on the mice, we used Moultrie I40XT GameSpy Digital infrared-triggered game cameras (EBSCO Industries, Inc., Birmingham, Alabama), which provided both still shots and video footage. The cameras are triggered when they detect a difference between ambient background temperature and heat generated by a moving animal. Two cameras were directed at each enclosure. The cameras were mounted on trees at a 90° angle from each other at a height of 40 cm above the ground, and approximately 2 m from the enclosure (Swann et al. 2004). Each camera was leveled and focused on the enclosure and the surrounding ~ 50 m² area. We set the sensitivity of the

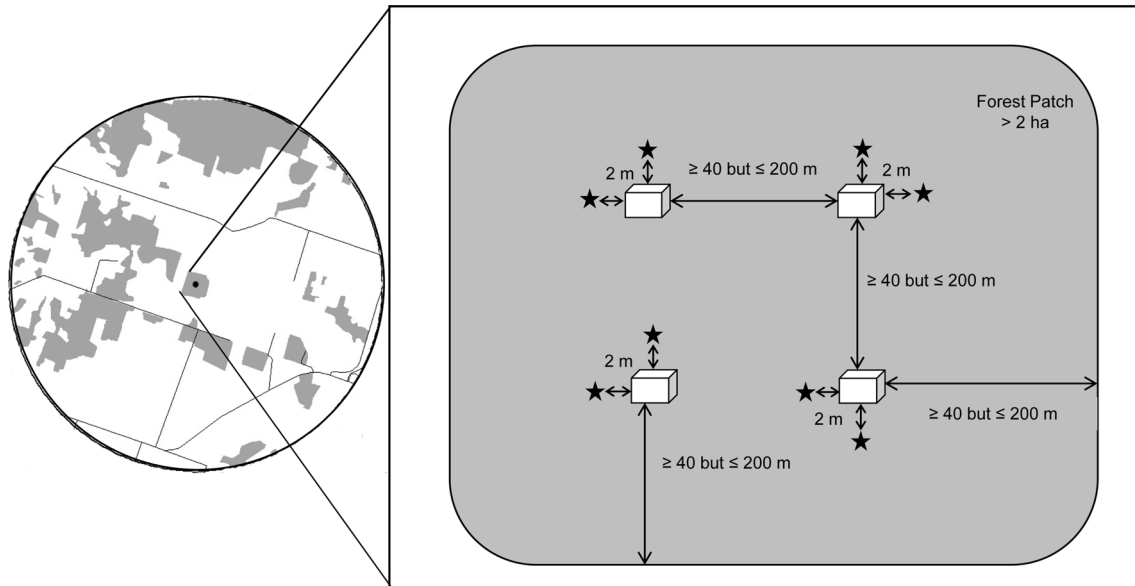


Fig. 2 Experimental set-up at each of the 28 sites. Four wire mesh enclosures were placed at each site within the center of a focal forest patch > 2 ha. Focal forest patches were centered within rural landscapes that were defined as the area within a 2 km radius from the center of each focal patch (*black dot*). Each of the three enclosures contained a single trapped mouse. A fourth enclosure was included as a no-mouse control. Enclosures were placed at least 40 m and at most 200 m from each other and from all forest

edges. To monitor predation attempts on the mice, two Moultrie I40XT GameSpy Digital infrared-triggered game cameras (*stars*) were directed at each enclosure. The cameras were mounted on trees at a 90° angle from each other at a height of 40 cm above the ground, and approximately 2 m from the enclosure. Each camera was leveled and focused on the enclosure and the surrounding ~ 50 m² area

cameras to high, the video duration to 20 s and the video delay for the re-set of the camera to 60 s.

