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Effect of paved road density on abundance of white-tailed deer

Keith G. Munro[A], *Jeff Bowman*[B] *and Lenore Fahrig*[A,C]

[A]Geomatics and Landscape Ecology Research Laboratory, Carleton University, 1125 Colonel By Drive, Ottawa, ON K1S 5B6, Canada.
[B]Wildlife Research and Development Section, Ontario Ministry of Natural Resources, DNA Building, 2140 East Bank Drive, Peterborough, ON K9J 7B8, Canada.
[C]Corresponding author. Email: lenore_fahrig@carleton.ca

Abstract

Context. Although ~3% of white-tailed deer are killed on roads each year, no previous study has tested for an effect of roads on deer abundance. This is difficult to do because road density is generally negatively correlated with deer habitat availability.

Aims. Our goal was to determine whether roads affect deer abundance.

Methods. First, we used an existing dataset from Pennsylvania, USA, to determine a range of paved road densities representing a significant range in deer per capita mortality. We then conducted a field study in eastern Ontario, Canada, with sample sites for relative deer abundance selected such that (1) road density in the surrounding landscapes varied over this same range, and (2) there were low correlations across landscapes between road density and deer habitat availability. The latter allowed us to isolate the effects of roads from the effects of habitat on deer abundance. We indexed relative deer abundance using a combination of pellet samples and track counts.

Key results. Unexpectedly, we observed a positive relationship between relative deer abundance and paved road density.

Conclusions. We speculate that this positive relationship is due to (1) reduced deer predation and/or perceived predation risk and/or hunting pressure in landscapes with higher road density and/or (2) provision of a resource or service by roads, the benefits of which outweigh the road mortality.

Implications. We found no evidence that road mortality places deer populations at risk of decline, at least over the range of road density values in our study. Therefore we conclude that road mortality is not a conservation concern for white-tailed deer in ecological contexts similar to our study areas.

Additional keywords: deer–vehicle collisions, habitat fragmentation, *Odocoileus virginianus*, Ontario, Pennsylvania, reproductive rate, road mortality.

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Introduction

Although dozens of studies have documented the negative effects of roads on population abundances of a wide range of animals, different species are not equally susceptible to road and traffic effects (reviewed in Fahrig and Rytwinski 2009). It is important to determine which species or species groups are most susceptible to negative road effects so that mitigation measures can be targeted to those species. For mammals, Rytwinski and Fahrig (2011) showed that, in a cross-species comparison, mammal species with lower reproductive rates are much more likely to show negative population-level effects of roads than are species with higher reproductive rates. They suggested that populations of mammals with low reproductive rates are less able to rebound from road mortality.

In much of eastern North America, the most frequently road-killed large mammal is the white-tailed deer, *Odocoileus virginianus*. For example, Conover *et al*. (1995) estimated that there were over 700 000 deer–vehicle collisions in the USA during a single year (1991), which resulted in over 600 000 mortalities, because ~91.5% of deer–vehicle collisions are fatal for deer (Allen and McCullough 1976). Like other large mammals, the reproductive rate of white-tailed deer, 1–1.5 fetuses per female per year (Mundinger 1981; Kie and White 1985; Garroway and Broders 2007), is low relative to the reproductive rates of smaller mammals. Therefore, based on Rytwinski and Fahrig's (2011) analysis we might expect to see negative effects of road mortality on population abundances of white-tailed deer.

On the other hand, a range of factors in North America have favoured white-tailed deer over the past few decades. These include the near elimination of its predators (Taylor 1956; Roseberry and Woolf 1998), reductions in hunting pressure in some locations (McCabe and McCabe 1984), and increases in food and habitat availability in the form of agricultural crops and forest edge habitat (Dusek *et al*. 1989; Roseberry and Woolf 1998). In fact, over the past few decades, white-tailed deer populations have undergone rapid increases in many parts of eastern North America (e.g. Roseberry and Woolf 1998; reviewed in Côté *et al*. 2004). These increases can be particularly marked in exurban areas, where browse is available and hunting and predation are minimal (Storm *et al*. 2007).

Despite overall population increases, it is possible that road mortality is negatively affecting white-tailed deer populations. Deer populations in areas with high road mortality may be increasing less quickly than would be expected if road density were lower, or populations could even be decreasing in areas of high road mortality. This would be observed as lower abundances in areas with high road density than in areas with low road density. Despite a long history of studies of road mortality on white-tailed deer (e.g. Bellis and Graves 1971; Puglisi *et al*. 1974; Romin and Bissonette 1996; Finder *et al*. 1999; Hubbard *et al*. 2000; Grovenburg *et al*. 2008; McShea *et al*. 2008), no study has tested for an effect of roads on deer abundance. A difficulty in testing for such an effect is that road density may be negatively correlated with deer habitat variables such as forest amount and forest edge amount, making it difficult to isolate the effects of roads on deer abundance.

Our goal was to determine whether roads affect deer abundance. Experimental manipulation of road density, traffic volume, or road mortality (while controlling for habitat amount) was not feasible. The next best approach would have consisted of obtaining deer abundance estimates and estimates of deer road mortality in multiple landscapes varying widely in road density (and therefore in road mortality) (Farrell and Tappe 2007), but containing similar amounts of deer habitat. If there were a negative correlation between deer per capita road mortality and deer abundance across such a set of landscapes, we could conclude that road mortality negatively affects deer abundance, despite the current overall population increases in deer due to the factors listed above.

