

# Reproductive rate and body size predict road impacts on mammal abundance

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**Abstract.** It has been hypothesized that mobile species should be more negatively affected by road mortality than less-mobile species because they interact with roads more often, and that species with lower reproductive rates and longer generation times should be more susceptible to road effects because they will be less able to rebound quickly from population declines. Taken together, these hypotheses suggest that, in general, larger species should be more affected by road networks than smaller species because larger species generally have lower reproductive rates and longer generation times and are more mobile than smaller species. We tested these hypotheses by estimating relative abundances of 17 mammal species across landscapes ranging in road density within eastern Ontario, Canada. For each of the 13 species for which detectability was not related to road density, we quantified the relationship between road density and relative abundance. We then tested three cross-species predictions: that the slope of the relationship between road density and abundance should become increasingly negative with (1) decreasing annual reproductive rate; (2) increasing home range area (an indicator of movement range); and (3) increasing body size. All three predictions were supported in univariate models, with  $R^2$  values of 0.68, 0.50, and 0.52 respectively. The best overall model based on AIC<sub>c</sub> contained both reproductive rate ( $P = 0.008$ ) and body size ( $P = 0.072$ ) and explained 77% of the variation in the slope of the relationship between road density and abundance. Our results suggest that priority should be placed on mitigating road effects on large mammals with low reproductive rates.

**Key words:** body size; landscape connectivity; landscape fragmentation; landscape structure; mammal; mobility; population abundance; reproductive rate; road density; road mitigation; road mortality; road network.

## INTRODUCTION

Over the last 100 years, North America's landscapes have become increasingly fragmented by roads. As road networks continue to increase worldwide, so too has the interest in their effects on wildlife populations (Trombulak and Frissell 2000, Forman et al. 2003). In their research agenda for road ecology, Roedenbeck et al. (2007) identified five critical road ecology research questions that need to be addressed, the most pressing being: "Under what circumstances do roads affect population persistence?"

Several hypotheses have been suggested for predicting the types of species whose populations should be most negatively affected by roads. Species that make frequent, long-range movements over the landscape should be more negatively affected by roads because they interact with roads more often than do less-mobile species (Carr and Fahrig 2001, Gibbs and Shriver 2002, Forman et al. 2003). Similarly, species with larger territories or home ranges should be more susceptible to road effects than those with smaller territories/home ranges. Species with

lower reproductive rates and longer generation times (i.e., species having  $K$ -selected life histories), should also be more susceptible to road effects because they will be less able to rebound quickly from population declines (Gibbs and Shriver 2002). Since species with large home ranges and low reproductive rates naturally occur at low densities, we also expect that species that naturally occur at low densities should be more susceptible to road effects.

These hypotheses can be summarized into two main mechanisms that should affect both the magnitude and direction of the road effect on mammals: (1) reproductive rate, which affects a species ability to rebound from low numbers resulting from road mortality, and (2) mobility (movement range and/or home range), which affects a species encounter rate with roads. Since both mechanisms are related to a species natural density, as outlined above, density is indirectly captured in these two mechanisms. Taken together, these hypotheses also suggest that, in general, larger species should be more affected by road networks than smaller species because larger species generally occur naturally at lower densities, have lower reproductive rates, longer generation times, and are more mobile than smaller species (Gibbs and Shriver 2002, Forman et al. 2003). Interestingly,

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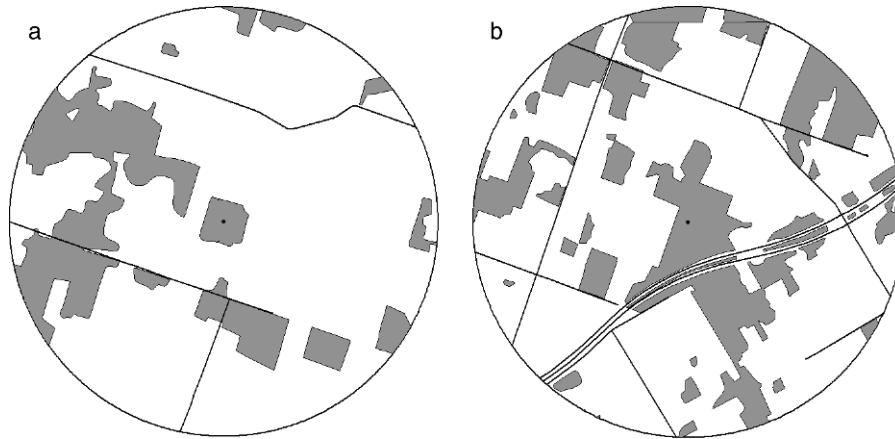


FIG. 1. Examples of two landscapes (the area inside the circles in each panel): (a) low road density and (b) high road density. Landscapes for the 2005 and 2009 sampling period were 2 km radius areas around each of 14 and 24 forest patches, respectively. During 2005 and 2009, small mammals were sampled in a 100-m<sup>2</sup> grid and a 140-m<sup>2</sup> grid (respectively) in each patch. For the 2008 sampling period, landscapes were 3 km radius areas around the center of each of the 29 sampling sites, each arranged as outlined in Appendix A: Fig. A1. The sample site is represented by a black dot, roads by lines, and forest cover by gray shading.

since larger species are often predators on smaller species, it is also possible that negative effects of roads on populations of large animals could lead to reduced predation on small animals in areas of high road density. This could indirectly reduce the impact of roads on small mammals, further strengthening the prediction that negative road effects should increase with increasing body size. In fact, release from predation has been suggested as a possible cause for the frequently observed positive effects of roads on small mammal populations (Johnson and Collinge 2004, Rytwinski and Fahrig 2007, Bissonette and Rosa 2009, Fahrig and Rytwinski 2009).

