

The effect of roads on white-tailed deer (*Odocoileus virginianus*)

By

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ABSTRACT

White-tailed deer, *Odocoileus virginianus*, exhibit a positive relationship with road density when populations are compared between human-developed and natural disturbance areas. Within human-developed areas this relationship is not as well understood. I examined this relationship in three steps. I established a positive relationship between the number of deer-vehicle accidents (DVA) and road density using 1982-1997 records of DVA counts in Pennsylvania. Using a mensurative experimental design I measured relative deer abundance for twenty-four landscapes in eastern Ontario where road density varied but percent cover of forest, forest edge, cropland and pasture were controlled. I found a significant positive relationship between deer abundance and road density. Comparison of foetus counts of roadkilled does in Nova Scotia with DVA rates showed no evidence of reproductive compensation for this increased mortality. My results suggest that roads themselves provide deer with a resource or service, resulting in higher abundances in high road density landscapes.

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Introduction

Since the cessation of unrestricted hunting and the establishment of hunting legislation and conservation programs in the early 1900s, white-tailed deer, *Odocoileus virginianus*, population numbers have increased dramatically (McCabe and McCabe 1984). Cook and Daggett (1995) estimated the current white-tailed deer population of the United States to be in excess of 20 million deer, a staggering increase over the 500,000 deer estimated to be present in the early 1900s. There are many examples of high growth: the deer population in Virginia, USA has increased from approximately 575,000 in 1987 to an estimated 1,000,000 by 1995 (West and Parkhurst 2002); in Nova Scotia, Canada, deer populations have shown annual increases of up to 130% (Nova Scotia Department of Natural Resources, unpublished data); there was a 153% increase between 1986 and 1990 in the white-tailed deer population on Rocky Mountain Arsenal, Colorado, USA (Whittaker and Lindzey 2001). In many areas, populations have become so large that white-tailed deer are considered a nuisance species, responsible for crop and property damage (West and Parkhurst 2002; Ontario Ministry of Natural Resources 2004; Nova Scotia Department of Natural Resources 2006; Pennsylvania Game Commission 2007).

The major driver behind these population increases is that anthropogenic modification of landscapes has inadvertently created an ideal deer environment. In many regions the continuous forests have been fragmented as the land was cleared for logging, agriculture and residential development. This benefited deer as they are commonly described as a species of the forest edge. This designation comes from their use of browse as a major food source, feeding on woody and succulent growth up to 2 m above ground level (Krefting et al. 1966). In late stage forests, thick canopy cover limits the amount of

understory and thereby limits the amount of available food. In the natural setting deer take advantage of clearings caused by fallen trees or fire as a main source location of browse (McCabe and McCabe 1984). Fragmenting the continuous forest increases the amount of low-growing vegetation along the forest edge. Furthermore, with the replacement of forest with agricultural land, the food resources available to deer grow beyond the increase in browse as deer feed on crops to supplement or even replace their traditional diet (Gladfelter 1994). Lastly, in our drive to protect both ourselves and the livestock being raised on the formerly forested land, we have extirpated the wolf, *Canis lupus*, from many areas thereby largely freeing deer from a major predatory pressure (Taylor 1956). Ironically in many regions this elimination of wolves was carried out with the goal of improving the deer hunt (Young 2002). Roseberry and Woolf (1998) suggest this release from predation may be a major factor in allowing deer to exploit areas fragmented by forest clearing.

Roads have played a major role in these anthropogenic landscape modifications although, as suggested by Forman and Alexander (1998), it is much debated whether roads drive development or development drives roads. Even in the absence of agricultural development, roads fragment the continuous forest and increase the amount of forest edge with relatively little actual forest loss. As forest is cut down and farms are created, roads are built to link them but roads also allow access to previously undisturbed forest, opening them up to agricultural development. Lastly, by increasing hunter access to previously remote areas, roads can facilitate the extirpation of predators. Jensen et al. (1986) found evidence that wolf populations cannot sustain themselves in areas where road density exceeds 0.6 km of road/km². Essentially, a human-developed landscape

including roads offers superior habitat when compared to stretches of undisturbed continuous forest. Roseberry and Woolf (1998) found that deer benefit from a moderately fragmented landscape. Bowman et al (in review) show this in northern Ontario where the region dominated by white-tailed deer effectively ends where human development for logging ends.

In addition to their relationship with landscape changes that benefit white-tailed deer, roads also exhibit negative influences on deer populations through deer-vehicle accidents (DVA). About 91.5% of DVAs are fatal for the deer (Allen and McCullough 1976). Conover et al. (1995) estimated that in 1991 726,000 deer, *Odocoileus* spp. (including both white-tailed deer and mule deer, *Odocoileus hemionus*), collided with cars in all US states excluding Hawaii. Romin (1994 as cited in Conover et al. 1995) suggests that if estimates of deer that survive the initial collision but die later are included, and if corrections are made for the chronic under-reporting of DVAs (approx. 50% go unreported), the total number of deer killed in DVA in the United States in 1991 exceeds 1 million.

Whereas there is a significant body of research on deer-road interactions, the long term effect of these interactions on deer population size has not been studied. Most research has focused on analysing and predicting the locations of DVAs. Many such studies consider only extremely small scales both spatially (only including one portion of a road and its immediate surroundings) and temporally (only considering how the deer interact with the landscape just prior to a DVA) (Finder et al. 1999; Hubbard et al. 2000; McShea et al. 2008). These small-scale studies likely do not capture the full range of landscape features with which the deer interact. For example, the studies mentioned

above looked at individual road segments and quantified the landscape characteristics up to 800 m from the road. As white-tailed deer are reported to occupy summer home ranges with radii up to 1.6 km (Smith 1991), these studies almost certainly do not quantify all landscape variables with which the deer have interacted prior to the DVA. A study by Grovenburg et al. (2008) did examine the effect of landscape characteristics on DVA counts in South Dakota at a county level but did not look directly at the influence of road density.

My first research question was: within human-modified areas, how does road density affect white-tailed deer abundance? There are two main ways this may be manifested. First, I hypothesized that as DVAs occur on roads, increasing the number of roads should increase the occurrence of DVAs. From this I predicted (Prediction 1) that the proportion of the estimated white-tailed deer population that is killed in deer-vehicle accidents should have a positive relationship with road density. Secondly, I hypothesized that this increased mortality in higher road density areas is sufficient to affect population size. From this I predicted (Prediction 2) that, within developed areas, deer abundance should be negatively related to road density once the effects of the amounts of forest, forest edge, cropland and pasture on deer abundance are controlled for.

There exists the possibility that any negative effects of road mortality could be reduced if deer possess the ability to increase their reproductive efforts to replace lost individuals. Two possible mechanisms could allow for this. White-tailed deer exhibit a high reproductive rate with females breeding as fawns and producing twins most commonly and triplets often as well (Smith 1991). By removing individuals from the population, road mortality may release resources to other deer and may reduce social

pressure, a situation their rapid reproductive rate is well suited to take advantage of through increased recruitment of fawns. Therefore, the deaths due to road mortality may be quickly replaced. The second mechanism is that the removal of fawns due to DVAs could release resources to the mother of the roadkilled fawn. Work by Clutton-Brock et al. (1989) has shown that the majority of the cost of reproduction in red deer, *Cervus elaphus*, is in lactation as opposed to gestation. Females who avoided the cost of lactation, by being either barren or losing their calf early, gained an advantage the following year over females who had successfully reared calves, in terms of overwinter survival, fecundity, calving date and calf size. In this manner, female white-tailed deer that lost fawns to DVAs and therefore avoided even part of the cost of lactation should be able to invest more energy in improving their own body condition and potentially respond by producing more offspring the following year.

My second research question was: do deer exhibit reproductive compensation in the face of traffic mortality? I hypothesized that, based on either of the mechanisms presented above; deer will increase reproductive output in the face of higher mortality. From this I predicted (Prediction 3) that female deer killed in areas of higher road mortality should exhibit higher reproductive rates measured by foetus counts compared to those killed in areas of lower road mortality.

These two research questions and their three associated predictions were tested using a combination of pre-existing and new data. Prediction 1 was tested using data from Pennsylvania, USA of DVA occurrences and estimated winter deer densities. These data were used to calculate the proportion of each county's estimated deer population killed annually in DVAs. I then tested the relationship between this proportion and the

density of paved roads for each county. Prediction 2 was tested by selecting landscapes in eastern Ontario, Canada such that paved road density varied widely across landscapes but the other major landscape predictors of deer abundance were controlled for. Deer abundance was measured across these landscapes and tested against road density. Lastly, Prediction 3 was tested using location and necropsy data of road killed deer in Nova Scotia, Canada. I compared foetus counts of adult does in areas of high and low estimated traffic mortality.

Methods

Prediction 1: proportion of deer population killed in DVAs vs. paved road density

Deer data

Two datasets on the Pennsylvania deer populations were provided by the Pennsylvania Game Commission's (PGC) Deer Management Section (DMS). All data were at the county scale. The first dataset provided counts of all reported deer mortalities resulting from DVAs by county from 1963 to 1997. The second dataset provided winter deer densities for all PA counties from 1982 to 2001 expressed as deer/forested square mile. These deer densities were the product of a DMS population model using the age and sex characteristics of hunter-harvested deer. An important point to note is that no road effects were included in this model.

From these deer densities and forest cover per county (also provided by the DMS), the estimated deer population for each county was calculated. County area was measured using ArcMap v9.2 (ESRI, 2006) and the Pennsylvania Spatial Data Access (PASDA) website. Deer population size per county was calculated by multiplying the

number of deer per forested square mile by the total number of forested square miles per county.

The proportion of each county's estimated population killed annually in DVAs was then calculated by dividing the DVA count by the county's deer population. Hereafter this will be referred to as "proportional DVA mortality." The overlap in the two DMS datasets allowed me to calculate annual proportional DVA mortality for the years 1982 to 1997.

Road density

Vector-based spatial data were obtained from PASDA for State (2008) and Local (2005) paved road layers. This represented the data available closest in time to the DMS datasets. Using the Python-based script BatchClip in ArcCatalog v 9.1 (ESRI, 2005), the road layers were clipped using the spatial boundaries of the counties (Fig. 1). Using another Python script (CalculateLength) the length of each road segment was measured and road lengths were summed across the county, providing a total paved road length (km) for each road type for each county. Paved road density (km/km^2) was then determined by dividing paved road length by county area.

Data analysis

The relationship between proportional DVA mortality and paved road density was tested in a simple linear regression analysis using the DVA data from 1997. 1997 was chosen because it was closest in time to the available road density data.

Prediction 2: deer density vs. paved road density

I. Pennsylvania data

To uncover the relationship between paved road density and deer density it was necessary to control for other major predictors of deer density: forest, row crop and pasture/grass. A raster landcover image (PAMAP, 2005) which included these variables was obtained from the PASDA website. Once again this was the spatial data closest in time to the DMS datasets. Using the counties as the defining areas I used the tool Tabulate Area in ArcMap v9.2 (ESRI, 2006) to calculate the percent cover of each landcover type. The raster image originally included three categories of forest, deciduous, coniferous and mixed, but I combined these into a single cover type since they were highly inter-correlated.