Potential confounding variables

In their site selection process, Rytwinski and Fahrig (2007, 2011) attempted to control for possible confounding variables that might affect white-footed mouse abundance. However, there were several variables that could affect mouse abundance and/or predation attempts that did vary among sites. These included local habitat characteristics [number of woody tree species, percent cover of coarse woody debris (CWD), and mean tree diameter at breast height (DBH)], landscape characteristics [focal forest patch size and percent forest in the landscape (including the focal forest patch)], and Julian date. The habitat characteristics were taken from Rytwinski and Fahrig (2007, 2011) [see Rytwinski and Fahrig (2007, 2011) for vegetation survey methods, and see Table S1 for raw data]. Although our experiment was conducted 3–5 years following these measurements, we assumed they would have changed slowly enough to be still representative of relative differences among the sites. Size of the focal patch (ha) and percent forest in the landscape were determined using Ontario Ministry of Natural Resources thematic data (Ontario Ministry of Natural Resources 2012b).

Data analysis

Predation attempts

The “raw” number of video clips could not be used to represent the number of predation attempts because occasionally the camera recorded the mouse moving with no predator present, or it recorded a passing non-predator animal (e.g., deer). Therefore, all video clips were filtered to ensure that they contained a predator on or approaching the experimental enclosure. In addition, a difficulty in quantifying the number of predation attempts from the video footage was that the same predation attempt by the same individual predator could be recorded in subsequent video clips if the individual remained at the enclosure for more than the 60 s video delay period. We were concerned that this might inflate the apparent number of predation attempts at sites containing a very persistent individual predator. Since predators were not marked, we could not reliably identify individuals. However, we reasoned that a large time gap between video clips of the same species of predator indicated either that the predator went away and then returned later to make another predation attempt or that a different individual predator of the same species made the second attempt. We therefore reduced the number of sequential same-species predation attempts by applying a minimum time gap between same-species

predation attempts. We tried different minimum time gaps (5, 10, 20, 60, 120 min between video clips of the same species). The estimates using different time gaps were highly correlated (Table S2), and using different minimum time gaps did not qualitatively change our results. Here we present only the analyses using the 20 min minimum time gap.

Four response variables were examined: the total number of predation attempts by all species per enclosure-day, the number of predation attempts by mammal species other than raccoon (*Procyon lotor*) per enclosure-day, the number of raccoon predation attempts per enclosure-day, and the presence/absence of an avian predation attempt. We combined the number of predation attempts by mammal species other than raccoon because each species accounted for $\leq 5\%$ of the total number of predation attempts we recorded. Since there were only three predation attempts by birds, each from a different avian predator species, we combined these predation attempts into one response variable. Data for the three enclosures containing a mouse in each focal patch were combined, producing one value for each response variable for each focal patch. For the total number of predation attempts, the number of predation attempts by mammals other than raccoon, and the number of predation attempts by raccoon, we used the number of attempts per enclosure-day at each site, to account for the fact that at three sites we were only able to trap two (rather than three) mice. For avian predation attempts, where there was never more than one attempt per site, we used the presence/absence of an avian predation attempt as the response.

Potential confounding variables

Although we tried to control for potential confounding variables during site selection and study design, there were still some variables potentially affecting predation attempts that might mask an effect of paved road density or distance to the nearest paved road. We calculated the correlations between the potential confounding variables—percentage CWD, number of tree species, mean tree DBH, size of the focal patch, amount of forest in the surrounding landscape, and Julian date—and paved road density and distance to the nearest paved road, to determine which of the potential confounding variables might mask a road effect on the response variables. We intended to include in further analyses any variable that showed a significant correlation with paved road density or distance to the nearest paved road.

Effects of road density and proximity on predation attempts

To test our predictions that white-footed mice placed in sites with higher surrounding paved road density and closer to a paved road would experience fewer predation