The purpose of this study was to test the predictions that the effects of roads on mammal populations should be increasingly negative with (1) decreasing reproductive rate, (2) increasing mobility, and (3) increasing body size. We did this by estimating relative abundances of 17 mammal species from landscapes ranging in road density within eastern Ontario, during three sampling periods: 2005, 2008, and 2009. For each of the 13 species for which detectability was not related to road density, we estimated the slope of the relationship between road density and relative abundance. We then tested for relationships between these slopes and reproductive rate, home range area as an indicator of mobility (Bowman et al. 2002), and body size.

#### METHODS

In each of three field seasons (2005, 2008, and 2009) we targeted a particular set of mammal species representing a particular range of body sizes. In 2005 we targeted very small mammals (up to 22 g), in 2008 we targeted mid-sized to large mammals (up to 9500 g), and in 2009 we targeted the larger small mammals and smaller mid-sized mammals (up to 600 g). To obtain abundance estimates of these different species across a

large number of landscapes, we needed to use different sampling techniques for the different species groups. This resulted in a data set in which the relative abundance estimates for a single species within a single year are comparable across landscapes, but relative abundance estimates are not comparable across species or within species across years. However, since our objective was to evaluate effects of reproductive rate, mobility, and body size on the slope of the relationship between relative abundance and road density (not on abundance itself), we did not need absolute abundance estimates, or abundance estimates that are comparable across species; we only needed relative abundance estimates that are comparable within species across landscapes.

#### Surveys conducted during summer 2005

*Site selection.*—In 2005 we surveyed small mammals (*Peromyscus leucopus*, *Zapus hudsonius*, *Napaeozapus insignis*, *Blarina brevicauda*, *Tamias striatus*) in 14 forest patches selected such that they were centered in 14 landscapes that varied widely in road density (km/km<sup>2</sup>). We defined each landscape as the area within a 2-km radius of each sampled patch (Fig. 1). This size of landscape was based on reported long-distance movements of small mammals. Such reports are rare (Diffendorfer and Slade 2002), but *Peromyscus* sp. has been reported to travel over 1 km in under a month (Murie and Murie 1931, Howard 1960, Bowman et al. 1999, Maier 2002). In selecting the 14 sample patches, we attempted to maximize the variation in road density among the surrounding landscapes while controlling for landscape variables other than road density. We selected only rural landscapes, containing no urban development, and approximately 20–35% forest (Fig. 1). We chose 20–35% forest because it allowed the largest possible range of road density values, given the variation

in forest cover and road densities in eastern Ontario. Landscapes also contained limited or no water (i.e., no rivers or lakes) and no railways, to avoid the possibility of additional barrier effects. We sampled forest patches that were located at least 3 km apart to minimize overlap of the landscapes. Sampled patches were all larger than 1 ha and of similar forest type (deciduous/mixed deciduous). Landscapes with lower and higher road densities were interspersed across the Ottawa region as much as possible to avoid possible confounding effects of regional trends (Fig. 2).

**Mammal sampling.**—We sampled small mammals between 6 June and 29 July 2005 using footprint tracking tubes (Merriam 1990). The proportion of tracking stations containing small mammal tracks has been shown to be a good estimate of relative abundance (Fahrig and Merriam 1985, Brown et al. 1996, Drennan et al. 1998, Glennon et al. 2002).

We lined 30-cm lengths of 3.75 cm (inside diameter) plastic water pipe (PVC tubing) with a strip of white paper (28 × 7 cm). To the center of each paper, we stapled a 6 × 6 cm square of waxed paper with a smear of powdered carbon black (decolorizing) and paraffin oil (Nams and Gillis 2002) in a ratio of 1:3 (by mass). Each sample patch contained a 10 × 10 grid of tubes at 10-m spacing. Tubes were not baited. We checked tubes weekly for tracks and replaced tubes with newly prepared papers weekly. Relative abundance was estimated as the total number of tracks found at the site over the eight-week tracking period; the maximum possible value was 800 (i.e., 100 tubes for eight weeks at each site).

**Sample patch characteristics.**—To assess whether local habitat variables differed among sampled patches, we carried out vegetation surveys in each patch from 13 July to 22 July 2005. For each patch, we estimated the number of woody tree species, density of shrub vegetation, percent cover of coarse woody debris (CWD), patch size, and patch shape (see Rytwinski and Fahrig [2007] for vegetation survey methods).

#### *Surveys conducted during summer 2008*

**Site selection.**—In 2008, we selected 29 landscapes within eastern Ontario to sample mid-sized and large mammals (*Mustela ermine*, *Tamiasciurus hudsonicus*, *Lepus americanus*, *Sylvilagus floridanus*, *Mephitis mephitis*, *Marmota lotor*, *Martes pennant*, *Vulpes vulpes*, *Procyon lotor*, *Ursus americanus*). Each landscape was centered on a sampling site containing a stream/creek and a forest patch greater than 6 ha within 150 m of each other. This was done to cover the reported habitat preferences for all target species. Landscapes were defined as the area within a 3-km radius of each sampling site. Since the home range sizes (and reported movement distances) of our target species range widely (e.g., in Ontario home range size for adult male and female short-tailed weasels [*M. ermine*] are 21.3 ha and 8.3 ha, respectively [Simms 1979], compared to 4020 ha

for adult female black bears [*U. americanus*; Maxie 2009]), we could not select a landscape size that would encompass the entire home ranges of all species due to the logistical constraints of monitoring a large number of sites. We chose a 3-km radius (2826 ha) landscape to encompass the entire home range of the species with the second largest home range, the red fox (*V. vulpes*). We selected landscapes containing no urban development and similar forest amounts (approximately 20–35%) and forest types (deciduous/mixed deciduous), and varying as widely as possible in road density (km/km<sup>2</sup>). Landscapes were at least 2 km apart to minimize the chance of sampling the same individual at different sites. Landscapes with lower and higher road densities were interspersed across eastern Ontario as much as possible to avoid possible confounding effects of regional trends (Fig. 2).

