MAMMALIAN ROAD CROSSING PATTERNS ALONG A MAJOR HIGHWAY WITHIN ADIRONDACK PARK OF NEW YORK STATE, USA

by

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ABSTRACT

I studied mammalian movements across a major highway within Adirondack Park of New York, USA, by recording successful and unsuccessful road crossings using snow tracking surveys and road-kills, and by monitoring 19 under-road passageways. After one year, I completed 46 road-kill surveys and four snow tracking surveys, yielding 220 and 116 unsuccessful and successful crossing locations, respectively. Both unsuccessful and successful crossing locations were spatially clustered, albeit at different locations, and were significantly associated with features of the adjacent landscape and characteristics of the highway. One year of under-road passageway monitoring yielded 823 detections made by 19 different species. Mammals responded significantly to the geographic location, adjacent landscape, and the under-road passageway characteristics. The results presented here demonstrate how mammals respond to at least three different spatial scales – geographic, landscape, and local – and how these results can be incorporated into future mitigation strategies for this study area.

Key words: Adirondack Park, corridors, landscape, mammals, road-kills, roads, snow tracking, underpass

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PREFACE

The expanding global road network is forcing conservation biologists to recognize the ecological consequences of roads in the landscape. These consequences include at least three main effects: (1) direct mortality, (2) habitat fragmentation, and (3) habitat loss. These effects may profoundly influence mammalian movement patterns. A better understanding of these patterns, especially with respect to roads, is necessary to conserve mammalian populations.

The major goal of this thesis is to investigate the degree to which the spatial arrangement of mammalian road crossing locations along a major highway in Adirondack Park, New York, USA, is influenced by the characteristics of the highway and the adjacent landscape. This goal is accomplished through three principal components of the investigation. First, I studied the locations of successful winter road crossings (as indicated by snow tracking) and road-kills (i.e., unsuccessful road crossings) to determine whether crossing locations were randomly distributed or clustered in space. Secondly, I tested whether the locations of these successful and unsuccessful road crossings were significantly associated with characteristics of the highway (i.e., traffic volume, locations of under-road passageways, and width of the right-of-way) and the surrounding landscape (i.e., area of forest, area of open habitat, area of open water, total length of streams, and total length of roads). Lastly, I documented mammalian usage rates of under-road passageways along the highway and investigated associations between usage rates and characteristics of the under-road passageway and the surrounding landscape.

This thesis is presented in three chapters, each according to the journal's format specified for each chapter. The first chapter is presented according to Conservation

Biology format, and serves as an informative introduction to the field of conservation biology in general, and road ecology in particular (specifically with respect to mammals). Here, I summarize results from previous work in this area, identify key gaps in our current understanding, and discuss promising lines of future research. Chapter 1 concludes with a brief summary of the methodology and major results of this thesis research.

Chapter 2 and 3 are both presented according to Biological Conservation format guidelines (Mark V. Lomolino is the co-author for both chapters). In Chapter 2 I provide a summary of our current knowledge of mammalian highway crossing patterns and how these patterns are influenced by the surrounding landscape. After describing the study area, field work, calculation of landscape variables, and data analyses in detail, I then present the results for the spatial patterning of both successful and unsuccessful road crossing locations. I analyze these patterns for all data combined, and then as subsets of these data for individual species, seasons, and lanes (north- and south-bound) of the highway. I then discuss the associations between the road crossing patterns and the under-road passageway and landscape characteristics. I conclude this chapter with a discussion of the implications of this spatial patterning and its association with the under-road passageway and landscape characteristics, and provide recommendations for future research in this area.

In Chapter 3 I investigate how mammalian usage rates of under-road passageways are influenced by the under-road passageway and landscape characteristics. I begin this chapter by summarizing the current literature on wildlife use of under-road passageways and highlight some areas that need improvement. I next describe the study area, under-road passageway monitoring procedures, and statistical analyses in detail. I conclude this chapter with detailed results for all mammal species combined and for individual species including my interpretations and general conclusions/recommendations.

In summary, this thesis is an attempt to describe the spatial arrangement of mammalian road crossing locations along a major highway, and investigates their associations with characteristics of the highway (including the use of under-road passageways) and the adjacent landscape. These characteristics influence mammalian movement patterns, thereby affecting the locations where mammals attempt to cross the highway. Likewise, the characteristics of under-road passageways also influence mammalian usage rates, causing some under-road passageways to be more effective than others. Understanding the local and landscape scale factors influencing wildlife road crossing patterns will ultimately reduce the ecological effects of roads within this landscape and others as well.