The annual county deer population calculated for Prediction 1 was divided by county area (km²) to get annual county deer density (deer/km²).

Data analysis

A correlation matrix of paved road density and the other landscape variables was first produced. I then ran a forward stepwise regression of the 2001 deer density on paved road density and the landscape variables.

II. Eastern Ontario data

Due to high collinearity between paved road density and the percent forest cover ($r=-0.754$) in the Pennsylvania data, it was impossible to isolate the effect of road density from this confounding factor. Therefore, I conducted a field study in eastern Ontario to test for a relationship between deer abundance and road density using a mensurative experimental approach to avoid correlations between road density and other major

predictors of deer abundance. Deer abundance, as estimated by deer sign (pellets and tracks), was sampled in the centre of each of 24 landscapes with varying levels of paved road density while controlling for the amount of forest cover, forest edge, cropland and pasture.

Site selection

The goal of site selection was to select landscapes of a given size, chosen to maximise variation in paved road density while minimising correlations between paved road density and the other landscape variables: forest, forest edge, cropland and pasture across landscapes. This was done by selecting landscapes based on the following criteria: a 30 to 200 ha forest patch in the centre of each landscape with the surrounding 3-km radius landscape composed of 30 to 40% forest cover, 3 to 5% forest edge cover and no correlations across landscapes between paved road density and the amount of cropland or pasture.

Site selection began by identifying potential forest patches and creating the study landscapes. Sites were initially chosen based on the size of forest focal patch, where the actual sampling would take place, with all selected patches ranging in size from 30 to 200 ha. Centroids, points placed at the centres of the forest polygons, were generated for all selected focal patches using ArcMap v9.2 (ESRI, 2006). These centroids were then buffered to 3 km to produce circular landscapes around the focal patches. The 3-km radius landscape was chosen based on the maximum reported radius of white-tailed deer summer home ranges of 1.6 km (Smith 1991). By choosing a larger landscape I ensured that a deer detected in a focal patch was unlikely to interact with landscape variables outside of the defined area, at least during the summer.

The first landscape variable to be controlled for was forest cover. Forest cover of eastern Ontario was obtained from 1:50 000 Natural Resources Canada (NRC, 2003) maps modified by cutting the forest shapefile using the road layer (Appendix J). This was necessary because in its original form forest was considered continuous across roads. Percent forest cover was obtained by dividing total forest area by the area of the 3-km radius landscape (28.274 km²). A selection criterion of 30 to 40% forest cover was used as it provided the most possible sites. The remainder of the landscapes were mainly agricultural fields (cropland: mean 31.77% (18.48-43.23) and pasture: mean 21.54% (11.74-39.77)).

Since white-tailed deer are commonly described as a forest edge species, I felt it necessary to control for forest edge as well. As no forest edge-specific spatial data were available I created a shapefile approximating this landscape feature. Using the spatial data for forest cover, forest edge was estimated as the area extending 10 m into the forest from the forest-field border. The arbitrary value of 10 m was chosen because forest edge effect can vary greatly depending on forest composition and matrix type. Once the forest edges were created, percent forest edge cover was calculated in the same manner as percent forest cover. A selection criterion of 3 to 5% forest edge cover was used as it provided the most possible sites.

Within each of the landscapes, total paved road length, also from the 1:50 000 Natural Resources Canada (NRC, 2003) maps, was calculated using the same BatchClip and CalculateLength scripts used with the Pennsylvania datasets. Paved road density was calculated by dividing total paved road length by the landscape area (28.274 km²). Landscapes were selected in two categories: Low road density landscapes had less than

0.6 km of paved road/km² of landscape and high road density landscapes had greater than 1.0 km of road/km².

Initial site visits were carried out between December 2007 and April 2008. These visits involved locating the appropriate landowners and obtaining permission to use their land for the upcoming season. After reviewing both the ArcMap data output and site visit notes, 24 sites were identified (Fig. 2) across eastern Ontario to the west and south of Ottawa. Initial site inspection showed all sites to be of deciduous or mixed-deciduous tree composition.

Field work site visits

Each site was visited once during each of two field work phases during the spring and summer of 2008. Phase 1 (12 May to 15 June) consisted of setting up the sampling plots and surveying for deer pellet groups and tracks, hereafter referred to as deer sign. Phase 2 (11 August to 20 September) consisted of re-surveying for deer sign and carrying out the vegetation surveys. The two separate field work phases were used to allow pellets to accumulate between the sampling visits. Sites were visited in a stratified random order based on paved road density. The high road density sites were divided into three subcategories (1.0-1.5, 1.5-2.0 and >2.0 km/km²). Within the low road density sites and the three subcategories of high road density, the sites were randomized using a random number generator. Then sites were chosen alternating a low road density site with one of the high road density sites, selecting from each subcategory consecutively. This schedule was held to as rigidly as possible but was occasionally disrupted by weather and landowner requests.

Deer sign collection

Pellet counts are among the most commonly used indirect methods for estimating deer abundance in closed environments such as forest patches (Putman, 1984). Pellet group counts were taken following Smart et al. (2004). At each site a 3 x 3 grid of 10 m x 10 m quadrats was arranged on the cardinal axes (Fig. 3) with 10 m between quadrats. The sampling grid was placed 100 m from the forest edge where the patch was entered and a minimum of 100 m from any other forest edge. This was done to eliminate any effect of forest edge on deer counts. White-tailed deer preferentially feed at the forest edge between forest and openings.

Each quadrat was numbered and marked by four 45 cm-long wooden stakes driven into the ground, marked A, B, C and D starting with the northwest stake and proceeding clockwise. A Global Positioning System (GPS) device was used to record coordinates for the 1A stake of every grid. Since all grids were identically oriented this allowed all grids to be accurately placed in ArcMap.

Quadrats were then roped off and surveyed completely for deer sign. When any sign was located it was recorded both in a data table and diagrammatically on a data sheet. Deer pellets were considered a group if there were six or more pellets present (Smart et al. 2004). During Phase 1, pellets located within the quadrats were removed from the focal forest patches. This allowed for new pellets to accumulate over the three month period between visits and ensured that the same pellet groups were not counted twice. Deer sign observed outside the quadrats was left untouched.

Vegetation surveys

Five vegetation variables were measured in each sample site: browse availability, canopy closure, ground cover, tree density and concealment cover. There were eight 10 m x 10 m vegetation quadrats at each site: four situated between the deer sign quadrats (Fig. 3: A, B, C and D) and four situated 20 m out from the sides of the grid in the cardinal directions (Fig. 3: E, F, G and H). With the exception of concealment cover, all vegetation variables were measured in the vegetation quadrats. I did not use the deer sign quadrats for the vegetation surveys because walking transects within the deer sign quadrats somewhat trampled the vegetation.

Browse availability was measured at ten points within each of the eight vegetation quadrats. At each point a 2-m bamboo pole was held vertically with one end on the ground. Two metres is approximately the height range within which a white-tailed deer will browse (Krefting et al. 1966). Each plant with leaves touching the pole was identified to species and the number of leaves from that plant in contact with the pole was recorded. For each site the number of individual plants and the number of individual leaves was calculated. Although this gave an overestimate of total availability the bias should be consistent across all sites. The level of browse damage per plant was also recorded as none, low, medium or high.

Canopy cover and ground cover were measured using a sight tube (a 30-cm length of 1 ¾ inch PVC pipe with wire crosshairs) with readings taken at the centre and at each corner of the vegetation quadrats. A reading consisted of looking through the sight tube (straight up for canopy cover and straight down for ground cover) and recording either hits (the crosshairs rest on vegetation) or misses (the crosshairs hit sky or ground,

respectively). Percent canopy cover and percent ground cover for each site were calculated by dividing hits by the total number of readings (40).

Tree density was calculated using a modification of the point centred quarter method. In each quarter of each vegetation quadrat the tree (trunk with a diameter at breast height (DBH) >10 cm) nearest to the central point was identified to species and its distance from the central point of the quadrat and its DBH were recorded. If there was no tree within the quarter the closest tree outside the quadrat was used. Tree dispersion for the site was calculated as the mean across all quadrats of the distances from the quadrat centre to the trees. Tree density was calculated as the inverse of squared tree dispersion (Waite 2000).

Concealment cover was observed using a vegetation profile board (VPB). This was a 2.5 m by 25 cm board of 1.6 cm plywood divided into ten 25 cm sections alternately painted black and white (Fig. 4) (modified from Nudds 1977). Spikes made from shelving brackets were affixed to the bottom to allow it to stand, thereby requiring only one person to take the readings. The VPB was set up on each of the four forest edges of each grid and observed from 10 and 15 m away. Nudds (1977) carried out test observations from six distances (5, 10, 15, 20, 25 and 30 m) and chose 15 m because readings at this distance showed the greatest variability across sites. Time constraints did not allow for these test observations so an additional observation distance, 10 m, was used. At both distances the number of sections that were more than 50% obscured by vegetation was recorded. For each site at each distance the mean number of sections obscured was used as the measure of concealment cover.

Post-hoc landscape data

Following the completion of the field work, the composition of the landscapes was analysed in detail as more data became available. From the 28-class Ontario Landcover Database (Ontario Ministry of Natural Resources, 1998), raster coverage of both cropland and pasture was acquired and transformed into vector shapefiles. The NRVIS/OLIW Data Management Model (Land Information Ontario, 2007) provided current data on eastern Ontario forested areas from which values for forest edge area were calculated. The percent landscape cover of all landscape variables (cropland, pasture, forest and forest edge) were re-quantified using the methods described above under *Site selection*.

I also created a variable called “accessible area” (Eigenbrod et al. 2007). This was the total area within which a deer located at one of my study forest patches could move without crossing a paved road.

Traffic density was estimated for the landscapes using annual average daily traffic (AADT) values previously obtained by Carr and Fahrig (2001) from the city of Ottawa and the municipalities and counties of eastern Ontario. However, since the available AADT data only covered a portion of the roads from my landscapes, I also obtained spatial data on the eastern Ontario road network, DMTI v8.3 (DMTI, 2009), which divided roads into five categories based on type (expressway, primary highway, secondary highway, major road and local road). Using the AADT data I had for a subset of these roads I calculated mean AADT values for each road type and applied these values to all roads of that type in my landscapes. Traffic density was then calculated following Carr and Fahrig (2001). For each road segment the AADT value was

multiplied by the length of the road segment within the 3-km radius landscape. This value was summed across all road segments in the landscape and divided by the area of the landscape (28.274 km²) to get traffic density expressed as AADT·km/km².

Data analysis

As the primary goal of this portion of the study was to assess the relationship between deer density and road density in an experimental design that controlled for other commonly correlated landscape predictors of deer abundance, it was first important to ensure that these correlations did not occur in the eastern Ontario data. Site selection was designed to ensure this. However as the statistical analysis was to be done using more recent spatial data and incorporating several new landscape measures, supporting analysis was required. To carry this out I examined the correlations between paved road density and estimated traffic density, the percent cover of each of the above mentioned landscape variables (forest, forest edge, cropland and pasture), the vegetation characteristics (browse availability (both the number of plants and the number of leaves), canopy cover, ground cover, tree density and concealment cover), and forest patch area.