**Mammal sampling.**—At each site, we placed three tubes, two enclosed track boxes and one semi-enclosed track box (described in next paragraph), to detect the presence of mammals at each site, near the center of each landscape (Appendix A: Figs. A1 and A2). All tubes and track boxes were placed at least 50 m apart. We placed one tube and one enclosed track box along the stream/creek edge, one tube and one semi-enclosed track box within 10 m of the forest edge (inside the forest patch between the forest and the stream), and one tube and one enclosed track box farther than 100 m from all edges in the interior of the forest patch (Appendix A: Fig. A1).

We used enclosed track boxes to exploit the need of some mid-sized mammals to investigate confined spaces to locate food, den locations, and/or resting/shelter sites (Zielinski and Kucera 1995, Foresman and Pearson 1998, Loukmas et al. 2003, O'Connell et al. 2006). However, since other species may be reluctant to enter enclosed tracking boxes (Zielinski and Kucera 1995, Manley et al. 2006), we developed a modified open track plate (semi-enclosed) to promote visits from these species.

We constructed enclosed tracking boxes (30 cm wide × 30 cm high × 85 cm long) from sheets of coroplast. Four wooden stakes 45 cm long were hammered into the ground and tied with twine around the enclosed track plates to help provide stability (Appendix A: Fig A2b). The tracking plate was composed of 1.6 mm thick polystyrene plastic sheets (29 × 81 cm) which were partially covered with brown butcher paper (contact paper) and placed inside the enclosed coroplast box. We aligned the contact paper at the center of the plastic sheet leaving about 13 cm of exposed plate at either end to which we painted a smear of powdered carbon black (decolorizing) and paraffin oil. The semi-enclosed tracking boxes were made from two 1.1 cm thick wood chip board sheets. The top sheet (1.0 × 1.0 m) was raised 35 cm above ground over a bottom sheet (0.8 × 0.8 m) by four 45 cm long 5 × 5 cm diameter wooden stakes that were screwed into the top sheet and then hammered

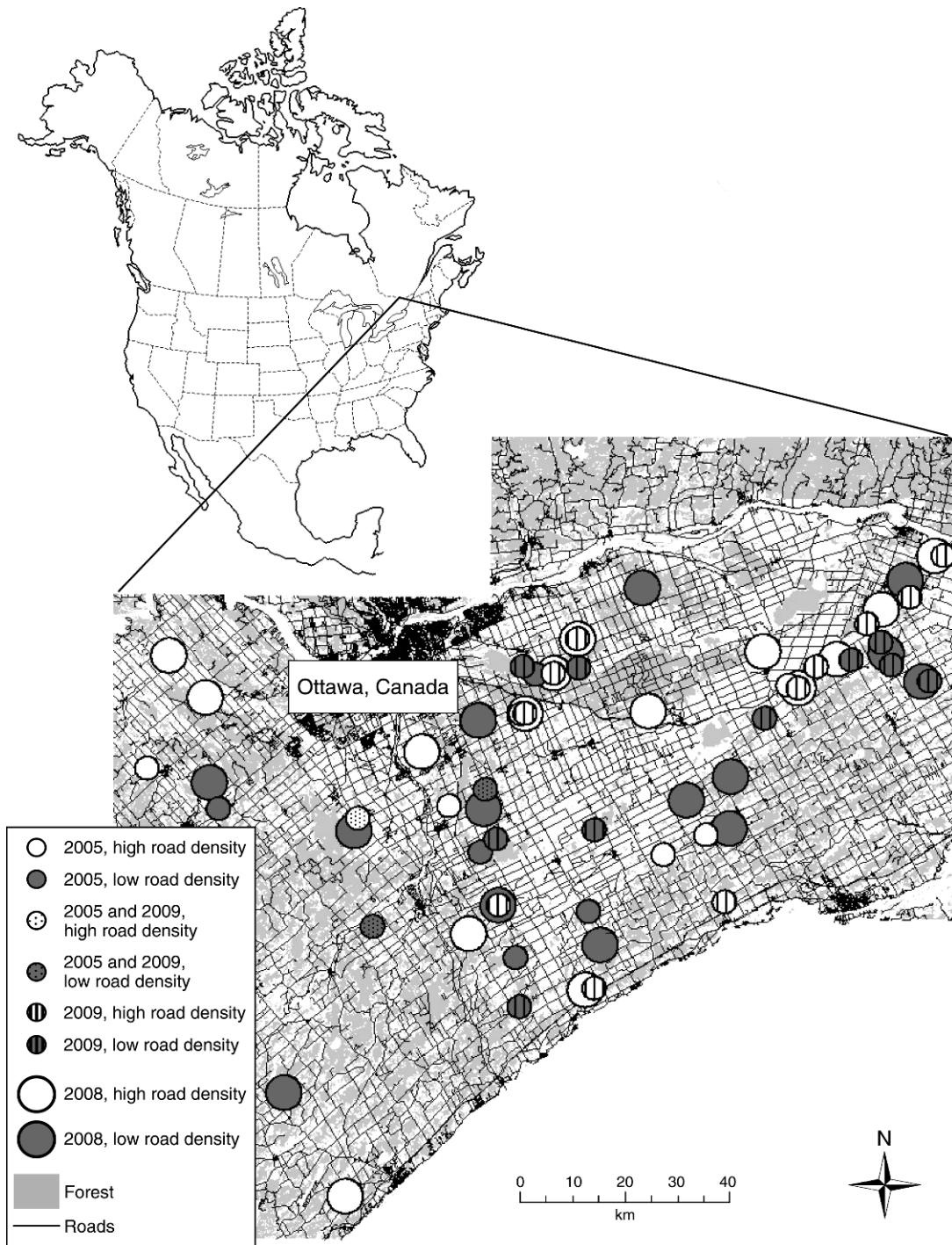


FIG. 2. Distribution of landscapes studied across eastern Ontario. Smaller circles represent the 2 km radius landscapes at the centers of which small mammals were sampled during summers of 2005 and 2009 (note that the smaller dotted circles correspond to those landscapes that were used for both the 2005 and 2009 sampling seasons), and larger circles represent the 3 km radius landscapes at the centers of which larger mammals were sampled during the summer of 2008. Gray-filled circles correspond to lower road density landscapes, and white circles correspond to higher road density landscapes. All landscapes were in rural areas.