CHAPTER 1

Ecological Impacts of Roads and their Significance in the Conservation of Mammalian Species

Abstract: *The ecological impacts of roads on mammals include many significant threats to individuals, populations, and entire species. The purpose of this chapter is to summarize our current knowledge on the ecological effects of roads in general, and how mammalian species, in particular, are affected by the presence of roads. I begin with an introduction to the field of conservation biology and a list of six major biodiversity threats that are of interest to conservation biologists. I then discuss one of these threats, habitat fragmentation, in more detail, specifically acknowledging roads as one form of habitat fragmentation. I summarize the ecological effects of roads (specifically with respect to mammals), including a discussion on mitigation strategies employed to reduce these effects. I highlight the potential influence of the adjacent landscape in affecting road-mammal interactions, and indicate a few shortcomings within this area in current road ecology research. Also, I emphasize the need for more landscape- to regional-scale, and long-term studies on wildlife-road interactions. Finally, I present a preview of the remaining chapters of this thesis, including a list of the hypotheses and predictions, a general description of the methodology, and a summary of the principal results and conclusions.*

Introduction

Conservation biology

The biodiversity crisis refers to the mass extinction event that is currently taking place across the globe (Myers 1979; Leakey & Lewin 1996; Singh 2002). This ongoing wave of extinctions is unlike any other in the fossil record in that it is primarily anthropogenic (Lawton & May 1995). Conservation biology is a relatively new field of science that arose primarily in response this current biodiversity crisis (Soulé 1986; Primack 2004). This field uses both applied and theoretical approaches to conserve rare species. While drawing on theory from many other fields, conservation biology also is a science whose principal focus is protecting species from extinction (Primack 2004), and it is this focus that separates it from other biological sciences that tend to be more utilitarian in nature.

Conservation biology has at least three principal goals (taken from Primack 2004):

1. to document the full diversity of the Earth's species,
2. to investigate the threats to biodiversity, and
3. to develop approaches to reduce or halt these threats.

Conservation biologists currently acknowledge at least seven global threats to biodiversity, including but not limited to, pollution, global climate change, overexploitation, exotic species, and loss, isolation and degradation of natural habitat, in no particular order (Soulé 1986; Primack 2004). It is the last three of these anthropogenic threats, collectively termed habitat fragmentation (sensu Wilcove et al. 1986), that I focus on in this thesis.

Habitat fragmentation

Of the threats listed above, fragmentation of natural communities is one of the most significant threats to populations of native species (Wilcox & Murphy 1985; Saunders et al. 1991; however, see Fahrig 2003). This global phenomenon includes two synergistic processes which are often difficult to separate: (1) direct habitat loss through the conversion of one habitat type into another, and (2), habitat subdivision, which, to varying degrees, isolates an individual or population from an area, whether it is a physical, behavioral, or psychological exclusion. In other words, habitat fragmentation partitions formerly continuous landscapes into smaller, potentially isolated patches, while also dividing resident wildlife populations into smaller subpopulations. These smaller and more isolated subpopulations in turn, become more susceptible to extirpation by a suite of demographic, genetic, and environmental events, including the loss of genetic diversity through drift and inbreeding, increased predation, edge effects, movement restrictions, reduced mating opportunities, and inadequate resource availability (Soulé 1986; Karieva 1987; Saunders et al. 1991; Andrén 1994; Gerlach & Musolf 2000).

Corridors

George Gaylord Simpson (1940, p149) described corridors as "…wide-open, nonselective connection[s]…" that allow bi-directional movements of a balanced diversity of fauna (Simpson 1940). Over the last few decades, Simpson's definition has been modified by conservation biologists. For example, Forman and Godron (1986) describe conservation corridors solely in a spatial context "…narrow strips of land which differ from the matrix… [and] are usually attached to a patch of somewhat similar vegetations". In contrast, Rosenberg and others (1997) require a more ecologically functional component to define a corridor, i.e., a corridor "… provides for movement between habitat patches…". Thus, a true conservation corridor, supposedly, must meet two criteria: form and function.