While this ideal dataset is not available, we assembled a compromise consisting of two studies that, when combined, represent an approximation of the ideal study. First, we obtained county-level paved road density data, deer mortality data and deer abundance estimates in the state of Pennsylvania, USA. From these we estimated the relationship between deer per capita road mortality rate and paved road density. We then selected forest patches in eastern Ontario within landscapes representing a similar range of paved road density values as in the Pennsylvania dataset, but such that the correlations between paved road density and deer habitat were low across these Ontario landscapes. We estimated deer relative abundance in forest patches centred in these landscapes, to test for a negative relationship between deer relative abundance and paved road density, independent of effects of deer habitat on relative abundance. The main advantages of our Ontario study design are that (1) the landscapes were selected across a range of paved road densities that we knew *a priori* (from the Pennsylvania data analysis) represented a wide range of deer per capita mortality rates and (2) we avoided the usual correlations between paved road density and deer habitat, thus allowing us to test for an independent effect of roads on deer abundance.

Materials and methods

Part I. Deer per capita road mortality versus paved road density (Pennsylvania)

The purpose of Part I was to document the relationship between paved road density and deer per capita road mortality. This required the rare combination of three datasets across multiple areas: (1) paved road density values, (2) deer road mortality values, and (3) deer population estimates that were independent of the deer road mortality values. Note that independent population estimates were needed in order to convert the deer road mortality data into per capita road mortality, i.e. to correct for the effect of different deer population sizes in different areas on the number of deer fatalities on roads. The three datasets required were available at the county scale for 61 of the 67 counties in Pennsylvania, USA. The state of Pennsylvania has a diverse topography within a total area of 119 000 km^2 divided fairly evenly into 67 counties (Fig. 1). The human population density is on average 110 km^{-2}, with counties ranging from highly urbanised to largely agricultural (corn, wheat, soybeans) to mainly forested (deciduous hardwoods).

For paved road density in each county, we used publicly available data from the Pennsylvania Spatial Data Access website for state paved roads (2008) and local paved roads (2005). These represented the available road density data closest in time to the deer mortality and population datasets (from 1997; see below). We clipped the paved road data using the boundaries of each county, summed the road lengths across the county, and divided by county area to get paved road density by county. For the deer road mortality and population estimates we obtained 1997 data from the Pennsylvania Game Commission's Deer Management Section. Note again that the 1997 data were the available data closest in time to the road density data. The Game Commission provided us with all reported deer road mortalities by county in 1997 along with estimated deer densities (independent of road mortality data) for each county in the same year, for 61 counties. The Game Commission estimated deer density for 1997 using a change-in-ratio procedure based on deer hunting statistics: harvest rates, age distribution, and sex ratio of harvested deer (described in Diefenbach *et al*. 1997). While these deer density estimates have high associated uncertainty, they were the only estimates available for the whole state on a per-county basis. The deer density values were provided to us as number of deer per forested area; they ranged, across counties, from 6.9 to 29.3 deer per forested square kilometre. The Game Commission also provided us with the forested area per county. For each county we therefore multiplied the deer density per forested area by the forested area of the county to obtain estimates of total deer abundance per county; these ranged across counties from 3.7 to 13 deer per county km^2. We divided the deer road mortality numbers by the deer abundance estimates to obtain estimates of the proportion of each county's 1997 deer population that was killed by road mortality, i.e. the deer per capita road mortality rate. We then used regression analysis to estimate the