into the ground alongside the bottom sheet (Appendix A: Fig A2c). We constructed tracking plates from 1.6 mm thick polystyrene plastic sheets ( $0.8 \times 0.8$  m) which were partially covered with brown butcher paper ( $56 \times$

$56$  cm) and placed on the bottom sheet. The 12-cm exposed border around the perimeter of the tracking plate was then painted with the carbon black and paraffin oil mixture (1:3 ratio by mass). We constructed

tracking tubes from 50 cm long plastic water pipes with 7.62 cm inside diameter. Tubes were lined with a strip of white paper (48 × 14 cm). At each end of the paper, a square piece of waxed paper (11 × 11 cm) was stapled and smeared with powdered carbon black and paraffin oil (1:3 ratio by mass). To prevent tubes from rolling on the ground, two 28 cm long, 5 × 5 cm wooden stakes were placed under and perpendicular to the tube and secured by attaching 33-cm lengths of metal strapping around the tubes (Appendix A: Fig A2d).

Track stations had a lure of mink gland and salmon oil (1:1 mixture) presented in a non-reward manner (Loukmas et al. 2003), to entice visitation by short-tailed weasels (*Mustela erminea*), striped skunks (*Mephitis mephitis*), raccoons (*Procyon lotor*), and fisher (*Martes pennanti*; see Plate 1) We chose a lure with no reward over bait to reduce the chance of the same individual revisiting track stations every week. The lure mixture was placed inside a housing capsule constructed from galvanized plumbing supplies attached to the roof of each track station. Lure capsules released the lure scent without allowing the animal to ingest the lure.

Tracking began 2 June 2008 and continued for 11 consecutive weeks, ending 22 August 2008. Tracking stations were checked once a week for a total of 11 checks. During weekly checks, the butcher paper was collected and replaced and the tracking stations were repainted and fresh lure was added. Tracks were identified using Rezendes (1999) and compared to the Carleton University footprint library. Relative abundance was taken as the number of weeks that a mammal species tracks were identified at each sample site.

*Local site characteristics.*—We carried out vegetation surveys from 28 July to 15 August 2008, based on vegetation associations of target species, *Mustela erminea*, *Mephitis mephitis*, *Procyon lotor* and *Martes pennant* (Pedlar et al. 1997, Larivière and Messier 1998, Gehring and Swihart 2003, Zielinski et al. 2004, 2006, Baldwin et al. 2006). Four 10 × 10 m plots were created 25 m from the two tracking boxes in the forest patch in each cardinal direction. Within each of the eight 10 × 10 m plots, all trees and snags (dead standing trees) ≥ 10 cm diameter were identified and their diameter at breast height (dbh) recorded. Tree and snag density was measured as the combined total of all trees (or snags) from the eight plots divided by the area sampled. Average tree and snag dbh was the sum of all tree (or snag) dbhs for the eight plots, divided by the total number of trees (or snags). Within each of the eight 10-m<sup>2</sup> plots, the lengths of all fallen dead and down CWD ≥ 10 cm diameter were recorded. The average length of CWD was the sum of all lengths recorded from the eight plots, divided by the total number of CWD. At each 10 × 10 m plot, one tree within the forest stand was randomly selected and its height was determined using a clinometer. Average canopy height was the average height of the eight trees from the eight plots. Canopy cover was measured by walking the perimeter of the 10-

m<sup>2</sup> plots and stopping at 2-m intervals to record 20 “hit” or “miss” readings using an ocular tube for the presence or absence of canopy cover sighted (James and Shugart 1970). Percent canopy cover was the percentage of the 160 sightings that were “hits.”

A 3 × 3 m plot was sampled for woody and herbaceous vegetation at the center of each 10 × 10 m plot. The number of woody and herbaceous stems was counted (separately) and separated into height intervals: 0.5 to <1 m, 1 to <2 m, and >2 m with <10 cm dbh, the latter for woody stems only. Stem density was estimated for woody and herbaceous vegetation within each height interval as the number of stems for all 3 × 3 m plots divided by the total area sampled (i.e., 24-m<sup>2</sup> area). Percent ground cover was estimated in a 1 × 1 m ground cover frame placed in the center of each 10 × 10 m sampling plot. Percent ground cover was averaged over the eight 1-m<sup>2</sup> sampling plots in each site. The number of potential dens was estimated by walking a 30 × 10 m plot 5 m from each of the two tracking boxes, in each cardinal direction and recording the number of ground dens (holes in ground with openings ≥ 5 cm diameter), CWD that were ≥ 30 cm dbh at their maximum diameter, snags that were ≥ 30 cm dbh, brush piles, and rock piles. The total number of potential dens for a site was the number of all potential dens from the eight 30 × 10 m walked plots.

#### *Surveys conducted during summer 2009*

*Site selection.*—In 2009, we surveyed small mammals and smaller mid-sized mammals (*Peromyscus leucopus*, *Zapus hudsonius*, *Napaeozapus insignis*, *Blarina brevicauda*, *Clethrionomys gapperi*, *Mustela ermine*, *Tamias striatus*, *Tamiasciurus hudsonicus*, *Sciurus carolinensis*, *Procyon lotor*) in 24 forest patches selected such that they were centered in 24 landscapes that varied in road density (km/km<sup>2</sup>), using the same criteria for landscape and site selection as in 2005 (above; Fig. 2) with the exception that sampled patches were all larger than 4 ha.