Since Simpson's work, corridors have been suggested as potential mitigation strategies for reducing the isolating effects of habitat fragmentation (Harris 1984; Saunders & Hobbs 1991; Beier 1993; Noss et al. 1996; Beier & Noss 1998). However, the utility of corridors in conservation has been debated (Simberloff et al. 1992; Rosenberg et al. 1997; Beier & Noss 1998). Opponents highlight their potential role in the spread of disease and exotic species, as potential population sinks, and as habitat for edge species (Simberloff et al. 1992).

Most of this debate stems from past studies that have provided species-specific recommendations for the optimal design of corridors. For example, contrary to Harrison's (1992) suggestion that wider corridors are more efficient, Andreassen and others (1996) found intermediate corridor widths to facilitate greater inter-patch movements of root voles (*Microtus oeconomus*) in southeast Norway. Laurance and Laurance (1999) found corridors of 30 - 40 m in width supported movements by most arboreal mammals in the Atherton Tableland of Queensland, Australia, except one species which required a corridor width minimum of 200 m. This same study also found different vegetation types within the corridor to facilitate movements of different species (Laurance & Laurance 1999). Similarly, Arnold and others (1991) found typical corridor habitat design recommendations to be inconsistent with kangaroo species' habitat requirements in western Australia, concluding that vegetated corridors restricted kangaroo movements (see also Lomolino et al. 2005 p. 167). Finally, based on non-volant mammal studies in the Olympic Peninsula of Washington, Perault and Lomolino (2000) suggested corridor effectiveness should be considered individually with attention given to the width and the surrounding habitat types, highlighting the influence of the surrounding landscape.

Roads

Roads are a significant contributor to habitat fragmentation, but function differently from more classical forms of fragmentation (e.g., deforestation) in that their isolation and barrier effects impact wildlife before their contribution to habitat loss becomes significant (Forman 2000; Forman & Deblinger 2000; Trombulak & Frissell 2000). Roads have a general filtering effect on wildlife, with the permeability of any single road varying with its particular characteristics (e.g., width, traffic volume, and characteristics of the adjacent habitat), and with the species' vagility or propensity to cross the road (Mader 1984; Saeki & MacDonald 2003; McDonald & St. Clair 2004; Ramp et al. 2005). This filtering effect acts in two principal ways: (1), by altering animal movements and, (2), as a direct mortality source (i.e. "road-kills") for individuals. Affected movements might include, daily activities, such as foraging behavior or territory maintenance, seasonal movements, such as mate selection or migratory behavior, or long term movements such as dispersal and range expansion (Spellerberg 1998; Sherwood et al. 2002; Forman et al. 2003). Road mortality has the potential to significantly reduce populations, thereby increasing the likelihood of extirpations due to the loss of genetic and demographic diversity, and increased susceptibility to environmental stochastic events (e.g., fires, floods, or disease outbreaks) (Forman & Alexander 1998; Trombulak & Frissell 2000).

Thus, because of the nature of these barrier effects, roads impact more than just their area (approximately 38,000 km^2 within the conterminous United States), in that their isolation effects are more a function of their length (6.2 million km with the conterminous United States) (Forman 2000).

Roads and mammals

Mammal species, like all other terrestrial animals, are subject to the ecological effects of roads and have received a good deal of attention in the literature. Forman (2003) estimated that 1 million vertebrates are road-killed annually on roads within the conterminous United States. Trombulak and Frissell (2000) suggested that “few if any terrestrial species of animal are immune” to the ecological effects of roads. Road fatality has been documented as the leading cause of mortality in many mammalian species, including Florida panthers (*Felis concolor coryi*) (Taylor et al. 2002), Eurasian lynx (*Lynx lynx*) (Schmidt-Posthaus et al. 2002), moose (*Alces alces*) (Bangs et al. 1989), European badgers (*Meles meles*) in Britain (Gallagher & Nelson 1979), eastern quolls (*Dasyurus viverrinus*), and Tasmanian devils (*Sarcophilus laniarius*) in northern Tasmania (Jones 2000).

The ecological impacts of roads also vary within species. For example, Coulson (1997) reported that males accounted for 65-92% of all road-killed individuals in six species of macropods in Australia. Road-kills also reflect seasonal and dial activity patterns of some species. For example, road-kills of the raccoon dog (*Nyctereutes procyonoides*) in Japan peaked in spring and fall months coinciding with their seasonal activity peaks (Saeki & Macdonald 2003), and road-kill patterns strongly reflected seasonal and dial activity patterns in armadillo (*Dasypus novemcinctus*) in central Florida (Inbar & Mayer 1999).