attempts than white-footed mice placed in sites with lower surrounding paved road density and farther from a paved road, we first conducted simple linear regressions of the total number of predation attempts per enclosure-day, on each of paved road density and distance to the nearest paved road. For both the number of predation attempts by mammal species other than raccoon and the number of raccoon predation attempts, we ran separate simple linear regression of the number of predation attempts per enclosure-day on each of paved road density and distance to the nearest paved road. For avian predation attempts, we conducted simple logistic regression analysis (logit link) of presence/absence of a predation attempt on each of paved road density and distance to the nearest paved road. For the total number of predation attempts, the number of predation attempts by mammal species other than raccoon, and the number of predation attempts by raccoon, where we had sufficient sample sizes to allow for the inclusion of multiple predictors, we then conducted multiple regressions including, as covariates, any of the confounding variables that showed a significant correlation with paved road density or distance to the nearest paved road. We performed all statistical analyses using R v 3.0.3 (R Development Core Team 2014). To meet model assumptions, the response variables—the total number of predation attempts per enclosure-day, the number of predation attempts by mammal species other than raccoon per enclosure-day, and the number of predation attempts by raccoon per enclosure-day—were log transformed for all analyses. Before taking logs we added 1 so that zero values were still zero following transformation. Due to its skewed distribution, the predictor variable distance to the nearest paved road was also log transformed for all analyses. We used *P* values and confidence intervals to evaluate significance.

Results

Altogether there were 1039 video clips showing predation attempts, at 25 of the 28 focal patches. This was reduced to 228 predation attempts after we applied the 20 min minimum time gap between successive predation attempts by the same predator species. We recorded predation attempts by eight predator species: raccoon (198 attempts), domestic cat (*Felis catus*) (12 attempts), short-tailed weasel (*Mustela erminea*) (9 attempts), striped skunk (*Mephitis mephitis*) (3 attempts), fisher [*Pekania (Martes) pennanti*] (3 attempts), red-tailed hawk (*Buteo jamaicensis*) (1 attempt), eastern screech owl (*Megascops asio*) (1 attempt), and barred owl (*Strix varia*) (1 attempt) (Fig. 3b–d; Table S1). 98.7 % of recorded predation attempts were made by mammals. Most (87 % of all attempts) were made by raccoons. We recorded only three predation attempts by avian predators, each at a different focal patch. Control en-

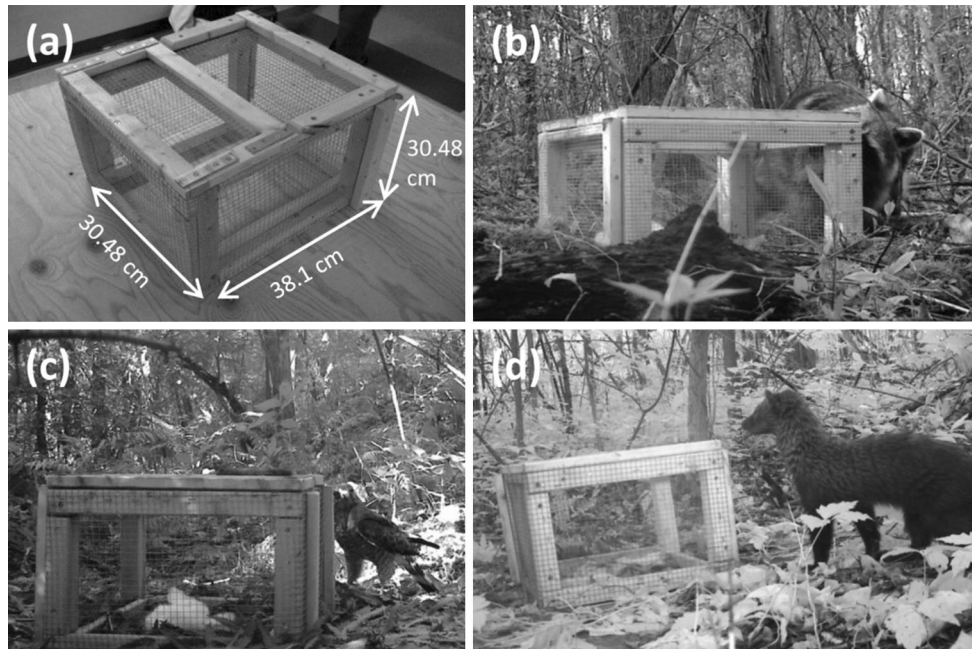


Fig. 3 **a** Mouse enclosure (38.1 × 30.48 × 30.48 cm) built to allow predators to detect the mouse visually or by olfaction. Example photos of predation attempts on *Peromyscus leucopus*: **b** raccoon

(*Procyon lotor*); **c** red-tailed hawk (*Buteo jamaicensis*); and **d** fisher [*Pekania (Martes) pennanti*]

closures were much less likely to attract predator species than enclosures containing a mouse; 6 % of video clips were recorded at control enclosures.