To test for the relationship between deer abundance and road density, I used three different abundance indices representing three different time periods: Phase 1 pellet counts (over-winter deer abundance), Phase 1 track counts (spring abundance) and Phase 2 track counts (summer abundance). During Phase 2, pellet groups were found at only 4 of 24 sites, which was not sufficient data for analysis. Since only track presence or absence per quadrat was noted for most sites (21 out of 24) in Phase 1, I converted all Phase 1 track counts at each site into a score from 0 to 9 representing the number of quadrats at that site in which tracks were found (Phase 1 track score). During Phase 2,

individual tracks were recorded so for that period the total number of tracks was used. To provide an overall index of deer abundance per site I combined all three indices in a single ranked measure called abundance rank. To obtain the abundance rank values, I first ranked the sites according to each of the three abundance indices individually. Then, for each site I summed the three rank values. Finally, I ranked these sums across sites. Note that abundance rank was calculated only for the 21 (of 24) sites for which I had data for each abundance index. The three individual abundance indices and the combined index, abundance rank, were each regressed on log transformed paved road density, traffic density, accessible area, patch area and the other landscape and vegetation variables using forward stepwise regression analysis.

In order to ensure that there were no patterns of spatial autocorrelations of deer, all-directional correlograms were produced for each of the individual abundance indices (Phase 1 pellet counts, Phase 1 track score and Phase 2 track counts) using Moran's I.

Prediction 3: testing for compensatory reproduction

The availability of location and necropsy data from deer killed in DVAs in Nova Scotia provided an opportunity to test for evidence of compensatory reproduction in response to road mortality.

Data source and filtering

As part of an ongoing program monitoring road kill on Nova Scotia's roadways, the Nova Scotia Department of Natural Resources (NSDNR) records the locations (UTM coordinates) and performs necropsies on all white-tailed deer killed in DVAs. I obtained a portion of this database containing 13,005 deer killed in DVAs in the province from 1999 to 2004 (*All Deer*). Deer were aged, sexed, evaluated for body condition and a

subset of the females were checked for the presence of foetuses. This subset was further filtered to include only those females who had their uterine contents checked between January and May, the period in which foetuses are expected and detectable (1,034 does) (*Checked Females*). Foetus counts per *Checked Female* ranged between 0 and 4.

Data manipulation and analysis

This data was tested for evidence of reproductive compensation in two ways; first, by testing the relationship between road density and foetus count and second, by examining if foetus counts differ in areas of high and low road mortality.

To test the relationship between road density and foetus count, it was necessary to quantify road density. This was done by the same procedure used during the site selection process in eastern Ontario. All *Checked Females* were projected into ArcMap v9.2. Using the BatchClip script in ArcCatalog v 9.1, all roads (Canada Census, 2006) within a 3-km radius landscape around each *Checked Female* were selected and their lengths summed using the CalculateLength script. Road density was calculated as km of road/km² of landscape by dividing the total road length by the area of the landscape (28.274 km²). Foetus count was then regressed on road density using a Poisson regression.

To determine whether females in areas with estimated higher road mortality had higher reproductive rates (number of foetuses), I needed to estimate the local deer kill rate around each *Checked Female*. I projected both *Checked Females* and *All Deer* into ArcMap v9.2 and calculated the distances between each *Checked Female* and her five nearest neighbours in the *All Deer* dataset. The inverse of the mean nearest neighbour distance served as an index of local DVA mortality: smaller mean nearest neighbour distances represented clustering of DVA and therefore signified higher local DVA

mortality than areas with larger mean nearest neighbour distances. The foetus counts of *Checked Females* with the highest (n=200) and the lowest (n=200) local DVA mortality (Fig. 5) were compared using a two-sample t-test.

All statistical analyses were performed using SPSS v.16 (SPSS Inc., 2007).

Results

Prediction 1: proportion of deer population killed in DVAs vs. paved road density

Deer deaths occurring in deer-vehicle accidents were a large source of mortality of Pennsylvania white-tailed deer, averaging 6.6% but frequently exceeding 40% and reaching as high as 60% of the estimated population in some counties (Fig. 6). Proportional DVA mortality increased significantly with increasing road density ($F=25.960$, $df=60$, $p<0.001$, $slope=0.019$, $SE=0.004$, $R^2=0.306$; Fig. 7).

Prediction 2: deer density vs. paved road density

I. Pennsylvania data

It was not possible to test for a relationship between road density and deer population size using the Pennsylvania data because of the high collinearity of paved road density and the percent landcover of forest across counties (Table 1). Therefore, it was impossible to isolate the effect of road density on deer abundance. While the simple regression of paved road density on the 2001 deer density showed a negative relationship ($F=7.426$, $df=60$, $p=0.008$, $slope=-0.805$, $SE=0.295$, $R^2=0.112$), this relationship disappeared when percent forest cover was included in the model. Stepwise regression suggested that percent forest cover was the only significant predictor of deer density, showing a positive relationship ($F=15.742$, $df=60$, $p<0.001$, $slope=0.054$, $SE=0.014$, $R^2=0.211$).

II. Eastern Ontario data

The sites in eastern Ontario were selected to avoid or at least reduce correlations between paved road density and other landscape variables. This was largely successful, particularly with percent forest cover (Table 1); however, percent forest edge cover was significantly positively correlated with paved road density ($r=0.480$, $df=24$, $p=0.018$). In addition, both percent canopy cover ($r=-0.416$, $df=24$, $p=0.043$) and tree density ($r=-0.428$, $df=24$, $p=0.037$) in the sample forest patches were significantly negatively correlated with paved road density. As expected, traffic density was highly correlated with paved road density ($r=0.682$, $df=24$, $p<0.0001$).

All forest patches were of deciduous or mixed deciduous composition. Tree density varied from 0.02 to 0.14 trees/m². Concealment cover varied from 0.00 to 7.75 sections of the VPB >50% covered (out of 8) at 10 m and 0.00 to 8.00 sections covered at 15 m. Canopy cover varied from 60.00 to 92.50% and ground cover varied from 0.00 to 85.00%. Estimated browse availability varied from 78 to 381 leaves per site and 44 to 213 plants per site (Appendix E).

Deer presence was confirmed at all 24 eastern Ontario sites. During Phase 1 (May/June) 21 sites showed signs of deer presence with pellet groups found at 12 sites and tracks found at 14 sites. In Phase 2 (August/September) 23 sites showed signs of presence, 4 with pellets and 23 with tracks. The one site with no deer presence detected in Phase 2 showed signs of presence during Phase 1.

When included with all landscape and vegetation variables, neither log-transformed paved road density nor traffic density was a significant predictor of the three individual abundance indices (Appendix F). However, there was a significant positive

effect of log-transformed paved road density on the combined index, abundance rank ($F=4.382$, $df=20$, $p=0.050$, $slope=7.284$, $SE=3.480$, $R^2=0.187$; Fig. 8).

Correlograms demonstrated that spatial structure was not responsible for the distribution of any of the three individual abundance indices (Appendix G).

Prediction 3: testing for compensatory reproduction

Road density for the 1,034 *Checked Females* ranged from 0.13 to 8.68 km/km² with a mean of 1.38 km/km². Foetus count ranged from 0 to 4 with a mean of 1.35. The Poisson regression showed no evidence of a relationship between road density and reproductive output as measured by foetus count (Wald $X^2=1.589$, $df=1$, $p=0.207$, $slope=-0.036$, $SE=0.0285$).

Mean nearest neighbour distance for the 200 *Checked Females* designated as high DVA mortality deer ranged from 0 m to 271.2 m with a mean of 93.9 m. For the 200 *Checked Females* designated as low DVA mortality deer, mean nearest neighbour distances ranged from 1416.6 m to 7988.7 m with a mean of 2633.5 m. Foetus counts for high DVA mortality *Checked Females* had a minimum of 0, a maximum of 3 and a mean of 1.34 (Std. Dev.=0.893). Foetus counts for low DVA mortality *Checked Females* had a minimum of 0, a maximum of 4 (one deer only) and a mean of 1.36 (Std. Dev.=0.885). The two-sample t-test showed no significant difference in foetus counts between the high and low local DVA mortality *Checked Females* ($t=-0.167$, $df=398$, $p=0.866$), indicating no evidence for compensatory reproduction.

Discussion

I found that deer-vehicle accidents can account for a large proportion of a population's annual mortality, reaching as high as 60% in some years in several

Pennsylvanian counties and averaging 6.6%. In reality this value could be even higher as DVAs are chronically under-reported (Conover et al. 1995). Interestingly, when Fudge et al. (2007) calculated the annual proportion of the Nova Scotia deer population killed in DVAs for the years 1999 to 2003, they found a similar value of 6%.

The proportion of the deer population killed per county in Pennsylvania increased with higher paved road density, supporting Prediction 1. In areas with higher road density deer are required to cross roads more frequently as a part of their daily and seasonal movements, increasing the opportunities for a DVA to occur. Also, areas with higher road densities tend to be more developed for human use (agriculture and residential areas), creating a landscape pattern of forest patches and agriculture that has been shown to benefit deer (McCabe and McCabe 1984). This results in higher deer densities, which may cause yearlings to move farther from their mother's home range to set up those of their own. Nixon et al. (2007) reports yearling dispersal distances in Illinois up to 49 km. In this way, higher road densities could be creating more mobile populations, possibly increasing the frequency with which individuals must cross roads. Furthermore, in landscapes with more roads, the number of vehicles per km of road may be higher, thereby increasing the odds that when a deer crosses a road a car will also be there. All of these factors increase the opportunities for DVAs to happen in landscapes with high road densities.

It is important to recognize the potential source of error that exists in the calculation of proportional DVA mortality. Since neither the DVA counts nor the winter densities were my own data I must assume that they may be flawed estimations of the true deer situation in Pennsylvania. This error could be further compounded when deer

densities were scaled up to provide county populations, essentially estimates of estimates. Despite this they still represent a valuable and relevant source of information because any errors that exist can be expected to be constant. Since the same PGC population model was used for all estimates, they may be over- or under-estimates but this estimation error should be constant. Similarly, DVAs are chronically under-reported (Conover et al. 1995) leading to an underestimation but most likely a constant one. As my analysis focuses on trends, this error is less disruptive because the form of the trend should remain the same as long as the errors are constant.

Due to high collinearity between paved road density and forest cover across counties in Pennsylvania (Table 1), it was not possible to use this dataset to test for a relationship between deer abundance and paved road density. Therefore, to answer this question I carried out the mensurative experiment in eastern Ontario.

The lack of pellets during Phase 2 forced a reliance on tracks as the major estimator of deer abundance. This potentially introduced a source of error into these estimates as, unlike pellet counts, tracks are not limited by any physiological constraints. Using known defecation rates and accumulation periods it is relatively straightforward to accurately calculate deer densities. This is not so with track counts. It is impossible to say with utmost certainty that higher track counts are a result of increased deer densities and not simply more active deer. I attempted to control for this in two manners. First, my experimental treatment was designed to avoid influencing deer behaviour. During the three month period between site visits, the quadrats were only marked by unobtrusive wooden stakes. Because this treatment is unlikely to make my study patches more or less attractive to deer, the chance of having overly active deer should be equal for every site.