Not surprisingly, differential susceptibility to the ecological effects of roads reflects some species' avoidance of the road. For example, Lavallo and Anderson (1996) report that home ranges of bobcats (*Lynx rufus*) in Wisconsin exhibited a significant tendency to be located in sites with relatively low densities of secondary roads. Similarly, McLellan and Shakleton (1988) found that grizzly bears (*Ursus arctos*) in British Columbia and Montana used habitats near roads less frequently than habitat farther than 100 m from a road, but increased their activity near roads at night when traffic volumes were lower. Brody and Pelton (1989) suggested that black bears (*Ursus americanus*) in North Carolina also shifted their home ranges to avoid higher road densities and higher traffic volumes. Mladenoff and others (1995) found that eastern timber wolves (*Canis lupus lycaon*) in Wisconsin and Michigan exhibited a significant tendency to maintain territories at sites with relatively low road densities. For other examples of road avoidance by mammals, see Rondinini & Doncaster (2002) and Mader (1984).

Road mitigation

In response to the aforementioned negative impacts that roads have on wildlife, conservation biologists and transportation planners have developed several mitigation strategies. The most common approach is to erect fencing along the roadsides in an attempt to prevent wildlife from attempting to enter the road right-of-way (Forman et al. 2003). Few if any fences, however, are entirely effective in preventing road fatalities, as many species are able to dig beneath, pass through, or jump over the fencing. Even the most effective fences, while reducing mortality, do little to minimize the isolating effects of roads.

Other, largely experimental measures for reducing the ecological effects of roads include technologies to deter mammals from crossing the road and those to alert drivers to the presence of mammals within the adjacent habitat. For example, light reflectors, such as the Swareflex® reflectors, are designed to deflect some of the light from vehicle headlights into the surrounding habitat in an attempt to deter wildlife from approaching the road. There is little evidence however, to indicate that these reflectors are effective (Reeve & Anderson 1993). A similar approach is the use of sonic deterrents, such as the Shu Roo®, which produces an ultrasonic sound to alert kangaroos to oncoming traffic, but these too have received mixed reviews from tests of their effectiveness (Bender 2001). Animal crossing warning signs have been placed along road shoulders in order to increase the driver's awareness to the chance of an animal (usually a larger, game species such as deer) crossing the road, but their effectiveness has not yet been rigorously tested. Researchers in Washington, U.S.A., have taken this one step further by collaring elk (*Cervus elaphus*) with devices that will trigger yellow lights mounted on the warning signs to flash when the animal nears the road (Ament 2004).

Finally, perhaps the most promising mitigation approach is to construct wildlife underpasses (see Forman et al. 2003). Simply put, the purpose of a wildlife underpass (also called wildlife crossing structures, wildlife passages, ecopipes, and ecoculverts) is to reduce the number of vehicle caused mortalities while allowing cross-road movements, thereby increasing connectivity between two potential habitats (Forman et al. 2003).

Several studies have investigated the efficacy of wildlife underpasses in facilitating the movements of mammals, and concluded that larger, more natural looking wildlife underpasses are generally the most effective, provided they are placed in appropriate locations along the road (Foster & Humphrey 1995; Yanes et al. 1995; Rodriguez et al. 1996; Clevenger & Waltho 2000; Clevenger et al. 2001; McDonald & St. Clair 2004; Ng et al. 2004; Mata et al. 2005). However, these studies have considered different mammal species in different landscapes, making it difficult to assess optimal designs for wildlife underpasses. Also, most studies were conducted over a short temporal span, or often limited to a single season (e.g., spring or summer). Further still, the spatial extent of these studies usually did not extend to the landscape scale (Clevenger & Waltho 2003; Forman et al. 2003).

Spatial and temporal extent of typical road studies

The limited spatial and temporal extent of most studies of road-mammal interactions prompted some authors to call attention to the trade-off between the quality of the data and the extent of the study (Clevenger & Waltho 2003). A few studies, however, have used long-term data from road-kill databases maintained by transportation crews, which unfortunately suffer from inaccuracies in spatial data (e.g., most data collected in this manner lack geographic coordinates and usually use street names or townships) (Case 1978; Saeki & Macdonald 2003). On the other hand, most studies in which the data were collected systematically by the researchers using precise location information typically were limited to relatively smaller areas (Seibert & Conover 1991; Ashley & Robinson 1996).