Correlations between the potential confounding variables and both paved road density and distance to nearest paved road were weak ($r \leq |0.40|$, $P > 0.05$; Table S3), with the exception of two variables, mean tree DBH and Julian date, which showed significant associations with distance to nearest paved road ($r = -0.49$, $P = 0.01$ and $r = -0.39$, $P = 0.04$, respectively). Mean tree DBH and Julian date were therefore included in further analyses (below) to account for their potential effects on predation attempts.

For all predator species combined, there was no evidence of a relationship between predation attempts and paved road density ($\beta = 0.005$ (CI $-0.20, 0.21$), $F_{1,26} = 0.002$, $P = 0.966$; Table 1, Fig. 4a). In contrast, and opposite to the prediction of the predation release hypothesis, the total number of predation attempts decreased with the log of the distance to nearest paved road ($\beta = -0.386$ (CI $-0.63, -0.14$), $F_{1,26} = 9.311$, $P = 0.005$; Table 1, Fig. 4b). Including mean tree DBH and Julian date with paved road density in a multiple regression did not qualitatively change the results from the simple linear regression of road density on the total number of predation attempts. However, including these variables with distance to the nearest road in a multiple regression did change the results from the simple linear regression of distance to the nearest road on the total number of predation attempts, in that distance to the nearest road was no longer significant (Table 1).

For all mammalian predators other than raccoon, there was no evidence of a relationship between paved road density or distance to the nearest road for the number of predation attempts ($\beta = 0.076$ (CI $-0.02, 0.17$), $F_{1,26} = 2.680$, $P = 0.114$, Fig. 4c; $\beta = 0.012$ (CI $-0.12, 0.15$), $F_{1,26} = 0.029$, $P = 0.865$, Fig. 4d, respectively; Table 1). Including mean tree DBH and Julian date with paved road density or distance to the nearest road in multiple regressions did not qualitatively change the results from the simple linear regression of road density or distance to the nearest road on the total number of predation attempts (Table 1).

For raccoon, there was no evidence of a relationship between predation attempts and paved road density ($\beta = -0.044$ (CI $-0.25, 0.17$), $F_{1,26} = 0.167$, $P = 0.686$, Fig. 4e). Similar to when all predators were combined, and opposite to the prediction of the predation release hypothesis, the number of predation attempts decreased with the log of distance to nearest paved road ($\beta = -0.413$ (CI $-0.66, -0.16$), $F_{1,26} = 10.550$, $P = 0.003$; Table 1, Fig. 4f). Including mean tree DBH and Julian date with paved road density in a multiple regression did not qualitatively change the results from the simple linear regression of road density on the number of raccoon predation attempts. However, the effect of distance to the nearest road on the number of raccoon predation attempts was no longer significant when mean tree DBH and Julian date were included in the model (Table 1).

For predation attempts by predatory birds, there was a decline in the number of predation attempts with in-

Table 1 Model summaries of the relationship between (A) $\log[(\text{the total number of predation attempts per enclosure-day}) + 1]$, (B) $\log[(\text{the number of predation attempts by mammal species other than raccoon per enclosure-day}) + 1]$, (C) $\log[(\text{the number of predation attempts by raccoon per enclosure-day}) + 1]$, and (D) the presence of avian predators and each of (1) paved road density, and (2) $\log(\text{distance to the nearest paved road})$. For responses A-C, multiple regressions were conducted including, (3) paved road density, mean tree diameter at breast height (DBH) and Julian date, and (4) $\log(\text{distance to the nearest paved road})$, mean tree DBH and Julian date. Values in brackets are the 95 % confidence intervals for the coefficient estimates (β)