Second, I created the overall measure of abundance, abundance rank. This provides a more robust test by combining all three abundance estimates and therefore reducing the impact of any individual sources of error. I do acknowledge that error may still exist in my samples but feel that it is at a reasonable level and the conclusions drawn from the data remain valid.

In the eastern Ontario dataset I found a positive relationship between paved road density and the combined deer abundance index (abundance rank), rejecting Prediction 2 (Fig. 8). This result was surprising, especially in light of the positive relationship between paved road density and proportional DVA mortality found in Pennsylvania and the fact that care was taken to avoid correlations between road density and deer habitat in the Ontario study (Table 1). It appears that even in areas of high road density, with assumed higher DVA rates, deer populations are not negatively affected, at least not in eastern Ontario. These findings raise two questions about the eastern Ontario deer populations: 1) Why are we not seeing any evidence of the expected negative effects of road mortality? 2) Why are deer abundance estimates in fact higher in areas with higher road density?

With regard to the first question there are two potential explanations. First is the possibility that the deer may be compensating reproductively for the increased mortality due to DVAs. While there is evidence suggesting that white-tailed deer may possess the socio-dynamic or biological mechanism necessary to allow for reproductive compensation (Dusek et al. 1989; Clutton-Brock et al. 1989), no evidence for this was found from either of the tests of the Nova Scotia deer population, rejecting Prediction 3. This could be because these deer may not be in a resource limited environment, so the removal of an individual does not actually “free up” resources for compensatory

reproduction. Clutton-Brock et al. (1989) showed that female red deer, *Cervus elaphus*, can gain a short-term reproductive advantage by avoiding the cost of lactation but it is possible this may not translate into reproductive compensation in the Nova Scotia deer. While DVAs are a significant source of fawn mortality (Vreeland et al. 2004; Burroughs et al. 2006), not enough fawns may be killed in Nova Scotia to drive a noticeable trend or they may be killed too late into or after lactation and therefore do not convey a sufficient advantage to the mother. Alternately, white-tailed deer may be following the reproductive strategy of the red deer, i.e. investing any advantage gained into larger, as opposed to more, offspring (Clutton-Brock et al. 1989). The Nova Scotia dataset does not include information on foetus size or fawn weight so this idea could not be tested. Also, because data on deer density in Nova Scotia were only available at the level of the deer management zone, it was not possible to control for the effect of population size when calculating local DVA mortality rates. Therefore, perceived higher mortality rates may simply be driven by larger deer populations and may not reflect higher proportional mortality.

The second potential reason for the lack of the expected negative effect of road density on deer abundance is that the eastern Ontario data may be on too small a scale for the effects of the gradient in DVA mortality with road density seen in Pennsylvania to be observable in the Ontario deer populations. Given the movement potential of white-tailed deer, eastern Ontario could contain only a few populations that were repeatedly sampled in my landscapes. Similarly, deer populations in areas with severe winters may be best defined at the level of the deer yard. Both these situations could serve to mask the effect of DVA mortality on deer abundance if each year deer from the main population disperse

from the winter yards and fill in the gaps left by deer killed in DVAs. Aycrigg and Porter (1997) and Lesage et al. (2000) reported that deer, specifically females, exhibit substantial levels of philopatry towards their home ranges with summer philopatry exceeding winter philopatry. However, there is still a degree of dispersion, especially among yearlings (Nixon et al. 2007). If this is in fact what is happening, areas of higher road density with higher associated mortality should have a younger age structure than lower mortality areas. I was not able to test this with any of my datasets but it does present a future avenue of research to be explored.

So if deer populations in eastern Ontario are not suffering the negative impacts of road mortality, what aspect of roads results in the increased abundances in areas of higher road density? There are at least three potential explanations for this pattern. First, roads may act as semi-permeable barriers which contain dispersing yearlings closer to the ranges of their mothers. This would create temporary build-ups of populations in areas of high road density, possibly counteracting the effects of road mortality. The concept of roads acting as semi-permeable barriers was supported by the work of Curatolo and Murphy (1986) where it was found that caribou, *Rangifer tarandus*, would hesitate up to ten minutes prior to crossing a pipeline with an adjacent road after a vehicle had passed. If white-tailed deer exhibit similar behaviour, the presence of roads with traffic could slow down their dispersal speed and cause them to settle closer to their maternal home ranges. Roads could function as a net, trapping concentrations of deer in areas of high road density. In a resource limited system, competition for resources would drive yearlings away from deer with previously established home ranges. Eastern Ontario is not such a system, as agricultural development has produced a glut of available sources of

food. To test this theory, I created the variable called “accessible area” (Eigenbrod et al. 2007). However there was no relationship between accessible area and my deer abundance index (abundance rank), so my data do not support this explanation.

Secondly, there is the possibility that the positive relationship found between deer abundance and road density in eastern Ontario may actually be driven by the positive correlation between road density and the amount of forest edge habitat ($r=0.480$). However, forest edge amount was not a significant predictor of deer abundance, so my data do not support this idea.

Finally, it is possible that a positive relationship between road density and deer abundance is due to the provision of some resource(s) or service(s) to deer by the roadway itself. One such resource is a supplemental source of browse on the grassy road verge (Bellis and Graves 1971). Deer are commonly seen feeding along the grassy verges of highways, where they have been shown to take advantage of the earlier springtime green up of faster growing introduced plant species (Ng et al. 2008). Carbaugh et al. (1975) reported deer feeding on highway verges when forage in the forest is scarce. While the agricultural development of eastern Ontario has provided supplemental food sources, the period during which I found the greatest response of deer abundance, as measured by track score, to road density was in the spring (Appendix H(b)). This coincides with both the earlier green up and a period of relatively low crop availability as the crops have not yet matured. Another possible attractant is road salt left over from the winter. In the absences of natural mineral licks, deer obtain their required sodium intake from anthropogenic sources, mainly runoff from roadways (Pletscher 1987). Deer lick roadside gravel and drink from water sources on the side of roads that are high in sodium

(Fraser, 1979). Salt levels would be expected to be higher in the spring than in the late summer, again matching the time period when I found the strongest positive effect of roads on deer abundance (Appendix H(b)). Roads may also allow for year-round occupancy of summer home ranges by providing movement corridors free of snow in the winter. Typical winter deer behaviour in areas of significant snowfall is to congregate in forested areas of predominantly coniferous growth known as deer yards (Marchinton and Hirth 1984). This permanent canopy can reduce the snow depth on the ground by up to 50% and allow for more energy efficient movement (Blouch 1984). By serving as movement corridors between coniferous forest patches that are too small to act as independent deer yards, roads may link these patches and allow deer to exploit them during the winter with relatively low energetic cost. This, in turn, could lead to higher energetic investment by the deer in body condition and raise reproductive output resulting in a higher localised deer abundance.

The idea that roads provide resources/services and that this drives the positive relationship between road density and deer abundance agrees with the predictions of Fahrig and Rytwinski (2009: Fig. 2). Based on a literature review of 79 articles of road effects on 131 species and 30 species groups, they created a working hypothesis to predict the effect of roads on animal abundance, a catch-all term covering population size, density, species presence/absence and species richness. Part of this hypothesis predicts a positive response to roads for species that are attracted to roads but are also able to practice car avoidance. Car avoidance by deer is supported by Waring et al. (1991) who reported deer waiting for vehicles to pass before attempting to cross roads and by D'Angelo et al. (2006) who reported that deer stopped movement towards

roadways as vehicles passed. Both of these findings demonstrate that deer are aware of vehicles and will avoid crossing when they are detected.

An interesting but costly project would be to employ my eastern Ontario study design comparing areas with and without fencing excluding deer from roadways and grassy verges. Would the positive relationship between deer abundance and road density persist if the deer could not access the resource/service? This could shed light on whether deer are benefiting from some immediate aspect of roads or the broader associated landscape modifications.

My results support the use of mitigation fencing as an appropriate management strategy to reduce DVAs by keeping deer off roadways. In addition, proper placement of fencing could help lower local deer abundances by denying access to the resource(s) or service(s) provided by roads. The exact placement of the fencing would require further research to identify the exact aspect of roads that is beneficial to deer. For example, if it is the introduced plant species along the grassy verge that drive this relationship then mitigation fencing should be placed right at the forest border, assuming it is forested, denying deer access to this resource. If the roads are acting as movement corridors in winter, fences could be placed closer to roads as they would only need to exclude deer from the ploughed portions of the roadway. If my resource/service concept is accurate, simply denying deer access to roads may serve to partially control population growth while at the same time reducing DVA mortalities of deer and people.

Conclusion

It has long been accepted that roads and their associated modification of the landscape has benefited white-tailed deer, allowing them to rapidly increase in population

size and to expand across North America. My research has shown that, in addition to their broad-scale modifications of the environment, roads themselves offer something positive to deer. Although the exact nature of this beneficial aspect is unknown, it does highlight the amazing ability of deer to take advantage of altered landscapes. Aside from direct cases of domestication, large mammals rarely benefit from these massive anthropogenic landscape modifications. Deer are among the unique few that thrive in a human-dominated world.

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Table 1. Correlations between paved road density and other landscape variables for 67 counties in Pennsylvania, and correlations between paved road densities and other landscape variables and vegetation variables for 24 study sites in eastern Ontario.

Variable	Pennsylvania paved road density (km/km²)	Eastern Ontario paved road density (km/km²)
% forest cover	-0.754**	-0.180
% cropland cover	0.246*	-0.248
% pasture cover	0.035	-0.277
% forest edge cover	n/a	0.480*
% canopy cover	n/a	-0.416*
% ground cover	n/a	0.158
Tree density (trees/m²)	n/a	-0.428*
Concealment cover (mean # of sections >50% obscured at 10 m)	n/a	0.248
Concealment cover (mean # of sections >50% obscured at 15 m)	n/a	0.238
Browse availability (number of leaves)	n/a	0.274
Browse availability (number of plants)	n/a	0.218
Focal patch area (ha)	n/a	-0.163
Traffic Density (AADT·km/km²)	n/a	0.682**