Temporal issues, similar to those of spatial extents, arise when the study duration is relatively short. Specifically, many studies have been conducted within just one or two seasons (Hunt et al. 1987; Clevenger et al. 2001; Taylor & Goldingay 2003; McDonald & St. Clair 2004; Mata et al. 2005). In areas with colder climates, many species shift their home ranges and or adjust their foraging behaviors seasonally. Road-kill surveys become complicated when transportation crews remove snow (and, unintentionally, road-kills) from roads. Therefore, most road-kill based studies conducted in temperate climates are limited to non-winter field surveys. However, snow cover during winter provides a perhaps unrivaled opportunity to directly study successful, cross-road movements. Despite its great potential, no published studies on the ecological effects of roads have included snow tracking surveys. That is, most wildlife road crossing studies have relied solely on road-kill data, and have not incorporated extensive information on successful mammal road crossings.

The landscape influence

In order to reduce mortalities and the isolating effects of roads, conservation biologists and transportation planners need to better understand how mammal road crossing locations are affected by characteristics of the adjacent landscape. A number of studies reveal that landscape context has a strong influence on the natural history of mammals, including individual movement patterns and behaviors (Gross et al. 1995; Johnson et al. 2002; Kie et al. 2005). Individuals can minimize energy expenditure during movements by moving downhill, or by moving along natural contours of the landscape (e.g., elk, *Cervus elaphus* [Parker et al. 1984]). For example, Kie and others (2005) documented a significant relationship between elk movements and the landscape topography in Oregon, suggesting elk move more frequently along ridge lines and stream corridors. The influence of topography on individual movements creates a "funneling" effect, thereby channeling individuals through the landscape in somewhat predictable patterns (Malo et al. 2004). This funneling is often documented by relatively high numbers of road-killed individuals at particular locations, or "mortality hotspots" along a road (Bashore et al. 1985; Forman & Alexander 1998; Clevenger et al. 2003). Documented "mortality hotspots" can then be targeted for mitigation measures, especially under-road passageways, in order to reduce mortalities and facilitate natural movements, thereby contributing to the conservation of mammalian species.

Purpose

This study is designed to evaluate the hypothesis that wildlife movement patterns are influenced by major highways and by features of the adjacent landscape. More specifically, this study focuses on non-volant, terrestrial mammal movement patterns along Interstate 87 (I-87) within Adirondack Park of New York, United States. In order to evaluate this hypothesis, the following predictions will be tested:

Prediction 1. Wildlife road crossing locations along I-87 (as indicated by road-kills and snow tracking) will be significantly clustered in space, Prediction 2. The frequency of road crossings within a particular area will be associated with traffic volume and with characteristics of the adjacent landscape, including the following variables:

- the total length of streams,
- the total length of roads,
- the number of under-road passageways,
- the area of the highway right-of-way,
- the area of open water,
- the area of forested habitat, and
- the area of open habitat, and

Prediction 3. Mammalian usage rates of under-road passageways will be influenced by the characteristics of the under-road passageway and the surrounding landscape, including the following variables:

- the size of the under-road passageway opening,
- the amount of canopy closure at the under-road passageway,
- the frequency of water occurring within the under-road passageway,
- the proximity of the under-road passageway to other under-road passageways,
- the distance from the under-road passageway to the nearest forested cover,
- the amount of forested area near the under-road passageway,
- the topographic complexity of the landscape, and

- the geographic (easting and northing) location of the under-road passageway.

Methods

Detailed descriptions of the methods are presented in each of the remaining chapters. Here I describe the general approach of the field methods and some of the salient features of the study area.