Model	Response	Predictors				R^2	F	df	P
		β paved road density	$\beta \log(\text{distance to paved road})$	β mean DBH	β Julian date				
A1	All predators	0.005 (-0.20, 0.21)				0.000	0.002	1, 26	0.966
A2			-0.386 (-0.63, -0.14)**			0.264	9.311	1, 26	0.005
A3		0.047 (-0.13, 0.22)		0.036 (0.005, 0.07)**	-0.003 (-0.005, 0.000)*	0.366	4.620	3, 24	0.011
A4			-0.205 (-0.48, 0.07)	0.026 (-0.007, 0.06)	-0.002 (-0.004, 0.000)	0.411	5.584	3, 24	0.005
B1	All mammals but raccoon	0.076 (-0.02, 0.17)				0.094	2.680	1, 26	0.114
B2			0.012 (-0.12, 0.15)			0.001	0.029	1, 26	0.865
B3		0.072 (-0.004, 0.003)		-0.003 (-0.02, 0.02)	0.0002 (-0.001, 0.002)	0.105	0.935	3, 24	0.439
B4			-0.020 (-0.005, 0.003)	-0.004 (-0.02, 0.02)	0.0004 (-0.001, 0.002)	0.024	0.196	3, 24	0.898
C1	Raccoon	-0.044 (-0.25, 0.17)				0.006	0.167	1, 26	0.686
C2			-0.413 (-0.66, -0.16)**			0.289	10.550	1, 26	0.003
C3		0.002 (-0.17, 0.17)		0.040 (0.01, 0.07)**	-0.003 (-0.05, -0.000)**	0.422	5.843	3, 24	0.004
C4			-0.205 (-0.47, 0.06)	0.030 (-0.002, 0.06)*	-0.002 (-0.005, -0.000)*	0.473	7.169	3, 24	0.001
D1	Presence of avian predators	-4.490 (-13.31, 0.06)					Wald z	n	P
D2			5.080 (-0.01, 12.58)*				-1.433	28	0.152
							1.656	28	0.098