* Correlation is significant at the 0.05 level

** Correlation is significant at the 0.01 level

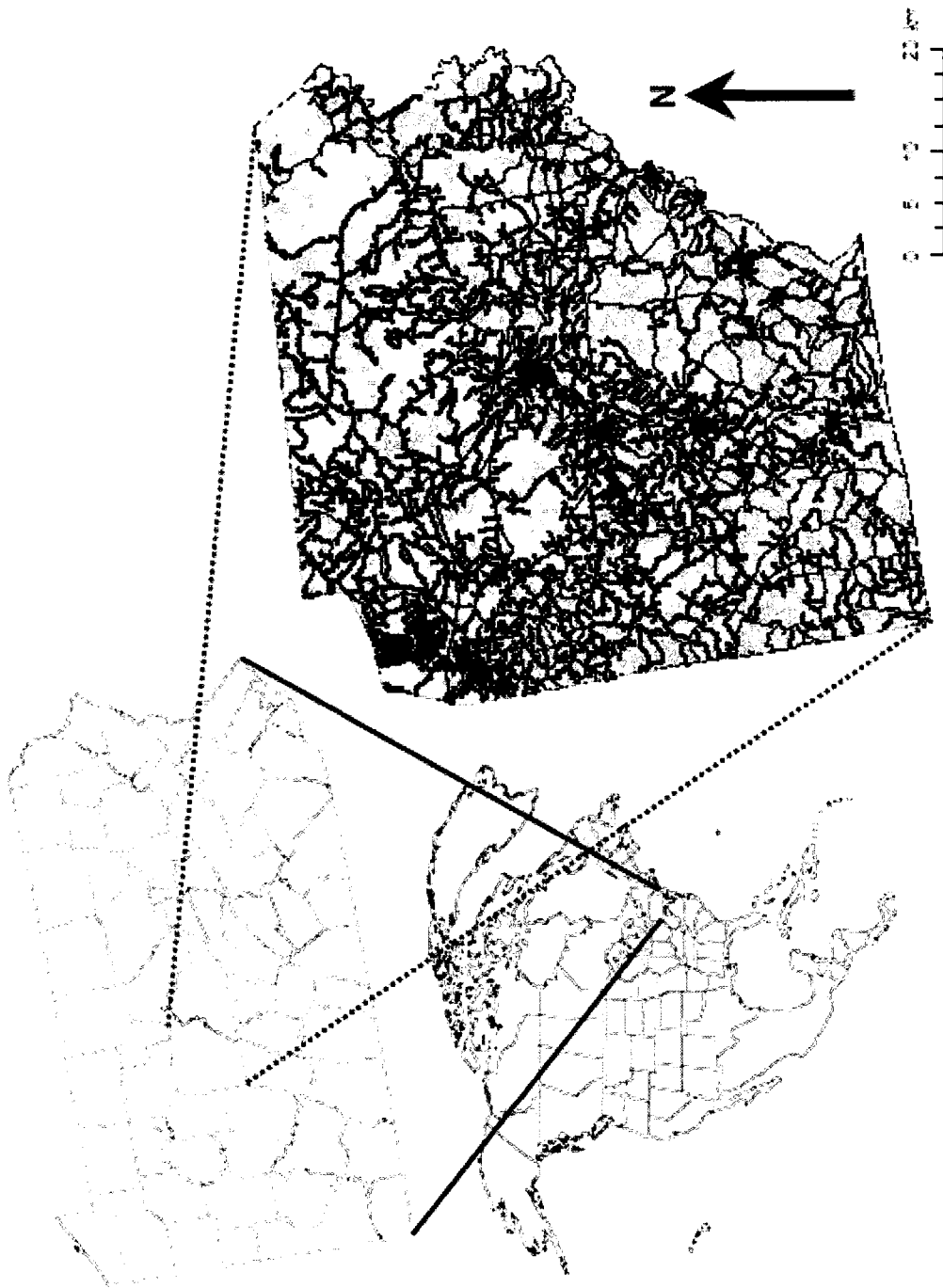


Figure 1. Map showing Bradford county of Pennsylvania as an example of the landcover analysis carried out. The thick lines represent county roads and the thin lines represent local roads. The grey shading represents forested land. Compared to other counties in Pennsylvania, Bradford county had a relatively high forest cover and low road density.

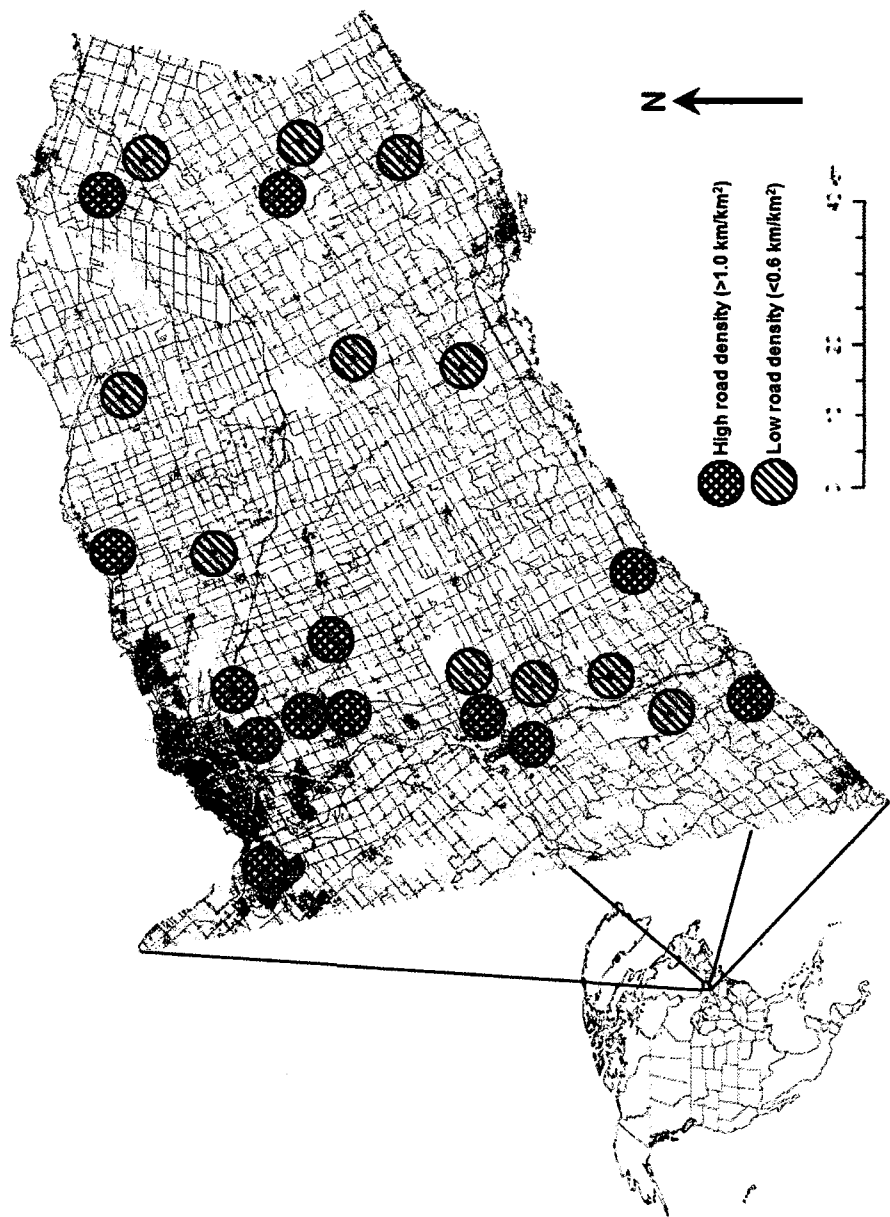


Figure 2. 24 landscapes in eastern Ontario. The black dots represent the focal forest patches where deer surveys took place and the circles represent the 3-kilometre radius landscapes within which the landscape factors were measured. Landscapes were chosen based on the following characteristics: focal forest patch between 30 and 200 hectares in size, 30 to 40 percent forest cover in the landscape and 3 to 5% forest edge cover in the landscape. All landscapes were in rural (mostly agricultural) areas.



Figure 4. Vegetation profile board (VPB). The VPB is a 2.5m by 25cm board divided into ten 25cm sections alternately painted black and white (modified from Nudds 1977). Concealment cover for each site was measured as the mean number of sections that were more than 50% obscured by vegetation.

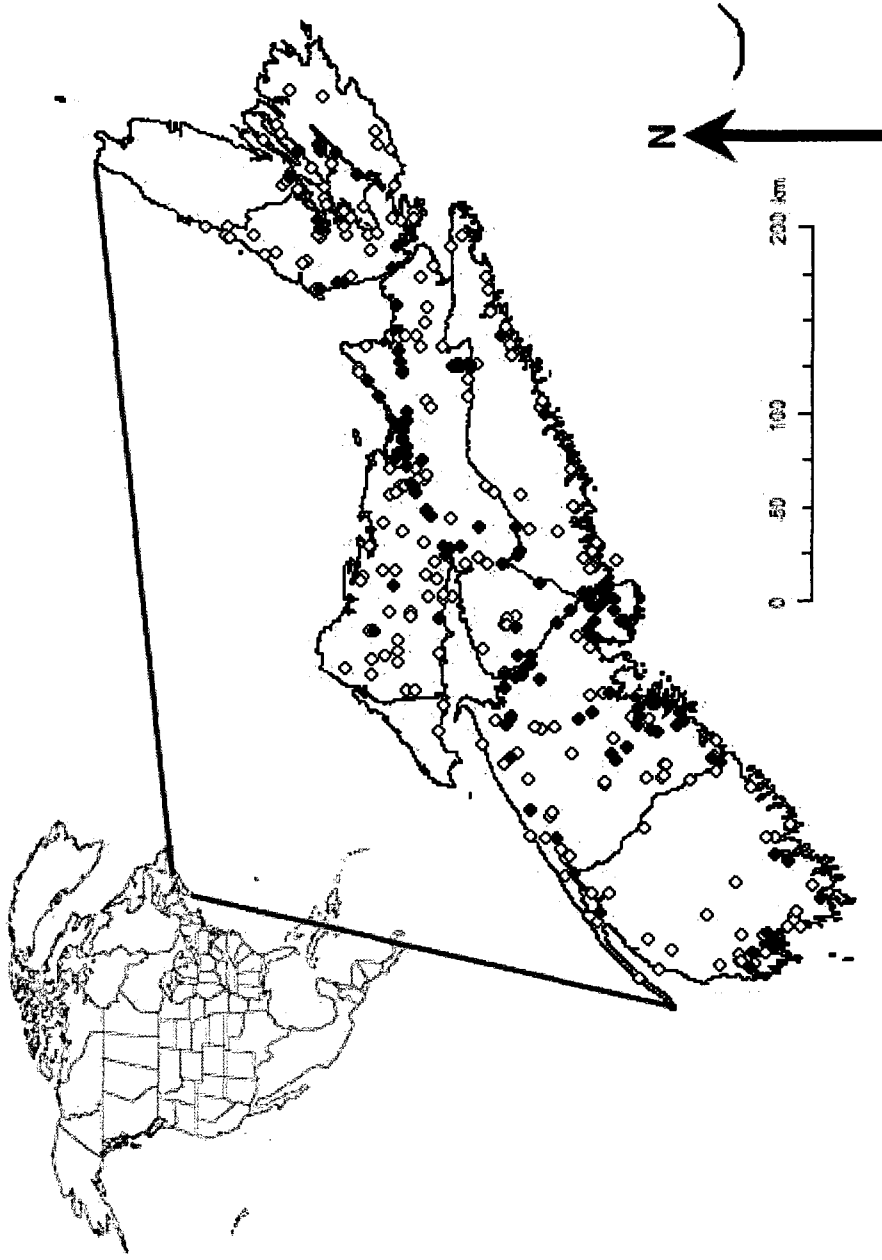


Figure 5. Map showing 400 female white-tailed deer killed in DVAs in Nova Scotia between January and May for the years 1999 to 2004 who had the contents of the uteruses checked for foetuses (*Checked Females*). For each *Checked Female*, local DVA mortality was estimated using the mean distances between the female and her 5 nearest neighbour DVAs. The foetus counts of the 200 *Checked Females* with the largest mean nearest neighbour distance, and therefore lowest local DVA mortality were compared to the foetus counts of the 200 *Checked Females* with the smallest mean nearest neighbour distance, and therefore the highest local DVA mortality (open and closed dots, respectively).