Study area

Interstate 87 (I-87) is a four-lane, divided highway connecting Plattsburgh, New York with Albany, New York. I-87 passes for 144 kilometers through the eastern portion of Adirondack Park (Figure 1). The Park is a predominantly forested, 2.5-million hectare state park, dominated by northern hardwood tree species, including yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and eastern hemlock (*Tsuga canadensis*). The land within the Park is constitutionally protected by the State, of which, approximately 57% is privately owned by seasonal and permanent residents (Adirondack Park Agency 2003). The climate of the Adirondacks is relatively moist (96 cm of rainfall per year) and characterized by cool summers with a short growing season, and cold winters producing substantial snow pack (average January and July temperature -9°C and 20°C, respectively) (Thaler 2004). Road density within the Park is approximately 1 km of roads per km^2, 73% of which are rural (compared to 3 km of roads per km^2 outside the Park; Jenkins 2004). The Adirondack Mountains reach their highest elevations at 1600 m, however, most of the study site ranged between 150 and 500 m above sea level (Jenkins 2004).

Data collection and analyses

I collected field data between October 2004 and October 2005 along I-87 within Adirondack Park (northern edge 44°33' N, 73°30' W, southern edge 43°22' N, 73°43' W). The three principal data collection techniques included road-kill surveys, snow tracking surveys, and under-road passageway monitoring. I conducted road-kill surveys from a moving vehicle once per week on Saturday or Sunday. I conducted snow tracking surveys within 24-hours of a significant snowfall event from a moving vehicle. I monitored under-road passageways for the entire year using both infra-red triggered cameras and a track-plate structure.

I used ArcGIS 9 (Environmental Systems Research Institute 2004) to calculate all of the landscape variables from data gathered from a variety of sources. I calculated traffic volume estimates based on New York Department of Transportation annual traffic volume data (New York Department of Transportation 2004). I measured the characteristics of the under-road passageway during field visits. I wrote randomization programs in Microsoft Excel (Microsoft 2000). I performed all statistical analyses within SYSTAT 10.2 (SPSS 2002) or Xlstat (Addinsoft 2007).

Summary of Results and Conclusions

Road crossing locations

Forty-six road-kill surveys yielded 220 individuals of 19 different species of mammals. Four snow-tracking surveys recorded 116 successful road crossings by six different species of mammals. Both road-kill locations and snow track road crossing locations were significantly clustered in space. Further analyses revealed significant spatial clustering of road-kills for six mammal species detected more than 10 times. Significant spatial clustering of road crossing locations also occurred within each season, and for each lane of traffic. Most successful crosses were made by coyotes (*Canis latrans*), whose movements were significantly clustered in space for each lane. Locations of successful road crossings were not significantly associated with those of road-kill locations, suggesting these locations occur in different areas along I-87. In addition, the frequency of road-kills was significantly higher in areas with less under-road passageways, a greater total length of roads, a greater area of open habitat, and a lower area of forested habitat within a 2 km buffer width around I-87. Successful crossings, on the other hand, were positively associated with under-road passageways. That is, successful winter crossings occurred more often at sites in closer proximity to under-road passageways. This information, especially the knowledge that mammalian road crossings are spatially clustered and associated with features of the adjacent landscape, will help to identify prime locations for mitigation and optimal means for modifying roads and the adjacent landscape for wildlife in this and other regions.

Under-road passageway monitoring

Under-road passageway monitoring documented 823 passes by 19 mammal species. Muskrats (*Ondatra zibethicus*), northern raccoons (*Procyon lotor*), and red squirrels

(*Tamiasciurus hudsonicus*) were detected most frequently. There was no documented under-road passageway use by the three largest mammal species inhabiting the area – moose (*Alces* alces), white-tailed deer (*Odocoileus virginianus*), and black bear (*Ursus americanus*), even though five exceeded 2 m in width and height. Detection rates of mammals were higher at under-road passageways which were farther from the nearest forest edge and had more open canopies within the immediate vicinity, but also had more forested habitat within the adjacent landscape (500 m radius). Species richness of detections increased toward the north, and was higher for underpasses with more open canopies and with lower costs of moving through the adjacent landscape. Individual species also demonstrated significant responses to the geographic location, and the characteristics of the adjacent landscape and the under-road passageway. Under-road passageways in this region did facilitate mammalian movements, and their potential for mitigating the impacts of roads can be improved for focal mammal species by managing the local habitat and considering the adjacent landscape.