* Coefficients were significant at the $P < 0.1$ level

** Coefficients significant at the $P < 0.05$ level

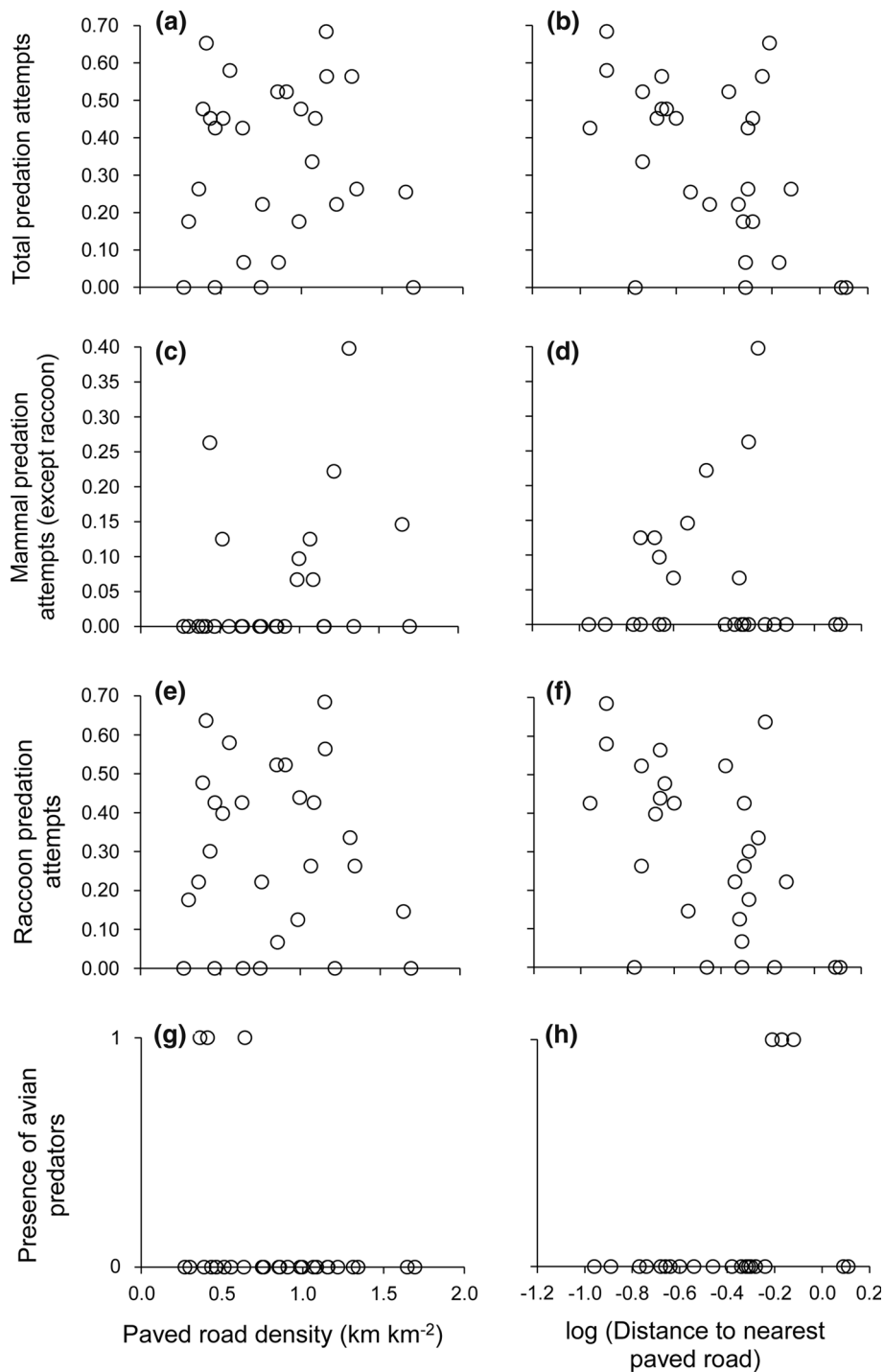


Fig. 4 Scatterplots of $\log[(\text{the total number of predation attempts per enclosure-day}) + 1]$ (**a, b**), $\log[(\text{the number of predation attempts by mammal species other than raccoon per enclosure-day}) + 1]$ (**c, d**), $\log[(\text{the number of predation attempts by raccoon per enclosure-day}) + 1]$ (**e, f**), and presence of avian predators

(**g, h**), on *Peromyscus leucopus* in experimental enclosures vs. paved road density (km/km^2) in the surrounding 2-km radius landscapes (*left panel*) and $\log(\text{distance to the nearest paved road})$ (*right panel*). Each point represents data from an experimental site ($n = 28$)

creasing paved road density, as predicted ($\beta = -4.488$ (CI $-13.31, 0.06$), Wald z -statistic = -1.433 , $P = 0.152$; Table 1; Fig. 4g) but the slope was not statistically significant. Similarly, as predicted, the number

of bird predation attempts increased with increasing distance from roads ($\beta = 5.080$ (CI $-0.01, 12.58$), Wald z -statistic = 1.656 , $P = 0.098$; Table 1; Fig. 4 h), with a marginally significant slope.

Discussion

The purpose of this study was to test the hypothesis that the observed positive response of white-footed mouse abundance to road density in the surrounding landscape (e.g., Adams and Geis 1983; Rytwinski and Fahrig 2007, 2011) is due to a negative effect of roads on predation (predation release), through a negative effect of roads on the abundance and/or activity of their predators. For all predation attempts combined, all mammalian predation attempts other than raccoon, and all raccoon predation attempts, we found no evidence for the predicted decline in predation attempts with increasing paved road density, or for the predicted increase in predation attempts with increasing distance to the nearest paved roads (Table 1; Fig. 4a–f). However, our results tentatively support the predation release hypothesis for predatory birds; there was weak evidence of a decrease in predation attempts with increasing paved road density and proximity to the nearest paved road, as predicted (Table 1; Fig. 4g, h).