*Mammal sampling.*—We conducted sampling between 1 June 2009 and 24 July 2009 using a combination of tracking tubes and semi-enclosed tracking boxes (all unbaited). Forty-five-cm lengths of tracking tubes were used in two different diameters (7.62 cm and 10.16 cm inside diameter) and lined with paper containing a square of carbon black-coated waxed paper. As in 2008, we included semi-enclosed tracking boxes (same construction as described for 2008, but smaller; top and bottom chipboard sheets were 40 × 40 cm) to promote visits from species that may be reluctant to enter confined spaces (e.g., arboreal species such as *Sciurus carolinensis*). Each focal patch contained a 7 × 7 grid of tubes and boxes at 20-m spacing (seven lines with seven tracking stations per line). Each line consisted of one semi-enclosed box, and either three 7.62-cm (inside diameter) tubes and three 10.16-cm (inside diameter) tubes or four 7.62-cm tubes and two 10.16-cm tubes.



PLATE 1. A fisher (*Martes pennanti*) visiting an enclosed tracking box. The photo was taken using an infrared digital trail camera. Photo credit: T. Rytwinski.

This resulted in a total of 25 7.62-cm tubes, 17 10.16-cm tubes, and seven boxes per grid (Appendix A: Fig A3).

We checked tubes and boxes weekly for tracks and replaced tracking papers weekly. Relative abundance was estimated as the total number of tracks found at the site over the eight week tracking period; the maximum possible value was 392 (i.e., 49 tracking stations for eight weeks at each site). Tracking procedures for all three years followed guidelines from the Canadian Council on Animal Care (CCAC) and were approved by the Carleton University Animal Care Committee.

*Sample patch characteristics.*—We carried out vegetation surveys on each sample patch from 16 July to 11 August 2009. Habitat variables measured were selected based on vegetation associations of target small mammal species (Dueser and Shugart 1978, Zollner and Crane 2003, Lee 2004, Holloway and Malcolm 2006). At each sample patch, we randomly chose six points within the sampling grid and centered a  $10 \times 10$  m plot over each point. We measured average tree and snag dbh, tree and snag density, canopy cover, and woody and herbaceous stem density as in 2008 except that we used  $2 \times 2$  m plots for woody and herbaceous stem density; and percent of ground covered by coarse woody debris as in Rytwinski and Fahrig (2007).

*GIS analyses (2005, 2008, and 2009 surveys).*—We calculated road density as the total length of all road types within each landscape divided by the total area of the landscape ( $\text{km}/\text{km}^2$ ), based on digital maps of public roads from the National Road Network of Canada vector road data sets for Ontario (Natural Resources Canada 2003). All road types were included: one and two-lane municipal and county roads (unpaved and

paved), and secondary and divided highways (paved). Road width ranged from  $\sim 4.5$  m for one-lane gravel roads to  $\sim 10$  m for two-lane secondary highways (paved surface width). Traffic volume varied across road types from  $\sim 25$  to  $\sim 20\,000$  average annual daily (24-h) traffic (AADT), though detailed traffic volume data are not available for all roads within our study area. Road verges were usually grasses and shrubs. Amount of forest within each landscape was obtained from digital 1:50 000 Natural Resources Canada topographic maps. GIS analyses were conducted using ArcView 3.2 (ESRI, Redlands, California, USA).

#### Statistical analysis

*Confounding variables.*—Before estimating the relationship between road density and abundance of each species, we first wanted to rule out the possibility of confounding vegetation and other habitat variables, by determining whether the local habitat characteristics were correlated with road density. We conducted Spearman rho correlations to determine the association between each local habitat variable and road density. We intended to include in further analyses any variable that showed a significant correlation with road density.

We also wished to rule out the possibility that any relationship we found between the effect of road density and our predictor variables (reproductive rate, home range size and body size) was due to a correlation between detection probability and road density, where detection probability is defined as the probability of detecting at least one individual during a particular sampling occasion, given the species is present in the area (MacKenzie et al. 2002). This could occur if, for

example, nearby roads increase or reduce the likelihood of an animal entering a tracking station. Therefore, we wanted to limit our analysis to species for which detection probability is clearly not affected by road density.

The objective of the detectability analysis was, for each species–year combination, to determine whether a model that assumes a relationship between road density and detectability fit our data better than a model that assumes no relationship between road density and detectability. To be as conservative as possible, we eliminated any species–year combination where the first model was selected over the second, regardless of model strength or significance and/or error associated with model parameters. We used a model developed by Royle and Nichols (2003) which accommodates heterogeneity in a species detection probability at a site as a result of variation in abundance. The model uses maximum likelihood estimation to find the most likely values for the two key parameters,  $\lambda$  (mean abundance across sites) and  $r$  (species detection probability). Assumptions are that abundance follows a given probability distribution (e.g., a Poisson distribution), and that the probability of detecting a species at a site is related to its detection probability and its abundance at the site.

We evaluated two models for detection probability for each species–year combination: (1) a model assuming a linear road density effect on detection probability ( $r$ ) and (2) a model assuming constant  $r$  (no relationship between road density and  $r$ ); in both cases we assumed a Poisson distribution. We determined the relative support for each model (i.e., model fit) using Akaike information criterion corrected for small sample size ( $AIC_c$ ; Burnham and Anderson 2002). As stated above, to be as conservative as possible, any species–year combination in which the road-density-effect model was selected as the better model (lower  $AIC_c$ ) was removed from the analyses below, regardless of model strength, error associated with model parameters, or the difference between the  $AIC_c$  values ( $\Delta AIC_c$ ).