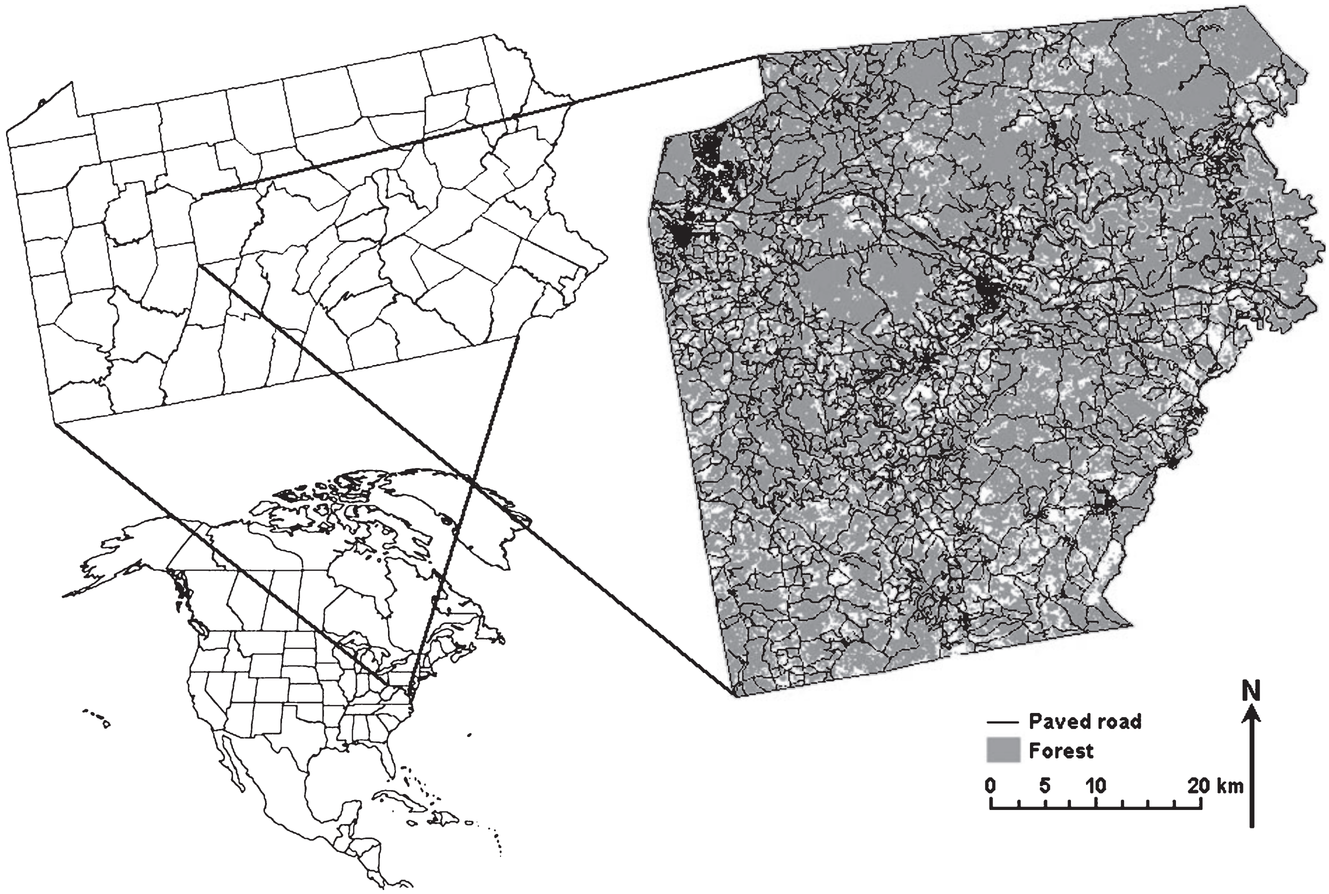

Fig. 1. The state of Pennsylvania within North America, with its 67 counties outlined, and an enlarged map of one of the counties, Clearfield County, showing paved roads in black and forest in grey. Clearfield County has relatively high forest cover and low road density compared with other counties of Pennsylvania.

relationship between deer per capita road mortality rate and road density across 61 counties in Pennsylvania.

Part II. Deer abundance versus paved road density, controlled for local and landscape habitat availability (eastern Ontario)

The purpose of Part II was to test for a negative relationship between paved road density and white-tailed deer abundance, while controlling for deer habitat amount at both local and landscape scales. In the Pennsylvania dataset there is a negative relationship between deer abundance and road density ($r = -0.33$, $P = 0.008$). However, we cannot infer from this that roads negatively affect deer populations, because in this dataset there is also a strong negative correlation between road density and forest cover ($r = -0.73$). While forest is not exactly equivalent to deer habitat, it is a component of deer habitat, and its high correlation with road density would make suspect any inferences about road effects on deer abundance, based on the Pennsylvania dataset. An apparent negative effect of road density on deer abundance could actually be caused by a positive effect of forest amount on deer abundance, making us unable to test independently for the effect of paved road density on deer abundance. Problems arising from strong correlations among landscape predictor variables are common in landscape ecology studies, where a single process (e.g. urban development) can lead to changes in multiple land covers (e.g. forest, roads). To uncover the effects of such variables on an ecological response (here, deer abundance), sample landscapes must be specifically selected to minimise these correlations, by searching for unusual combinations, e.g. landscapes with low forest and low road density and landscapes with high forest and high road density (e.g. Eigenbrod *et al*. 2008). Therefore, we collected new data on deer abundance in a sampling design specifically aimed at minimising correlations between paved road density and deer habitat variables. For logistical reasons we could not do this part of the study in Pennsylvania; instead, we conducted Part II in eastern Ontario (our region), but we used the paved road density values from Part I to inform our selection of landscapes for Part II. We selected 21 landscapes (here defined as circular areas of 3 km radius) for deer abundance surveys in the rural and exurban portion of eastern Ontario within 100 km of the city of Ottawa (Fig. 2). Each landscape was centred on a forest patch in which we sampled relative deer abundance, as estimated by deer sign (pellets and tracks). Road density and other landscape variables were measured within the landscapes surrounding each focal patch (i.e. a 'focal patch' landscape study: Brennan *et al*. 2002).