The overall lack of support for the predation release hypothesis when considering all predators combined is largely driven by the raccoon response, as raccoons were by far the most common mammalian predator we recorded (87 % of all attempts) (Table 1). Raccoon predation attempts increased with mean tree DBH and decreased with Julian date, and when these variables were included in a multiple regression, there was no apparent effect of road density or distance to nearest paved road on predation attempts by raccoons. These results suggest that there is no support for the predation release hypothesis for raccoons.

There was also no support for the predation release hypothesis for the other mammalian predators (combined), but as only small numbers of predation attempts were recorded for these species, we are less confident in this conclusion than in our conclusion for raccoons. Initially, we had hoped to investigate the predation release hypothesis for each predator species separately; however, there was too little information to do so. Relative abundance estimates have been obtained for some predators within our study area; however, as different sampling techniques/efforts were used in different years to target a particular set of mammal species, abundance estimates are not comparable across species or within species across years (see Table S4). Without accurate estimates of predator abundance for the sites used in this study, it is difficult to say whether the estimates of predation rate we recorded (even when combined) are in fact representative of predator numbers and/or activity in our study area. It is possible that some mammals that are prone to negative road effects have low detectability due to lower densities [e.g., fisher, red fox (*Vulpes vulpes*), coyote (*Canis latrans*)]. Although we did detect predation attempts by fisher, they were only 1.2 % of all predation attempts, and neither red fox, nor coyote were detected. Both fisher and red fox have shown negative

population-level responses to road density in past studies (Roedenbeck and Köhler 2006; Rytwinski and Fahrig 2011). If we had been able to leave the caged mice in place for a longer time, we would likely have obtained more accurate estimates of predation attempts by these rarer species, with possibly fewer attempts at sites with higher road density or closer to roads. Small mammals, including white-footed mice, do represent an important component in the diets of the lower density mammals in our study area (e.g., fisher: Powell 1981; Martin 1994; Bland et al. (2001), unpublished data; Powell et al. 2003; Bowman et al. 2006; coyote: Voigt and Berg 1987; Bekoff and Gese 2003; red fox: Cypher 2003). Therefore, the possibility remains that predation release by the rare, poorly detected predators (i.e., fisher, red fox, coyote) could be responsible for the positive road effects on white-footed mice. However, to our knowledge, there is not enough information to say whether predation by these predators is sufficient to influence white-footed mouse populations. We suggest that reduced predation by lower density mammalian predators in areas of high road density, either alone or in combination, as a cause for the positive effects of roads on small mammal abundance deserves further study. Regarding the other mammalian predators, previous studies have found no negative effect of roads on the short-tailed weasel or the striped skunk (Rytwinski and Fahrig 2011), so they are unlikely candidates for the predation release hypothesis. Finally, while there are no data on the relationship between domestic cats and road density, their numbers are likely positively related to road density as roads are indicative of presence of humans.

Our results do weakly support the predation release hypothesis for predatory birds. Raptors (hawks and owls), which are particularly efficient *Peromyscus* spp. predators (Errington 1932; Graber 1962; Marti 1976; Colvin and McLean 1986; Swengel and Swengel 1992), did show the predicted decline in predation attempts with increasing paved road density and proximity to nearest paved road (Fig. 4g, h). However, this conclusion is extremely tentative, as we recorded only three predation attempts by raptors. It is possible that our study design did not provide a true indication of the number of attempts by avian predators. Our cameras, being aimed at the enclosures containing the mice, may have missed many predation attempts by birds, which may have been attracted to the mouse but able to determine from a distance above it (e.g., perched above the enclosure) that it was inaccessible, and so they did not come down to within the view of the cameras. All three of the attempts we recorded were made at sites in landscapes with low road densities and far from the nearest paved road (Fig. 4g, h). We therefore suggest that our results are at least consistent with the notion that the positive effect of roads on white-footed mouse abundance is related to a reduction in abundance and/or activity of predaceous birds in landscapes with high road density. Previous studies have shown reduced abundance and/or activity of predaceous birds in the vicinity

of high traffic roads (Paruk 1987; Anthony and Isaacs 1989; Martinez and Zuberogoitia 2004; Boves and Belthoff 2012; Silva et al. 2012). Furthermore, Zabala et al. (2006) found that little owls (*Athene noctua*) in Biscay (SW Europe) were absent from areas of high paved road density. In addition, the typical low-flight behaviour of owls and their nocturnal hunting nature increases the risk of vehicle collisions (Grilo et al. 2012; Kociolek et al. 2015). Taken together, our results provide tentative support for the predation release hypothesis for predatory birds.