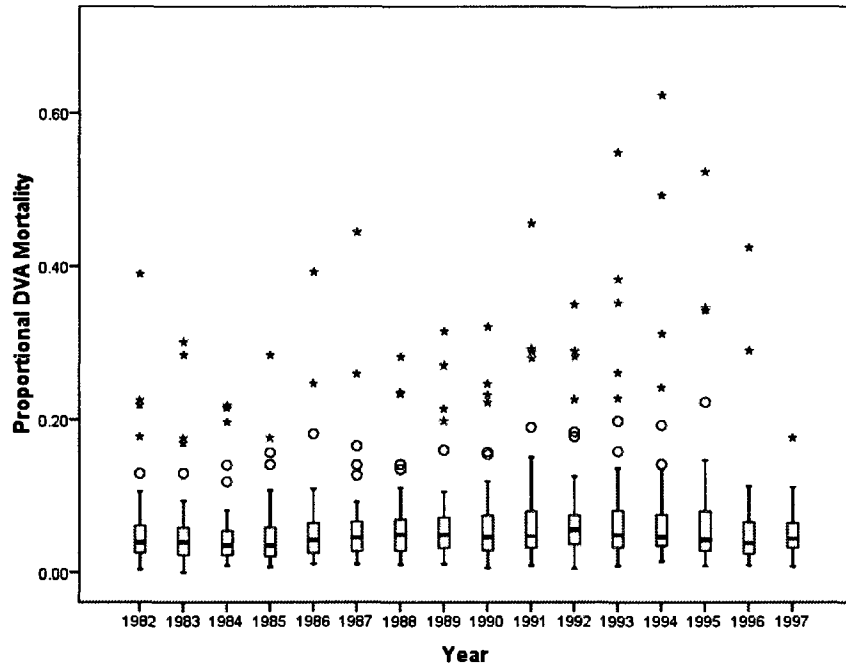


Figure 6. Proportion of estimated deer population killed by deer-vehicle accidents in 67 Pennsylvania counties by year. Mean proportional DVA mortality for 1982 to 1997 is 6.6%. The bars represent the mean proportional DVA mortality by year, the boxes represent 50% for that year's value and the whiskers represent the 95% confidence interval (CI). The circles and stars represent county values outside the CI but within 2 and 3.5 quartiles of the mean, respectively.

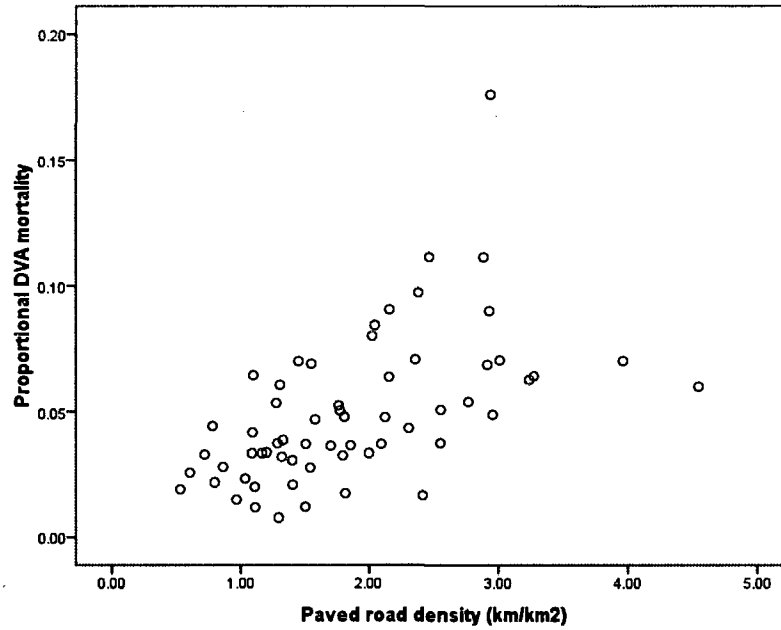


Figure 7. Proportion of estimated deer population that was killed in deer-vehicle accidents as a function of paved road density in the 61 Pennsylvania counties with reported DVA counts in 1997 ($F=25.960$, $df=60$, $p<0.001$, $slope=0.019$, $SE=0.004$, $R^2=0.306$).

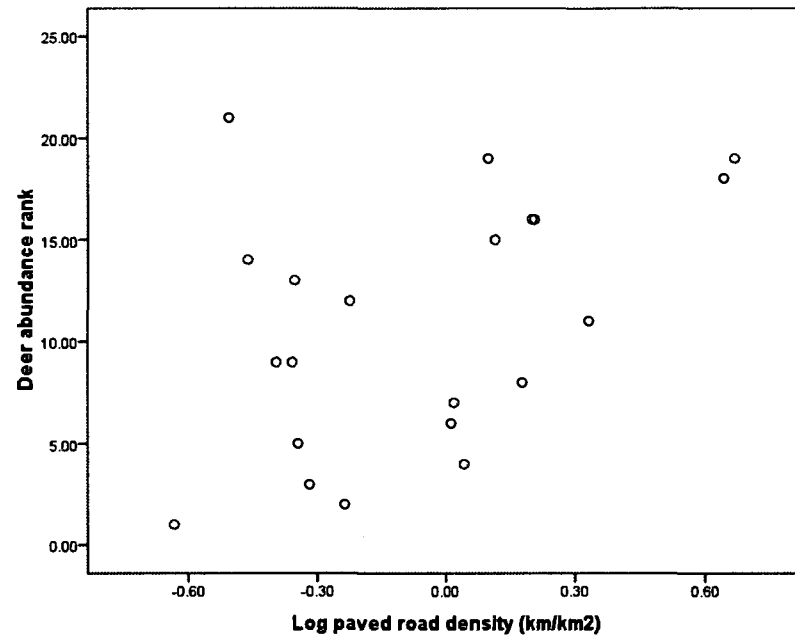


Figure 8. Relationship between deer abundance rank and log of paved road density (km/km^2) in eastern Ontario ($F=4.382$, $df=20$, $p=0.05$, $\text{slope}=7.284$, $\text{SE}=3.480$, $R^2=0.187$). Deer abundances were estimated using pellet and track counts in forest patches located at the centre of each of 21 3-km radius landscapes. Paved road density was calculated within each landscape.

Appendix A. Road density categories, location descriptions and UTM coordinates (NAD 1983 Zone 18N) for 24 forest patches in which white-tailed deer abundance was measured using deer sign counts in eastern Ontario to test Prediction 2. Road density was calculated for the 3-km radius landscapes centred on the forest patches. Low road density was defined as <0.6 km of paved road per km² of landscape. High road density was defined as >1.0 km of paved road per km² of landscape. Sites were numbered based on the order they were sampled. Bracketed numbers are the original site designations from ArcMap v9.2.

Site number	Paved road density	Location description	UTM Coordinates (NAD 1983 Zone 18N)	
			Easting	Northing
1 (62)	High	South of Little Third Rd. and Auld Macmillan Rd. intersection, west of Alexandria	0525713	5017187
2 (873)	Low	Due west of County Rd. 19 and Cedar Grove Rd. intersection, north of Williamstown	0531299	5001320
3 (1323)	High	West of County Rd. 44 and Bedell Rd. intersection, south of Kemptville	0499997	4982943
4 (875)	Low	East of County Rd. 12 and Cornwall TP 9 Rd. intersection, south of South Stormont	0501900	4992065
5 (1155)	High	Greely Sand and Gravel quarry, north of Albion Rd. and Mitch Owens Rd. intersection, Ottawa	0453133	5014140
6 (695)	High	West of Victoria Rd. and 9 th Line Rd. intersection, Metcalfe	0463980	5010323
7 (300)	Low	East of County Rd. 2 and Hurley Rd. intersection, west of Spencerville	0454235	4963289
8 (242)	High	North of Stampville Rd. and Carman Rd. intersection, Iroquois	0473385	4968078
9 (846)	Low	North of Grant Rd. and Dewar Rd. intersection, east of North Stormont	0503691	5006912
10 (275)	Low	North of Ventnor Rd. and Adams Rd. intersection, Ventnor	0459148	4971955
11 (1809)	High	Kanata Hill, south of Highway 417, Kanata	0432489	5019344
12 (633)	High	West of Stagecoach Rd. and Herbert Corners Rd. Herbert Corners	0454105	5008139
13 (1340)	Low	West of 9 th Concession and 1 st Line Rd. intersection, northeast of Green Valley	0532844	5014530
14 (1815)	High	South of Lester Rd. and Albion Rd. intersection, Ottawa	0449733	5020309
15 (34)	Low	West of Dalkeith Rd. and Breadalbane Rd. intersection, north of Breadalbane	0531336	5035882
16 (23)	High	North of Cassburn Rd. and County Rd. 10 intersection, Vankleek Hill	0525677	5041411
17 (443)	High	North of Baseline Rd. and Joannise Rd. intersection, Rockland	0476411	5040321
18 (259)	Low	North of County Rd. 22 and Edward Scott Rd. intersection, South Gower	0457865	4982158
19 (605)	Low	East of Loughlin Ridge Rd. and County Rd. 1 intersection, Hallville	0459244	4991260
20 (593)	High	North of County Rd. 22 and Highway 43 intersection, east of Kemptville	0452836	4989440
21 (1554)	Low	North of Route 14 and Concession 7 intersection, southeast of Rockdale	0497792	5038970
22 (519)	High	East of Highway 417 and County Rd. 27 intersection, Ottawa	0456287	5024100
23 (1183)	Low	South of County Rd. 26 and Ruissellet Rd. intersection, Bearbrook	0475869	5026509
24 (1366)	High	West of Merwin Rd. and McIntosh Rd. intersection, Maynard	0455802	4952135

Appendix B. White-tailed deer abundance estimates from deer sign counts collected in 24 forest patches in eastern Ontario during the spring and summer of 2008 to test Prediction 2. Phase 1 took place between 12 May and 15 June and Phase 2 took place between 11 August and 20 September.

Site Number	Phase 1 pellet count	Phase 1 track score	Phase 2 pellet count	Phase 2 track count	Abundance rank
1	2		0	0	
2	1		0	1	
3	0		0	5	
4	2	1	0	5	9
5	0	4	0	15	11
6	12	2	0	14	15
7	0	4	0	14	9
8	0	8	0	8	8
9	2	6	0	17	21
10	0	0	0	17	3
11	3	4	0	15	19
12	0	3	0	12	6
13	0	3	0	21	13
14	0	9	2	35	18
15	1	2	0	13	12
16	0	0	0	29	7
17	1	2	0	40	19
18	0	0	0	8	1
19	1	0	0	12	5
20	0	0	1	20	4
21	10	0	4	21	14
22	21	0	0	24	16
23	0	1	0	1	2
24	12	2	3	15	16

Appendix C. Geographic Information System (GIS) spatial data used for the selection of study sites in eastern Ontario to test Prediction 2. GIS number represents the original ArcMap designation. Paved road length, forest patch area and forest cover were obtained from 1:50 000 Natural Resources Canada (NRC, 2003) maps and forest edge cover was calculated from the spatial data for forest. All landscape variables except forest patch area were calculated for the 3-km radius landscape surrounding the forest patch.