Eastern Ontario has a diverse topography including hilly areas to the west and flatter agricultural areas in the centre and east. The

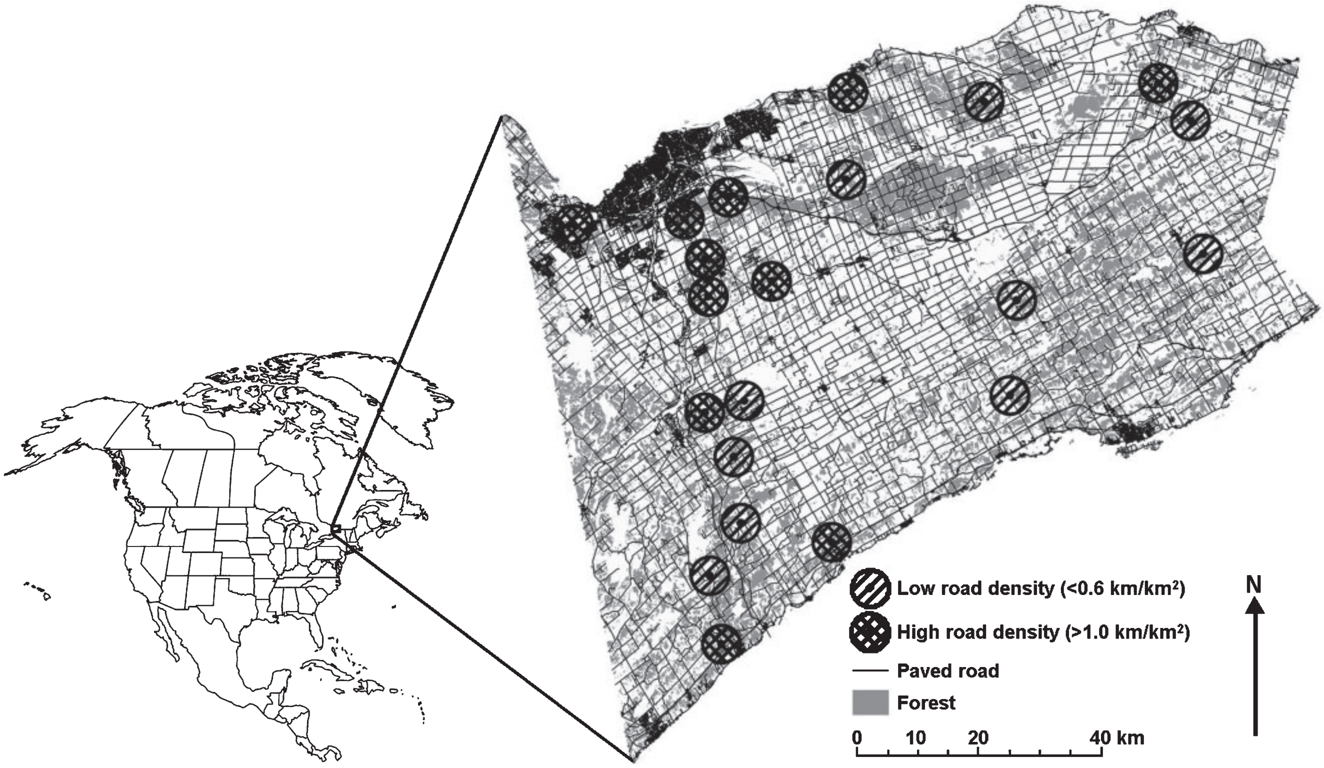

Fig. 2. The study area in eastern Ontario within North America, with the 21 sample sites. Each sample site contains a 'focal patch' of forest at its centre where relative deer abundance was estimated, surrounded by a circular landscape (3 km radius) in which road density and landscape covariables were measured. For the purposes of illustration the 21 landscapes are divided into high-road-density and low-road-density sites, but the effect of road density on deer relative abundance was analysed as a continuous variable (see Methods).

total area is 28 000 km^2 and the average human population density is 52 km^{-2}. Land uses include mainly agriculture (predominantly corn, soybean and hay), forest (mixed deciduous and coniferous) and urban areas.

We selected the focal forest patches and associated surrounding landscapes according to three main criteria. First, the range of paved road densities across the landscapes in eastern Ontario (0.23–4.65 km km^{-2}) was selected to be similar to the range of paved road densities across the 61 counties in the Pennsylvania dataset (Part I above) (0.53–4.54 km km^{-2}). Second, we selected the 21 landscapes in eastern Ontario to minimise correlations between paved road density and (1) sizes of the focal forest patches, (2) percentage cover of forest in the landscapes, (3) percentage cover of forest edge (total area within 10 m of all forest boundaries in the landscape, expressed as a percentage of the landscape area) and (4) percentage cover of crops in the landscapes. This was done by specifically searching for landscapes with unusual combinations (e.g. low road density and low percentage forest edge). Although it was not possible to select landscapes such that these correlations were zero, we were able to select them such that the correlations between road density and all these other variables were below 0.5. See Table 1 for the ranges of these covariables and their correlations with paved road density across the 21 landscapes. Finally, we ensured that all landscapes were spatially non-overlapping, i.e. the centre points of all landscapes were at least 6 km apart (rationale below; see Fig. 2).

Paved road density and the landscape covariables were calculated within circular areas ('landscapes') of 3 km radius (2800 ha), chosen on the basis of the maximum reported radius of white-tailed deer summer home ranges of 1.6 km (Smith 1991).