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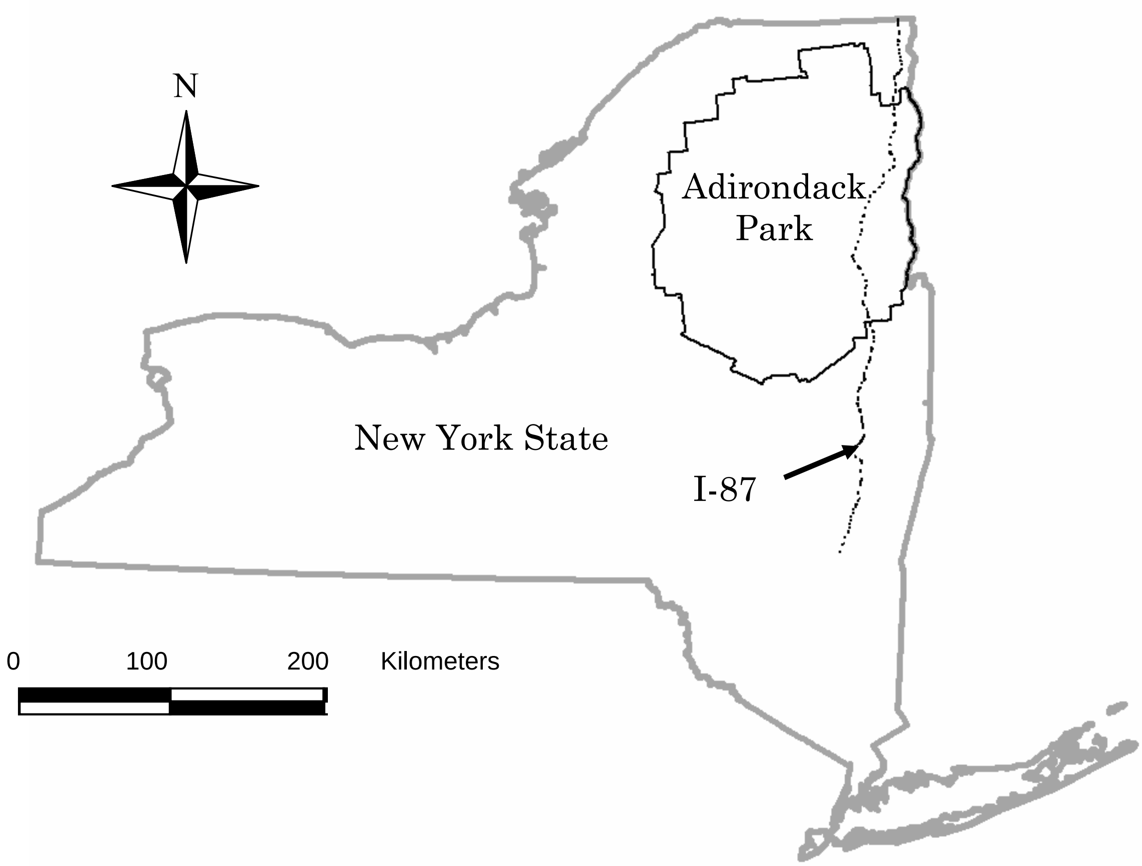
Figure 1. Map depicting the 144 km portion of Interstate 87 (I-87) within Adirondack Park of New York State, USA, that served as my study area. We documented mammalian road crossing patterns and their movements through 19 passageways from 17 October 2004 through 15 October 2005.Figure 1.



CHAPTER 2

Spatial distribution and landscape associations of mammalian road crossing locations along a major highway in Adirondack Park, New York, USA

Abstract

We conducted road-kill and snow tracking surveys for mammals along 144 km of an interstate highway (I-87) within Adirondack Park of New York State, USA, in order to evaluate the hypothesis that mammalian road mortalities and successful road crosses are influenced by characteristics of the highway and the adjacent landscape. Forty-six road-kill surveys conducted between 31 October 2004 and 22 October 2005, yielded 220 individual road-kills of 19 species of mammals, with striped skunk (*Mephitis mephitis*), northern raccoon (*Procyon lotor*), porcupine (*Erethrizon dorsatum*), and white-tailed deer (*Odocoileus virginianus*) being the most commonly detected species. Four snow tracking surveys conducted between 11 February 2005 and 3 March 2005, yielded 116 successful road crosses by seven species of mammals, with coyote (*Canis latrans*) and white-tailed deer being the most commonly detected species. Both unsuccessful and successful road crossing attempts were significantly spatially clustered, albeit along different sections of the highway. Road-kills tended to cluster in areas that had fewer under-road passageways, but more roads and open habitat in the surrounding landscape. On the other hand, successful crosses were not only much more likely (116 crosses versus 3 road-kills, when road-kills and snow tracking surveys were conducted simultaneously), but also tended to cluster in areas with more under-road passageways and forested habitat, but fewer roads and lower traffic volumes. Our results highlight the importance

of understanding where mammals are both successful and unsuccessful at crossing a major highway and the characteristics of the highway and the adjacent landscape at each of these locations.