*Reproductive rate, species mobility, and body size.*—Reproductive rate, mobility, and body size were taken from the literature for the 13 species for which detectability was not related to road density. Reproductive rate was the mean number of offspring per litter multiplied by the maximum reported number of litters per year; the values were taken from sources as close to our study region as possible (see Appendix B for values and sources). The most common measures of species mobility are dispersal distance (or movement range) and home range area. Bowman et al. (2002) found that mammal dispersal distance and home range area are significantly linearly related ( $R^2 = 0.74$ ), even after the effects of body size were removed ( $R^2 = 0.50$ ). Since for our species we had more confidence in the values available for home range area than the values available for dispersal distance, we used mean (of the two sexes) home range area as our measure of species

mobility, taken from studies as close to our region as possible. If more than one study was close in proximity to our study region, we calculated the mean across studies weighted by study sample size (see Appendix B for values and sources). Body size (Appendix B) was the average body size of the two sexes in grams. All values for body size were taken from Eder (2002).

*Road effect vs. predictor(s).*—We first standardized the relative abundance values for each of the 13 species (within year) and the road density values to z-scores (see Appendix C for raw data). We then performed separate simple linear regressions of each species' standardized relative abundance on standardized road density to obtain the standardized coefficients and standard errors of the coefficients from each regression. To perform a single analysis on species for which we had more than one year of sampling data (see Appendix F), we included year as a factor, to account for differences in sampling methodology and overall abundance between years.

We then tested the three cross-species predictions that the slope of the relationship between abundance and road density should become increasingly negative with decreasing reproductive rate, increasing home range area, and increasing body size, by performing three separate weighted regressions of the log-transformed (standardized coefficient + 2) for each species (response variable) on the log-transformed predictor variables (i.e., reproductive rate, home range area, and average body size). Before taking logs of the standardized coefficients we had to add a constant (here, 2) to all values, since we could not take logs of negative values. All variables were log-transformed to meet model assumptions. Each regression was weighted by the inverse of the standard error of the regression coefficients (of abundance on road density). Since the three predictor variables were correlated, we also fit multiple regression models to determine whether we could detect independent effects of predictor variables while controlling for the presence of the others. The detectability analyses were conducted using the Rmark 1.9.3 package (Laake and Rexstad 2008) in R (R Development Core Team 2009), and all other statistical procedures were conducted using PASW Statistics 18 (SPSS 2010).

## RESULTS

None of the possible confounding vegetation and habitat variables that we measured showed a significant correlation with road density (Appendix D); therefore, they were not included in further analyses. Seventeen mammal species were tracked during the combined sampling periods, ranging in size from the white-footed mouse (*Peromyscus leucopus*) and the meadow jumping mouse (*Zapus hudsonius*) at 20 g to the black bear (*Ursus americanus*) at 155 000 g. The road-density-effect model of detection probability was selected as a better model than the no-road-density-effect model for four of the 17 species (Appendix E): *Tamias striatus* (eastern chipmunk), *Sylvilagus floridanus* (eastern cottontail rabbit),

TABLE 1. Model summaries of cross-species relationships between the slope of the relationship between abundance and road density ( $\log[\text{regression coefficient} + 2]$ ; see Appendix F) and predictors  $\log(\text{reproductive rate})$ ,  $\log(\text{home range area})$ , and  $\log(\text{body size})$ .

Model	Model $R^2$	Predictor	$\beta$	SE	$F$	df	$P$	$AIC_c$
1	0.68	$\log(\text{reproductive rate})$	0.135	0.028	22.90	1, 11	0.001	-49.96
2	0.50	$\log(\text{mean home range area})$	-0.020	0.006	10.93	1, 11	0.007	-44.30
3	0.52	$\log(\text{average body size})$	-0.023	0.007	11.66	1, 11	0.006	-44.72
4	0.75	$\log(\text{reproductive rate})$	0.102	0.033	9.80	1, 10	0.011	-48.80
		$\log(\text{mean home range area})$	-0.009	0.005	2.81	1, 10	0.125	
5	0.77	$\log(\text{reproductive rate})$	0.101	0.030	11.00	1, 10	0.008	-50.02
		$\log(\text{average body size})$	-0.012	0.006	4.04	1, 10	0.072	

Notes: Each regression is weighted by the inverse of the standard errors of slope coefficients from single-species regressions of abundance on standardized road density (Appendix F: Table F1).  $AIC_c$  is the Akaike information criterion corrected for small sample size. Sample size = 13 mammal species. Note that 2 was added to the response variable (standardized regression coefficient) to make all values positive, so that we could take logs.

*Ursus americanus* (black bear), and *Clethrionomys gapperi* (southern red-backed vole). One of these species, *T. striatus*, was surveyed in more than one year, and the road-density-effect model was the better model in both years based on  $AIC_c$  values. We therefore excluded these four species from further analyses, leaving thirteen mammal species to test our predictions (see Appendix F for the model summary statistics and parameter estimates from the linear regressions of relative abundance on road density for each species-year combination).

Across the 13 species, as expected, reproductive rate and mean home range area were negatively correlated (Spearman's  $\rho = -0.549$ ;  $P = 0.026$ ), and average body size was positively correlated with mean home range area (Spearman's  $\rho = 0.893$ ;  $P < 0.001$ ) and negatively correlated with reproductive rate (Spearman's  $\rho = -0.521$ ;  $P = 0.034$ ). As predicted, there was a significant cross-species positive relationship between reproductive rate and the slope of the relationship between abundance and road density (Table 1; Fig. 3a); species with lower reproductive rates showed a more negative response to increasing road density. Mean home range area was negatively related to the slope of the relationship between abundance and road density (Table 1; Fig. 3b); species with larger home ranges showed a more negative response to increasing road density. There was a significant negative relationship between the body size and the slope of the relationship between abundance and road density (Table 1; Fig. 3c); larger species showed a more negative response to increasing road density. Based on model fit, the species trait that best explained variation in the coefficients relating mammal abundance to road density was reproductive rate (Table 1;  $AIC_c = -49.96$  compared to  $-44.72$  and  $-44.30$  for average body size and mean home range area respectively). A model including both reproductive rate and body size (the two species traits with the lowest  $AIC_c$  values and the least correlated) had an  $R^2$  of 0.77 and the lowest  $AIC_c$  value (Table 1), with reproductive rate being significantly positively related to the slope of abundance vs. road density and body size

being marginally significantly negatively related to the slope of abundance vs. road density.