Table 1. Covariables in the eastern Ontario dataset (Part II)

Landscape covariables were measured within 3-km-radius landscapes surrounding the central focal forest patches where deer abundance was surveyed, in each of 21 landscapes. Percentage forest edge is the length of forest boundary multiplied by a 10-m width divided by the area of the landscape. Browse availability index was measured in eight sampling quadrats in each focal forest patch (quadrat layout in Fig. 3; see Methods). 'Range' is the range of values of each covariable across the 21 landscapes. 'Correlation' is the Pearson correlation (r) between the covariable and paved road density across the 21 landscapes. Values of these variables and paved road density, along with the rank deer abundance index values for each of the 21 sites, are given in Appendix 1

Covariable	Range	Correlation
Landscape variables		
Percentage forest cover in the landscape	29.1–43.8	–0.20
Percentage forest edge in the landscape	3.2–5.0	0.49
Percentage crop cover in the landscape	18.5–41.9	–0.22
Local variables		
Focal forest patch area (ha)	5.6–257.6	–0.18
Browse availability index	78–381	–0.25

Typical home-range sizes are much smaller. For example, in forested areas Campbell *et al.* (2004) found average summer home ranges of ~100 ha, which expanded to ~150 ha in winter, and St-Louis *et al.* (2000) found winter home-range areas of ~60 ha for adults and 180 ha for fawns, although Lesage *et al.* (2000) found much larger home ranges (~1000 ha) in eastern Québec. Home-range sizes in agricultural areas appear to be larger: Grovenburg *et al.* (2009) found mean home-range sizes of 900 ha in summer and 1000 ha in winter. By choosing a landscape size larger than home-range sizes and by selecting landscapes with centres at least 6 km apart (the non-overlapping landscape criterion above), we ensured independence of the deer data and that a deer detected in a focal patch was unlikely to be affected by landscape variables outside of the defined landscape, at least during the summer. Road density values were taken from the 1 : 50 000 Natural Resources Canada 2003 topographic maps. Forest cover in the landscapes, forest edge cover in the landscapes (defined above), and the sizes of the focal forest patches were calculated using spatial data from the NRVIS/OLIW Data Management Model (Ontario Ministry of Natural Resources 2007). Crop cover in the landscapes was taken from the 28-class Ontario Landcover Database (Spectranalysis Inc. 2004).

To obtain an index of relative deer abundance we visited sampling plots within each focal forest patch twice in 2008, first during spring (12 May to 15 June) and then during summer (11 August to 20 September). To avoid problems of temporal correlations we randomised the site visits in time in the first survey and then used the same sequence for the second survey. During each period we surveyed for deer pellet groups and tracks, hereafter referred to as deer sign. These methods are reviewed in Putman (1984) and Kie (1988). At each site a 3 × 3 grid of nine 10 m × 10 m quadrats was arranged on the cardinal axes (Fig. 3) with 10 m between quadrats. We placed the sampling grid 100 m from the forest boundary where we entered the patch and a minimum of 100 m from any other forest boundary, to avoid effects of forest edge on deer counts. We surveyed each quadrat for deer pellet groups where deposits of six or more pellets together are considered a group (Smart *et al.* 2004). During the spring sampling, we removed pellets from the quadrats to allow us to distinguish new pellets that accumulated over the 3-month period between spring and summer visits. In addition to pellets, we recorded the number of sets of deer tracks in the quadrats during both spring and summer sampling. A set of deer tracks was defined as one or more hoof prints moving in a distinct direction. Pellet and track counts are not direct estimates of deer abundance, but rather indices of relative abundance, and conversion to actual abundance values would require many assumptions (Kie 1988). We therefore converted the deer sign data into a rank relative abundance index (which we call 'rank abundance' in short-hand). The rank abundance index summarised three measures (spring tracks, spring pellets, and summer tracks); summer pellets were not included because they were found at too few sites (4 of 21) to develop a meaningful ranking. We first ranked the sites according to each of the three measures individually. Then, for each site we summed the three rank values and reranked the sites based on these combined values (our overall estimated 'rank abundance'). We tested for spatial autocorrelation in rank abundance using an all-directional Moran's I correlogram with significance tested with a Bonferroni correction at $\alpha = 0.05$. The correlogram demonstrated no significant spatial structure in deer rank abundance.

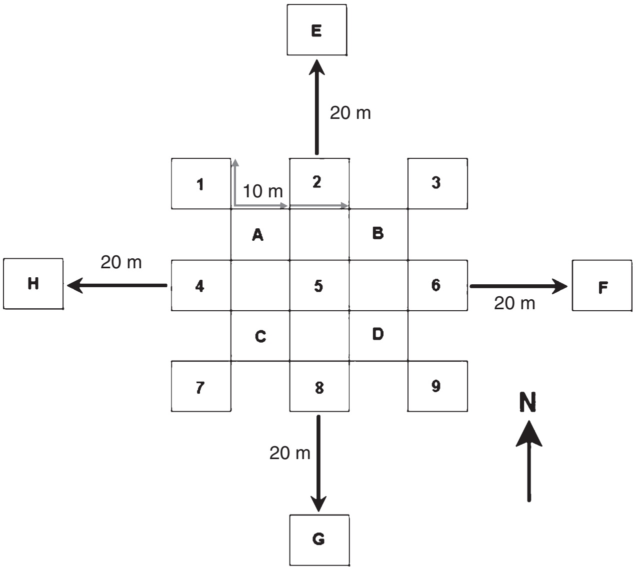

Fig. 3. Layout of the sampling grid used to measure deer sign (pellets and tracks) and browse availability in 21 focal forest sample sites in eastern Ontario. Sampling grids were placed >100 m from the forest boundaries. Quadrats were 10 m × 10 m and spaced 10 m from the adjacent quadrat. Grids were oriented on a north–south axis. Numbered boxes represent the quadrats in which the deer sign was sampled. Letters denote the quadrats where the browse availability index was measured.