Are there other factors that, combined with a weak predation release from avian predators, could explain the observed positive response of white-footed mouse abundance to roads? Rytwinski and Fahrig (2007) investigated a range of possible explanations and found a marginally significant positive effect of the number of buildings in the surrounding landscape on white-footed mouse relative abundance. They hypothesized that overwinter survival rates of white-footed mice might be higher in landscapes with more buildings, as buildings provide overwinter refuge sites against cold stress and lack of food (Witmer and Moulton 2012). However, the relationship between white-footed mouse abundance and number of buildings was weaker than the relationship between white-footed mouse relative abundance and road density, suggesting that the number of buildings alone did not cause the observed increase in white-footed mouse relative abundance with increasing road densities (Rytwinski and Fahrig 2007). We hypothesize that the positive effect of roads on white-footed mouse abundance could be due to the combination of a weak effect of predation release from predatory birds and a weak effect of a higher abundance of over-winter refuge sites in areas with more roads.

Is predation release the likely cause of positive effects of roads on abundances of other small mammal species in other regions (e.g., prairie vole (*Microtus ochrogaster*) in Illinois: Adams and Geis 1983; black-tailed prairie dogs (*Cynomys ludovicianus*) in Colorado: Johnson and Collinge 2004; kangaroo rat (*Dipodomys microps*) and great basin pocket mouse (*Perognathus parvus*) in Utah: Bissonette and Rosa 2009)? It is possible that release from predation by birds could be at least part of the explanation for several of these species. Since many of the above small mammals occupy open landscapes (e.g., open agricultural areas, short and mixed grass prairies, or open arid terrain), they may be particularly susceptible to high predation pressure from avian predators due to the low protective vegetation cover. Studies have shown that many species of rodents perceive greater predation risk in open habitats (less vegetation cover or structure) than bush habitats (more cover and structure) (e.g., North American desert rodents: Kotler 1984; Indian crested porcupines: Brown and Alkon 1990; squirrels and chipmunks: Bowers et al. 1993; Brown and Morgan 1995), and that rates of predation are higher on small mammals foraging in the open than on small mammals foraging with cover (Kotler et al. 1988). If

high road densities reduce avian predators in open areas, it is possible that reduced predation pressure could be the main driver for the positive effects of roads on abundances of some of these other small mammal species. While empirical data on population level effects of roads for raptors (owls and hawks) are limited, previous studies have reported negative road effects on an avian predator that inhabits open agricultural habitats (Zabala et al. 2006; Silva et al. 2012). Another possibility is that a combination of predation release and some habitat quality element that is correlated with roads is causing the positive effects of roads on abundances of other small mammal species in other regions. For example, Ruiz-Capillas et al. (2013) found that proximity to the road was the most important predictor of wood mouse (*Apodemus sylvaticus*) abundance, with greater abundance of mice in close proximity to a road that crossed a wooded landscape, but various microhabitat variables were also found to influence mice abundance. They suggested their results point to a refuge effect of increased small mammal abundance near roads that is associated with both microhabitat variables such as the cover and height of the tree and herbaceous layers and a lower intensity of predation near the road. Therefore, it is possible that the positive road effects on other small mammals (and possibly even the white-footed mouse) are due to a combination of predation release and a correlation between roads and habitat quality.

In conclusion, our results provide at best weak support for the hypothesis that reduced predation, specifically by birds, causes the positive relationship between road density and white-footed mouse abundance. In addition, we cannot rule out the hypothesis for larger mammalian predators, as they were not well sampled in our experimental setup. Future research should develop study designs that have a higher probability of detecting predation attempts by avian predators and low density mammalian predators.

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