## DISCUSSION

This is the first direct test of the hypotheses that the negative effect of road density at the population level decreases with reproductive rate, increases with movement range, and increases with body size. The results support our predictions (Table 1; Fig. 3a–c). In our study, the common negative correlation between forest cover and road density (e.g., Houlihan and Findlay 2003, Roedenbeck and Köhler 2006) was avoided through our experimental design, and none of the habitat variables we measured was correlated with road density (Appendix D). In addition, our results were not affected by species detection probabilities because we limited our analyses to species for which detection probability was not related to road density (Appendix E). Note that if we include the three species for which the difference in  $AIC_c$  for the road-density-effect model of detection probability relative to the no-road-density-effect model of detection probability was very small ( $\Delta AIC_c < 2$ ), our results did not change substantially: the direction of all relationships remained the same; for reproductive rate the  $R^2$  increased to 0.69 from 0.68; for home range size the  $R^2$  dropped to 0.49 from 0.50; for body size the  $R^2$  dropped to 0.47 from 0.52 (see Appendix G); and the model including both reproductive rate and body size, had an  $R^2$  that increased slightly to 79 from 77 and still had the lowest  $AIC_c$  value of all the models.

Our results provide strong support for the hypothesis that species with lower reproductive rates are more negatively affected by road density than are species with higher reproductive rates. Reproductive rate was the best predictor of population-level response to roads, explaining nearly 70% of the variation in the coefficients relating mammal abundance to road density (Table 1; Fig. 3a). The effect of reproductive rate remained strong in the model that included both reproductive rate and home range size, and in the model that contained both reproductive rate and body size (Table 1). Therefore, reproductive rate appears to have an effect on species

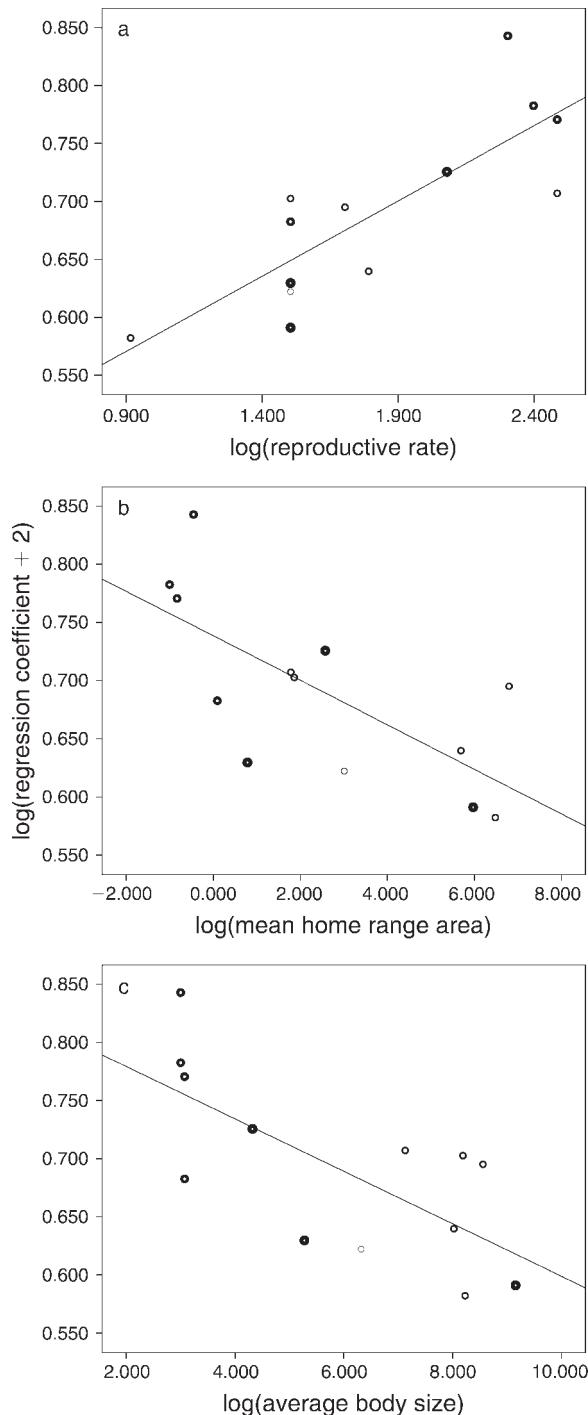


FIG. 3. Linear regressions of the  $\log(\text{regression coefficient} + 2)$  from single-species regressions of standardized relative abundance on standardized road density on (a)  $\log(\text{reproductive rate})$ ; (b)  $\log(\text{mean home range area})$ ; and (c)  $\log(\text{average body size})$ . Each regression is weighted by the inverse of the standard errors of the coefficients; heavier circles correspond to data points with lower standard errors (Appendix F: Table F1). Note that 2 was added to the response variable (standardized regression coefficient) to make all values positive, so that we could take logs. See Table 1 for a summary of the regression models.

response to roads, independent of its correlations with movement range and other life history attributes that are correlated with body size.