As explained above, the focal forest sample sites and associated landscapes were selected to minimise, to the extent possible, correlations between paved road density and measures of deer habitat availability. However, in selecting the sites we did not have prior information on local browse availability in the focal sample sites. Therefore, we collected this information during the field season to test for its correlation with paved road density and to statistically control for its potential effect on deer rank abundance, while testing for the effect of paved road density on deer rank abundance. During the second deer survey (summer) we established eight 10 m × 10 m quadrats at each site, four between the deer sign quadrats and four 20 m from the sides of the grid in the cardinal directions (Fig. 3). We measured browse availability at 10 points in each quadrat by holding a 2-m bamboo pole vertically with the end on the ground, representing the browsing range of a white-tailed deer (Krefting *et al.* 1966). We counted the number of leaves of all shrub species in contact with the pole. The number of leaves was summed across the 80 points per site to give an index of browse availability.

To test for a relationship between paved road density and deer rank abundance we conducted two analyses. The first was a simple regression of rank abundance on log(paved road density), where road density was logged due to its skewed distribution (Appendix 1). In the second analysis we included the covariables (local scale: browse availability, focal forest patch size; landscape scale: percentage forest, percentage forest edge, percentage crop), along with log(paved road density), in a multimodel analysis. We conducted multiple linear regressions of deer rank abundance on all 63 possible model combinations of these six predictor variables, and ranked the models by increasing AICc (i.e. top model has lowest AICc; see Burnham and Anderson 2002). We calculated model-weighted mean standardised coefficients to compare the relative effects of the predictor variables (Smith *et al*. 2009).

Results

Part I. Deer per capita road mortality versus paved road density (Pennsylvania)

The estimated per capita road mortality of deer in 61 counties in Pennsylvania in 1997 ranged from 0.008 to 0.176, and was strongly related to variation across counties in paved road density (slope = 0.019 (s.e. = 0.0038), $F_{1,59} = 25.960$, $P < 0.001$, $R^2 = 0.31$) (Fig. 4).

Part II. Deer rank abundance versus road density controlled for local and landscape habitat availability (eastern Ontario)

Deer presence was confirmed at all 21 eastern Ontario focal forest patch sites. During the spring (May and June) 17 sites showed signs of deer presence with pellet groups at 10 sites and tracks at 14 sites. In the summer (August and September) 21 sites showed signs of deer presence with pellet groups at 4 sites and tracks at 21 sites.

The simple linear regression of deer rank abundance on log (paved road density) indicated a significant positive relationship ($P = 0.05$, $R^2 = 0.19$) (Fig. 5). This positive relationship was also evident in the multimodel analysis. All models containing log(paved road density) had positive coefficients for log(paved road density). The top two models and eight of the top 10 models contained log(paved road density). The model-weighted mean standardised coefficient for log(paved road density) was 1.8. There was also evidence for a consistent negative effect of crop cover in the landscape: the coefficient for percentage crop was consistently negative across all models and the model-weighted mean standardised coefficient was –1.5. Crop cover was in seven of the top 10 models. Model-weighted mean standardised coefficients of all four other variables were near zero, with negative and positive estimates of the same coefficient in different models, indicating no evidence for effects of these variables.

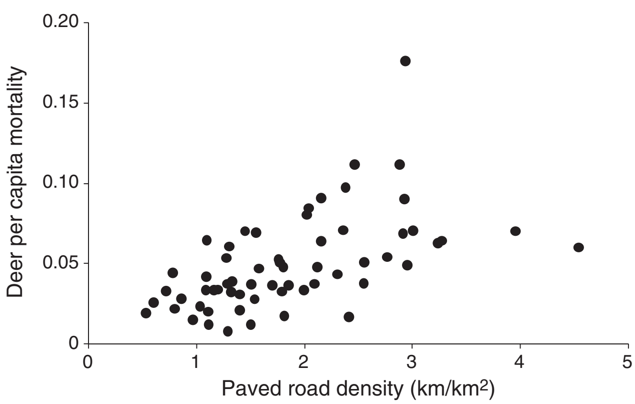

Fig. 4. Proportion of estimated deer population that was killed in deer–vehicle collisions (deer per capita road mortality rate) in 1997 versus paved road density for 61 Pennsylvania counties.

Discussion

Our analysis of the Pennsylvania data supports the suggestion that per capita deer road mortality is significantly related to paved road density, for paved road density values ranging from 0.5 to 4.5 km km^{-2}. The linear relationship over this range (Fig. 4) supports the use of paved road density as an index of deer per capita mortality. While additional information on traffic levels of each road in each county might have produced a tighter relationship, this information was not available. The strong relationship between primary road density and deer mortality (without inclusion of traffic data) is consistent with McShea *et al*. (2008), who found that, for a county in Virginia, most deer road mortalities occurred on primary roads and that, unlike secondary roads, the probability of a deer mortality on a primary road was unrelated to traffic volume. Paved roads in our study roughly correspond to primary roads in McShea *et al*. (2008), suggesting that paved road density is a good index of deer per capita road mortality.