Site number	GIS number	Paved road length (km ²)	Paved road density (km/km ²)	Forest patch area (ha)	Forest area (km ²)	% forest cover	Forest edge area (km ²)	% forest edge cover
1	62	30.29	1.07	35.22	8.27	29.24	1.05	3.72
2	873	12.81	0.45	43.47	8.31	29.39	1.20	4.23
3	1323	56.38	1.99	59.41	7.61	26.91	1.40	4.94
4	875	12.40	0.44	21.47	8.31	29.38	1.05	3.72
5	1155	60.69	2.15	15.13	8.34	29.48	1.17	4.13
6	695	36.73	1.30	38.16	7.98	28.22	1.12	3.96
7	300	11.37	0.40	35.43	8.84	31.28	1.20	4.23
8	242	42.51	1.50	71.35	8.35	29.54	1.04	3.69
9	846	8.83	0.31	185.57	9.59	33.92	0.97	3.43
10	275	13.58	0.48	50.32	8.16	28.86	1.04	3.69
11	1809	131.40	4.65	79.32	8.01	28.33	1.38	4.89
12	633	29.06	1.03	44.07	9.08	32.13	1.51	5.33
13	1340	12.51	0.44	37.70	8.72	30.83	1.20	4.24
14	1815	124.09	4.39	49.13	9.06	32.04	1.35	4.79
15	34	16.82	0.59	156.91	9.29	32.84	0.97	3.42
16	23	29.51	1.04	35.79	8.24	29.14	1.32	4.68
17	443	35.43	1.25	55.79	8.75	30.96	1.12	3.98
18	259	6.58	0.23	257.56	8.44	29.86	1.07	3.79
19	605	12.76	0.45	86.38	6.55	23.16	0.94	3.33
20	593	31.18	1.10	155.67	9.06	32.04	1.33	4.71
21	1554	9.75	0.34	33.26	10.95	38.72	1.04	3.67
22	519	44.76	1.58	70.54	9.54	33.75	1.03	3.65
23	1183	16.39	0.58	5.61	10.62	37.58	0.94	3.32
24	1366	45.33	1.60	26.98	10.27	36.33	1.45	5.14

Appendix D. Geographic Information System (GIS) spatial data used for the statistical analysis of the relationship between paved road density and deer abundance (Prediction 2) at 24 study sites in eastern Ontario. Sites were designated based on the order they were sampled. Forest patch area, forest area and forest edge area were obtained from the NRVIS/OLIW Data Management Model (Land Information Ontario, 2007). Cropland and pasture area were obtained from the 28-class Ontario Landcover Database (Ontario Ministry of Natural Resources, 1998). The same spatial data used for paved roads (1:50 000 Natural Resources Canada (NRC, 2003) maps) during the site selection process was used here as well. Accessible area was calculated using the paved road spatial data. Traffic density was calculated from annual average daily traffic (AADT) counts originally used by Carr and Fahrig (2001) and the paved road spatial data.

Site number	Forest patch area (ha)	Forest area (km ²)	% forest cover	Forest edge area (km ²)	% forest edge cover	Cropland area (km ²)	% cropland cover	Pasture area (km ²)	% pasture cover	Accessible area (km ²)	Paved road length (km)	Paved road density (km/km ²)	Log paved road density	Traffic density (AADT·km/km ²)
1	35.22	8.73	30.88	0.98	3.45	8.76	30.98	5.76	20.36	13.52	30.29	1.07	0.03	4733.58
2	43.47	8.31	29.39	1.20	4.23	12.22	43.23	5.87	20.75	25.09	12.81	0.45	-0.34	7796.10
3	59.41	8.04	28.44	1.36	4.82	9.34	33.04	7.24	25.62	15.37	56.38	1.99	0.30	22126.08
4	21.47	10.16	35.94	1.06	3.75	6.21	21.98	8.88	31.39	64.71	12.40	0.44	-0.36	3418.14
5	15.13	8.91	31.51	1.07	3.78	8.92	31.56	4.07	14.39	4.40	60.69	2.15	0.33	9031.91
6	38.16	8.97	31.73	1.07	3.79	8.40	29.71	6.81	24.08	23.23	36.73	1.30	0.11	5189.29
7	35.43	11.69	41.34	1.20	4.25	9.60	33.94	4.20	14.86	109.34	11.37	0.40	-0.40	3589.84
8	71.35	8.52	30.12	1.02	3.60	11.12	39.31	3.32	11.74	4.81	42.51	1.50	0.18	27100.35
9	185.57	9.59	33.92	0.97	3.43	7.94	28.08	6.59	23.31	35.85	8.83	0.31	-0.51	1316.36
10	50.32	8.27	29.24	1.04	3.67	10.26	36.28	4.77	16.87	21.44	13.58	0.48	-0.32	2660.66
11	79.32	9.09	32.14	1.29	4.56	8.77	31.01	5.46	19.31	4.34	131.40	4.65	0.67	47471.44
12	44.07	12.39	43.81	1.37	4.83	6.58	23.26	3.78	13.37	12.00	29.06	1.03	0.01	3514.47
13	37.70	8.76	30.97	1.20	4.24	8.08	28.57	7.00	24.75	51.92	12.51	0.44	-0.35	4728.60
14	49.13	9.46	33.45	1.34	4.75	5.22	18.48	3.68	13.01	3.68	124.09	4.39	0.64	18982.20
15	156.91	9.29	32.84	0.97	3.42	5.38	19.01	11.25	39.77	43.64	16.82	0.59	-0.23	28482.21
16	35.79	8.24	29.14	1.32	4.68	6.89	24.37	9.29	32.84	37.11	29.51	1.04	0.02	8049.98
17	55.79	8.85	31.32	1.10	3.88	9.03	31.94	8.36	29.57	8.37	35.43	1.25	0.10	6181.39
18	257.56	9.37	33.14	0.97	3.43	11.21	39.66	4.13	14.62	61.01	6.58	0.23	-0.63	3556.51
19	86.38	10.85	38.38	0.99	3.52	11.69	41.35	4.08	14.43	123.38	12.76	0.45	-0.35	4322.76
20	155.67	10.41	36.81	1.27	4.50	11.11	39.31	5.36	18.96	41.71	31.18	1.10	0.04	17594.46
21	33.26	10.95	38.72	1.04	3.67	8.19	28.98	9.72	34.38	52.35	9.75	0.34	-0.46	2980.39
22	70.54	10.29	36.40	1.00	3.54	11.85	41.90	5.13	18.16	3.76	44.76	1.58	0.20	33676.84
23	5.61	10.87	38.45	0.89	3.15	11.05	39.07	6.13	21.69	12.82	16.39	0.58	-0.24	5470.13
24	26.98	11.37	40.21	1.41	4.97	7.79	27.54	5.27	18.62	5.66	45.33	1.60	0.20	25256.79

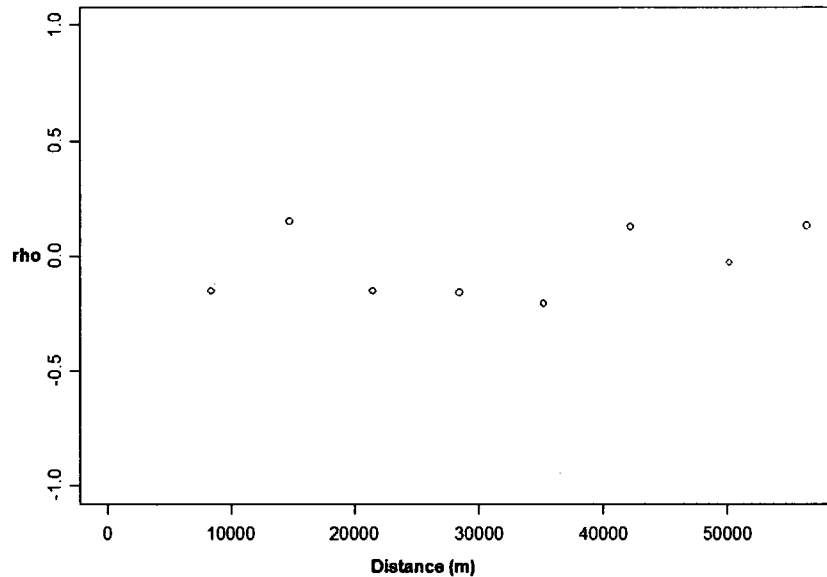
Appendix E. Vegetation survey data used for the statistical analysis of the relationship between paved road density and deer abundance (Prediction 2) at 24 study sites in eastern Ontario. Surveys were carried out during Phase 2 of field work (11 August to 20 September).

Site number	Tree dispersion (m)	Tree density (trees/m ²)	Concealment cover			% canopy cover	% ground cover	Browse availability (number of leaves)	Browse availability (number of plants)
			Mean # of sections >50% obscured at 10 m	Mean # of sections >50% obscured at 15 m					
1	3.77	0.07	6.25	8.00	72.50	0.00	170	92	
2	3.59	0.08	1.75	1.75	77.50	0.00	79	47	
3	3.60	0.08	2.00	4.75	80.00	45.00	191	60	
4	2.63	0.14	2.75	4.25	82.50	30.00	264	95	
5	4.20	0.06	6.75	8.25	65.00	85.00	381	213	
6	2.95	0.11	7.75	8.00	67.50	57.50	277	111	
7	2.74	0.13	0.75	2.25	77.50	70.00	239	87	
8	3.23	0.10	1.00	3.25	82.50	67.50	246	91	
9	3.33	0.09	2.50	4.00	85.00	60.00	145	84	
10	3.12	0.10	0.75	1.00	75.00	57.50	140	63	
11	4.57	0.05	1.75	3.00	80.00	27.50	78	44	
12	4.24	0.06	1.25	4.75	80.00	67.50	244	128	
13	4.95	0.04	0.50	3.50	72.50	57.50	173	101	
14	7.49	0.02	4.75	6.25	60.00	67.50	379	144	
15	3.61	0.08	0.25	0.00	85.00	27.50	129	76	
16	3.45	0.08	1.25	3.50	92.50	35.00	183	89	
17	3.91	0.07	3.25	4.75	72.50	72.50	240	104	
18	3.95	0.06	4.25	7.50	85.00	25.00	141	70	
19	4.86	0.04	4.50	6.75	82.50	50.00	295	98	
20	4.44	0.05	3.75	5.25	82.50	42.50	224	83	
21	3.63	0.08	0.75	2.00	85.00	52.50	160	78	
22	3.47	0.08	1.75	5.00	87.50	42.50	222	83	
23	4.52	0.05	0.00	0.25	92.50	20.00	93	52	
24	3.80	0.07	4.75	5.75	85.71	54.29	192	90	