Although this is the first test of the hypothesis that the negative effect of road density at the population level decreases with mammal reproductive rate, several previous studies—both theoretical and empirical—have found similar strong effects of reproductive rate on species response to habitat loss: species with lower reproductive rates require more habitat for population persistence than species with higher reproductive rates. For example, modeling studies suggest that reproductive rate has a larger effect than dispersal rate/ability on the amount of habitat required for population persistence (With and King 1999, Fahrig 2001). Vance et al. (2003) found a negative cross-species relationship between reproductive rate and the amount of forest in a landscape required for a 50% probability of presence of forest bird species. Similarly, Holland et al. (2005) found a strong cross-species negative relationship between reproductive rate of 12 species of longhorned beetles and the minimum habitat amount required for species presence, and this relationship was stronger than the effect of movement rate.

Our results are less clear for the hypothesized positive cross-species relationship between movement range and road impacts. In a univariate model, home range size explained 50% of the variation in species response to road density, but this was the weakest of the three univariate models (Table 1). Interestingly however, when either body size or home range area was combined in a model with reproductive rate, the model explained an additional 7–9% variation in comparison to the model with reproductive rate alone (Table 1). Since average body size and mean home range area were highly correlated ( $\rho = 0.893$ ) and body size and reproductive rate were only moderately correlated ( $\rho = -0.521$ ), the additional explained variance suggests that there is an added effect of mobility on top on the effect of reproductive rate. When comparing model fit however, the difference in  $AIC_c$  values between the combined models including either body size or home range area and reproductive rate, and the univariate model with reproductive rate alone, was very small; the combined model including body size and reproductive rate improved model fit slightly (lower  $AIC_c$ ) over the model including reproductive rate alone ( $\Delta AIC_c < 1$ ), while the  $AIC_c$  of the combined model with home range area and reproductive rate increased slightly compared to the model including reproductive rate alone ( $\Delta AIC_c \sim 1$ ; Table 1). Although this is the first direct test of this hypothesis, as for reproductive rate (above), there are analogous results in the habitat loss literature. Some modeling studies (Casagrandi and Gatto 1999, Fahrig 2001, Flather and Bevers 2002) and some empirical studies (Gibbs 1998, León-Cortés et al. 2003, Van Houtan et al. 2007) suggest that species with high dispersal rates and long dispersal distances are more

susceptible than less mobile species to habitat loss due to the higher risk of mortality in the matrix sustained by more mobile species. In the current study this increased risk results from increased road mortality rather than decreased habitat amount, but the mechanism linking the landscape change (road density or habitat loss) to movement range is the same, i.e., increased risk of mortality.

We had expected that body size would be the best predictor of mammal species responses to increasing road density because, through its correlations with reproductive rate and mobility, in a sense it “represents” all of the main mechanisms. However, in our data set, while body size was highly correlated with home range size, it was only moderately correlated with reproductive rate. Essentially, this allowed us to at least partially separate the effects of reproductive rate and mobility and to make conclusions about their relative importance on the effect of roads. We found evidence for both mechanisms, but the effect of reproductive rate was stronger than the effect of mobility.

In our analysis, 23% of the variation in the coefficients relating mammal abundance to road density was not explained by our predictor variables. Some of this variation is most likely explained by differences among species in their behavioral responses to roads and traffic (Jaeger et al. 2005, Fahrig and Rytwinski 2009). For example, species that are either attracted to roads or do not avoid roads, and that show low car avoidance (e.g., slow-moving species that are unable to avoid cars) are particularly vulnerable to road mortality (van Langevelde and Jaarsma 2005). This combination of factors is most likely responsible for the frequent negative effects of roads and traffic on abundances of amphibians and reptiles (Fahrig and Rytwinski 2009). Some turtles use roads and roadsides as nesting sites (Haxton 2000, Aresco 2005, Steen et al. 2007) and some snakes have been reported to come to the road surface to bask during the day or to thermoregulate at night (Sullivan 1981, Rosen and Lowe 1994). This proximity to roads and the slow movement of these species across roads leaves them vulnerable to very high road mortality rates (Hels and Buchwald 2001, Bouchard et al. 2009). Other species may avoid roads at a distance, due to traffic disturbances (noise, lights, and chemical emissions), a response that is commonly thought to explain the reduced abundances of birds near high-traffic roads (Reijnen et al. 1996, Forman et al. 2002, Rheindt 2003). Such species, while less likely to be killed on roads, are susceptible to habitat loss, as habitat quality within the vicinity of roads is reduced; the higher the traffic amount on the road, the more habitat is effectively lost to the species. In general, the degree to which behavioral responses to roads and traffic either obscure or reinforce the relationships between the road effect and reproductive rate, movement range, and body size will depend on how the behavioral responses are related to these three predictor variables.

In conclusion, we found strong support for the hypothesis that species with lower reproductive rates are more susceptible to negative road effects than species with higher reproductive rates, and moderate support for the hypothesis that more mobile species are more susceptible than less mobile species to negative road effects. Our results suggest that priority should be placed on mitigating road effects on larger mammals with lower reproductive rates.

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#### APPENDIX A

Setup of sample sites during 2008 and 2009, and example of tracking stations used to obtain mammal footprints (*Ecological Archives* A021-031-A1).

#### APPENDIX B

Reproductive rate, average body size, and mean home range area of mammal species used in this study (*Ecological Archives* A021-031-A2).

#### APPENDIX C

Raw relative abundance data for the 17 mammal species tracked during 2005, 2008, and 2009, and road density values (*Ecological Archives* A021-031-A3).

#### APPENDIX D

Correlations between habitat variables and road density for each sampling year (*Ecological Archives* A021-031-A4).

#### APPENDIX E

Detection probability analysis results (*Ecological Archives* A021-031-A5).

#### APPENDIX F

Model summaries and parameter estimates from the linear regressions of relative abundance on road density (*Ecological Archives* A021-031-A6).

#### APPENDIX G

Linear regression of the log-transformed standardized coefficient (response variable) from single-species regressions of standardized relative abundance on standardized road density for 16 mammal species on the log-transformed predictor variables (i.e., reproductive rate, home range area, and average body size) (*Ecological Archives* A021-031-A7).