Despite this, deer rank abundance was not negatively related to paved road density across our eastern Ontario landscapes, which were specifically selected to minimise correlations between paved road density and deer habitat variables. The landscapes in eastern Ontario covered a similar range of paved road densities, presumably representing a similar range in deer per capita road mortality rates, as those in Pennsylvania. In fact, our Ontario data suggest a positive relationship between deer abundance and paved road density. We reiterate that this positive response was not because, for example, the lowest road densities were in mostly forested areas, or at higher road densities the landscape was primarily agricultural; we selected our landscapes specifically to avoid this type of situation (Table 1; Appendix 1).

A potential reason for the lack of a negative effect of road density on deer relative abundance is that even in areas with high road density, the mortality on roads is a small component of overall mortality on deer. For example, harvest rates of adult male

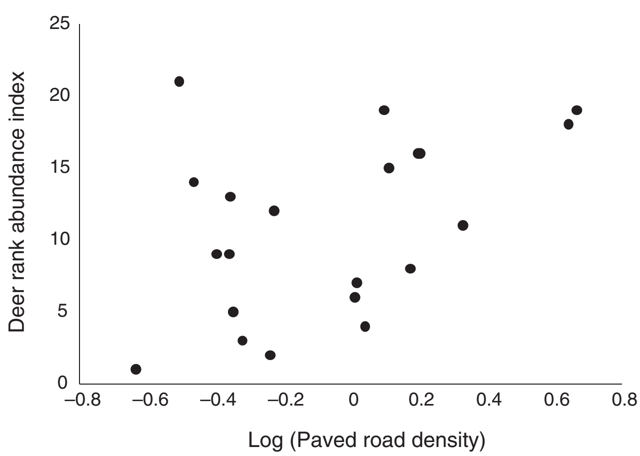

Fig. 5. Relationship between deer rank abundance and log(paved road density (km km^{-2})) in eastern Ontario. Deer rank abundance was estimated using pellet and track counts in forest patches located at the centres of each of 21 3-km-radius landscapes (Fig. 2). Paved road density was calculated within each landscape.

deer in Pennsylvania are estimated to range from ~0.3 to 0.6 depending on hunting effort and location (Norton *et al*. 2012), which is about 4–5 times the mortality rate due to road kill. The relative rates of harvest and road mortality in eastern Ontario are likely similar, although we do not have estimates for this area.

Another possible reason for the lack of negative effect of road density on deer relative abundance could be that our eastern Ontario data may cover too small a spatial extent for the effects of the gradient in deer road mortality to be observable. This could be an issue either if our landscapes were too small relative to the daily movement ranges of deer, and/or if most road mortality occurs during long-distance movements (e.g. dispersal movements) rather than during foraging movements. However, neither of these is likely. We selected our landscape size to be larger than typical home-range sizes for deer (see Methods), and it is known that white-tailed deer cross or attempt to cross roads frequently during their daily movements. Fritzen *et al*. (1995) estimated on average >1 road crossing per day per deer and Waring *et al*. (1991) estimated that 50% of individual deer observed next to roads crossed or attempted to cross the roads. This suggests that road mortality may be more strongly linked to frequent daily movements than to infrequent seasonal movements. We therefore infer that the spatial scale of our study in eastern Ontario was appropriate to detect the effect of road mortality on deer abundance.

We acknowledge that our measure of deer abundance, 'rank abundance', is not a true abundance estimate but is rather an index of relative abundance, and is subject to high uncertainty. Putman (1984) and Kie (1988) reviewed the use of pellets, and Kie (1988) reviewed the use of tracks, to estimate deer relative density. Despite many factors contributing to variability in these estimates, there is generally a positive relationship between pellet counts and deer abundance. Converting the deer sign counts to actual abundance estimates is fraught with assumptions, which is why we chose instead to combine them into a single rank relative abundance index (which we call 'rank abundance'). Note that we did not use other abundance indices (e.g. browse level, road mortality rate), as these would have been confounded with the predictor variables in our analyses.

Despite this uncertainty, our data do suggest a possible positive relationship between deer relative abundance and paved road density. We acknowledge that the relationship is not strong (Fig. 5) and could be spurious due to our relatively small sample size. For this reason, and also since we did not expect a positive relationship, any hypothesis explaining it (see below) is necessarily *post hoc* and speculative. Since we controlled for potential confounding variables through site selection (Table 1) and multimodel analysis, a correlation between road density and availability of deer habitat is unlikely to explain this positive relationship between deer rank abundance and paved road density. One possibility we considered is that, if deer behaviourally avoid roads or traffic (Long *et al.* 2010) then it is possible that, in landscapes with high road density, they become 'trapped' within small road-bounded areas (Jaeger *et al*. 2005). Following the season's reproduction, this could cause an apparent increase in abundance in these landscapes. We evaluated this hypothesis by testing (*post hoc*) for a relationship between deer rank abundance and 'accessible area' (Eigenbrod *et al*. 2008), or the size of the roadless area surrounding each of the 21 sampled patches. The relationship was not significant, providing no support for the idea that roads create temporary population build-ups.