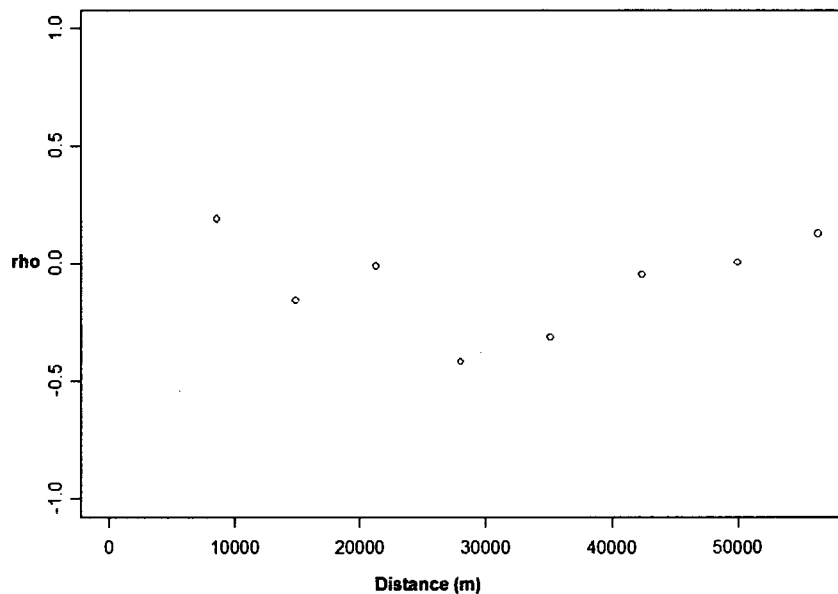
Appendix F. Main predictors of the three indices (Phase 1 pellet count, Phase 1 track score and Phase 2 track count) used to estimate deer abundance in eastern Ontario in order to test Prediction 2. The predictors were drawn from the regression of each of the individual abundances indices on log transformed paved road density, traffic density, the landscape variables (percent cover of forest, forest edge, cropland, pasture), patch area, accessible area and the vegetation variables (tree density, concealment cover at 10 and 15 m, percent canopy cover, percent ground cover and browse availability (both number of leaves and number of plants)) using a forward stepwise regression.

Abundance index	Main predictor variable	F-stat	Degrees of freedom	P-value	Slope(SE)	R²
Phase 1 pellet count	none	-	-	-	-	-
Phase 1 track score	% ground cover	6.569	20	0.019	0.074(0.029)	0.257
Phase 2 track count	% ground cover	9.549	23	0.005	0.250(0.081)	0.303

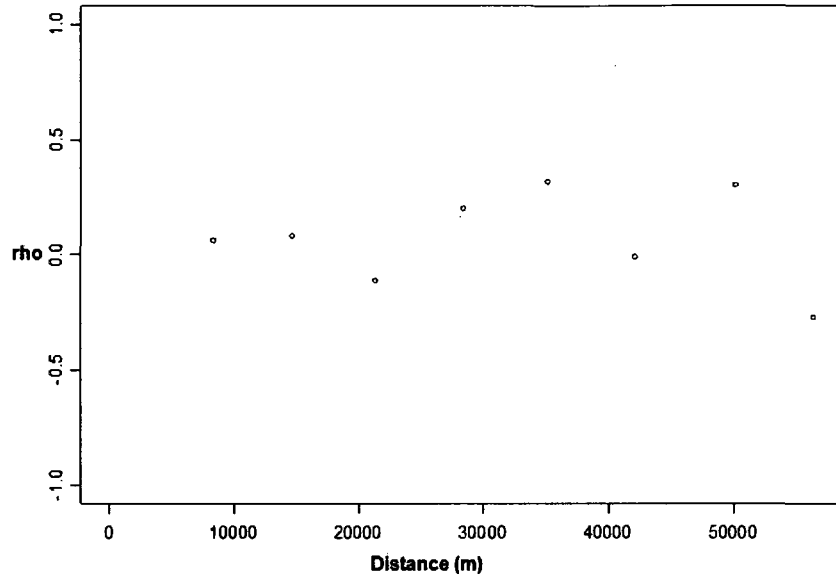
Appendix G. All-directional correlograms (Moran's I) produced using the individual abundance indices (Phase 1 pellet groups count, Phase 1 track score and Phase 2 track count) to test for spatial autocorrelation. The correlograms demonstrated that broad scale distributions of deer in eastern Ontario were not responsible for the patterns found through these abundance indices.



Appendix G(a). Correlogram of Phase 1 pellet counts showing no evidence of spatial autocorrelation.

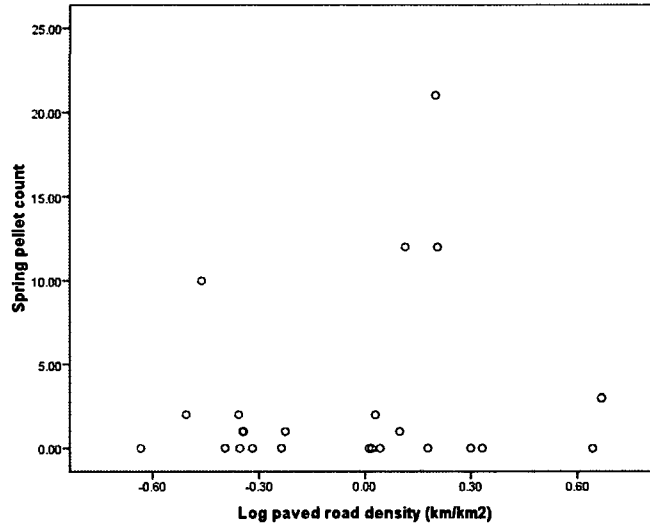


Appendix G(b). Correlogram of Phase 1 track score showing no evidence of spatial autocorrelation.

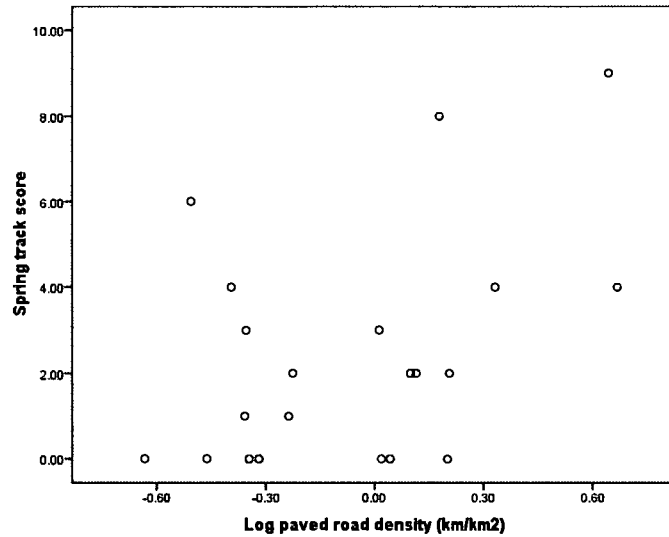


Appendix G(c). Correlogram of Phase 2 track counts showing no evidence of spatial autocorrelation.

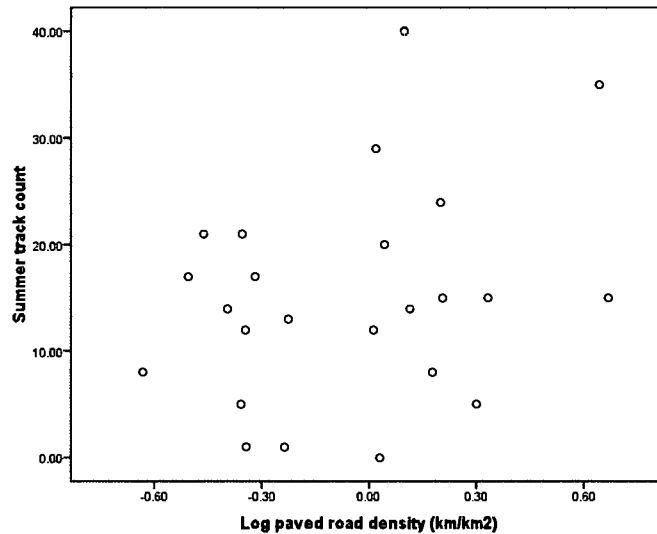
Appendix H. Preliminary results from the test of the relationship between white-tailed deer abundance and paved road density (Prediction 2). The test was a linear regression of log-transformed paved road density on each of the three abundance indices. Deer abundance estimates were collected using sign counts from 24 sites in eastern Ontario during the spring and summer of 2008.



Appendix H(a). Relationship between Phase 1 (12 May to 15 June, 2008) white-tailed deer abundance estimated by pellet group counts and log of paved road density (km/km²) in 24 sites in eastern Ontario ($F=0.538$, $df=23$, $p=0.471$, $slope=2.355$, $SE=3.210$, $R^2=0.024$). Deer abundances were estimated using pellet counts in forest patches located at the centre of 3 km radius landscapes. Paved road density was calculated for these landscapes.



Appendix H(b). Relationship between Phase 1 (12 May to 15 June, 2008) white-tailed deer abundance estimated by track scores (number of quadrats per site containing deer tracks: maximum score of 9) and log of paved road density (km/km²) in 21 sites eastern Ontario ($F=4.678$, $df=20$, $p=0.044$, $slope=3.256$, $SE=1.505$, $R^2=0.198$). Deer abundances were estimated using track counts in forest patches located at the centre of 3 km radius landscapes. Paved road density was calculated for these landscapes.



Appendix H(c). Relationship between Phase 2 (11 August and 20 September, 2008) white-tailed deer abundance estimated by track counts (number of sets of tracks detected per site) and log of paved road density (km/km²) in eastern Ontario ($F=2.136$, $df=23$, $p=0.158$, $slope=8.538$, $SE=5.842$, $R^2=0.089$). Deer abundances were estimated using track counts in forest patches located at the centre of 3 km radius landscapes. Paved road density was calculated for these landscapes.

Appendix I. Contact information for Nova Scotia and Pennsylvania white-tailed deer data

- Pennsylvania: Dr. Christopher Rosenberry, Pennsylvania Game Commission Deer Management Section, chrosenber@state.pa.us
- Nova Scotia: Anthony Nette, Nova Scotia Department of Natural Resources, netteal@gov.ns.ca

Appendix J. Splitting a polygon feature using a polyline feature in ArcMap v9.2 (ESRI, 2006): GIS technique developed to split the forest shapefile (polygon) using the road shapefile (polyline) during the site selection process to test for Prediction 2 in eastern Ontario. This technique requires an ArcInfo level license.

1. Use Create Route tool to combine all individual road polylines into a single polyline.
2. Use Create Feature Class tool to create a shapefile called Grid made up of five equal-sized abutting polygons that cover the road shapefile.
3. To Grid add a text field to the attribute table called Ident and assign a number to each polygon (1-5).
4. Using the Split tool with the single road polyline as the input coverage and Grid as the split coverage divide the road polyline into five sections based on the Ident values.
5. Perform a Select by Location on the forest shapefile using one of the road shapefiles created in step 4.
6. Start editing and use the Cut Polygon Features task with the forest shapefile as the target
7. Right click on the corresponding chunk of roads (one, two... etc) and select Replace Sketch.
8. Place your cursor over the red pixel and double click
9. Work in batches repeating steps 5 to 8 until complete.
10. Stop editing and save you edits.

Notes: You may have to change the size of the polygons created in step 3 in order to avoid overloading you computer. For this project I used five polygons. Shapefile coverage was of all of eastern Ontario. If you are using smaller areas steps 2-5 may not be necessary.