A second possible explanation for the apparent positive relationship between deer relative abundance and paved road density is that deer predator densities may be lower in landscapes with higher road densities (wolf, *Canis lupus*: Jędrzejewski *et al*. 2004; black bear, *Ursus americanus*: Nicholson 2009; coyote, *Canis latrans*: Kays *et al*. 2008), thus releasing deer from predation pressure. Reduced predator abundances in landscapes with high road densities has also been suggested as a possible explanation for the frequently observed positive relationships between road density and small mammal density (Rytwinski and Fahrig 2007, 2011). Similarly, a positive effect of road density on deer abundance could result from reduced predation by humans (hunting) in areas with higher road densities. In their review of causes of mortality of medium and large-sized mammals of North America, Collins and Kays (2011) found that while the probability of an animal–vehicle collision increases with increasing human footprint in the landscape, the rate of hunting decreases over the same gradient. Even if actual predation pressure is not substantially reduced in landscapes with high road densities, deer may be able to detect the presence of predators (the 'landscape of fear' concept: Hebblewhite and Merrill 2009; Manning *et al*. 2009; Laundré *et al*. 2010). In this case, if predators are less abundant in landscapes with high road densities, these landscapes could be more attractive to deer. This would result in higher deer abundances in these landscapes, not necessarily from reduced predation but from increased use of the landscapes by deer. If the resulting increase in abundance outweighs any decrease due to higher road mortality on deer in these landscapes, the net pattern may be a positive relationship between deer abundance and road density.

It is also possible that deer abundance is higher in landscapes with higher road densities due to the provision of some resource(s) to deer by the roadway itself, and that the benefits of this outweigh the higher road mortality in these landscapes. Since we controlled for forest edge area in our study design and analysis, an increase in browse at forest edges is not a likely candidate explanation. However, roads may also provide supplemental browse in the grassy road verge where deer are commonly seen feeding, particularly when forage in the forest is scarce (e.g. early spring) and after crops have been harvested (Bellis and Graves 1971; Carbaugh *et al*. 1975; Waring *et al*. 1991; Ng *et al*. 2008). Road salt is another possible resource provided by roads: in the absence of natural mineral licks, deer obtain sodium from anthropogenic sources, mainly runoff from roadways (Fraser 1979; Pletscher 1987).

In conclusion, our study is the first to test for an effect of paved road density on white-tailed deer abundance, while controlling for potentially confounding deer habitat variables. Using a dataset from Pennsylvania, we identified a range of paved road densities over which there is a marked increase in deer per capita road mortality. We then tested for a negative relationship between paved road density and relative deer abundance in landscapes selected across eastern Ontario. We selected these landscapes across the same range of road densities as in Pennsylvania, thus allowing interpretation of a relationship in terms of per capita road mortality. We also selected these landscapes to minimise correlations between road density and deer habitat, thus allowing us to unambiguously test for the effect of roads on deer abundance. Unexpectedly, we observed a positive relationship between deer abundance and paved road density. Two feasible explanations for this are (1) reduced deer predation and/or perceived predation risk and/or hunting pressure in landscapes with high road density and (2) provision of a resource by roads, the benefits of which outweigh the road mortality. These explanations are speculative, however, and we suggest that further research is needed both to confirm the positive relationship we found and to test possible causes.

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Appendix 1. Deer rank relative abundance index, and predictor variables at the landscape and local scales, for 21 sample sites in eastern Ontario
Deer rank abundance indexes are listed in order of increasing paved road density

Response variable	Landscape-scale predictors				Local-scale predictors	
Deer rank abundance index	Paved road density	Percentage forest cover	Percentage forest edge	Percentage crop area	Focal patch size (ha)	Browse index
1	0.23	33.14	3.43	39.66	257.56	141
21	0.31	33.92	3.43	28.08	185.57	145
14	0.34	38.72	3.67	28.98	33.26	160
9	0.40	41.34	4.25	33.94	35.43	239
9	0.44	35.94	3.75	21.98	21.47	264
13	0.44	30.97	4.24	28.57	37.70	173
5	0.45	38.38	3.52	41.35	86.38	295
3	0.48	29.24	3.67	36.28	50.32	140
2	0.58	38.45	3.15	39.07	5.61	93
12	0.59	32.84	3.42	19.01	156.91	129
6	1.03	43.81	4.83	23.26	44.07	244
7	1.04	29.14	4.68	24.37	35.79	183
4	1.10	36.81	4.50	39.31	155.67	224
19	1.25	31.32	3.88	31.94	55.79	240
15	1.30	31.73	3.79	29.71	38.16	277
8	1.50	30.12	3.60	39.31	71.35	246
16	1.58	36.40	3.54	41.90	70.54	222
16	1.60	40.21	4.97	27.54	26.98	192
11	2.15	31.51	3.78	31.56	15.13	381
18	4.39	33.45	4.75	18.48	49.13	379
19	4.65	32.14	4.56	31.01	79.32	78