1. Introduction

The 6.2-million kilometers of roadways cutting through the landscape ecologically impact approximately 20% of the total surface area of the United States (Forman, 2000). These roadways produce at least two significant, negative ecological impacts on mammals: barrier effects and direct mortalities (Forman and Alexander, 1998; Spellerberg, 1998; Trombulak and Frissell, 2000; Sherwood et al., 2002; Forman et al., 2003). Roads serve as barriers to animal movements, thereby fragmenting formerly continuous habitat and effectively isolating populations across once continuous landscapes (Oxley et al., 1974; Mader, 1984; Swihart and Slade, 1984; Brody and Pelton, 1989; Alexander and Waters, 2000; Dyer et al., 2002; Rondinini and Doncaster, 2002; McDonald and St. Clair, 2004; Riley et al., 2006). Direct mortality, chiefly through vehicle-animal collisions, or "road-kills", is perhaps one of the most obvious and best documented impacts (Case, 1978; Bangs et al., 1989; Seibert and Conover, 1991; Ferreras et al., 1992; Jones, 2000; Schmidt-Posthaus et al., 2002; Taylor et al., 2002; Saeki and Macdonald, 2004; Hell et al., 2005).

Much of the published studies on mammalian road-kills thus far, however, focus on a single taxon – ungulates (Puglisi et al., 1974; Reilly and Green, 1974; Fraser and Thomas, 1982; Bashore et al., 1985; Bangs et al., 1989; Romin and Bissonette, 1996; Putnam, 1997; Finder et al., 1999; Hubbard et al., 2000). Further, many studies only report anecdotal, albeit valuable, descriptions or tallies of road-kill locations along particular highways (i.e., the number of road-kills over a particular distance or over a period of time) (see Seibert and Conover, 1991; Clevenger et al., 2003; Hell et al., 2005). Such studies are insufficient if our goal is to better understand the relationships between mammalian road-crossing patterns and the surrounding landscape so that we might mitigate at least a fraction of the negative ecological effects of roads.

Because the energetic costs associated with locomotion vary with the physical characteristics (e.g., slope, cover type, etc.) of the landscape (Parker et al., 1984), individuals should prefer to move parallel to elevational contours and along riparian areas (Johnson et al., 2002; Kie et al., 2005). A better understanding of how these movement patterns relate to other landscape features, including roads and their adjacent habitats, is vital to the conservation of animal species. Unfortunately, only a few studies addressed these issues. Those that do, often identify non-random spatial clustering in mammalian road-kill locations, suggesting that landscape features influence movement patterns (Puglisi et al., 1974; Bashore et al., 1985; Finder et al., 1999; Hubbard et al., 2000; Clevenger et al., 2003; Saeki and Macdonald, 2004). Most of these studies focus on a single species (e.g., *Odocoileus virginianus* [Puglisi et al., 1974; Bashore et al., 1985; Finder et al., 1999; Hubbard et al., 2000], *Nyctereutes procyonoides* [Saeki and Macdonald, 2003], *Dasypus novemcinctus* [Inbar and Mayer, 1999]) or a single guild (e.g., small mammals [Clevenger et al., 2003]). A better understanding of how highway and landscape characteristics influence where mammals attempt to cross roads, both successfully and unsuccessfully, seems essential to the successful conservation of species inhabiting regions that are transected by major highways.

Unfortunately, there is a shortage of studies documenting the locations and frequency of successful mammalian road crossings in the published literature. Coupling road-kill data with successful road crossing data will allow us to calculate mammalian road crossing rates, versus simple tallies of unsuccessful crossing attempts. Further, knowing the crossing success rates for individual species, and the landscape and road characteristics influencing those movements, will increase our ability to mitigate many of the negative ecological impacts of roads within the landscape.

The purpose of this study is to document mammalian road crossing locations along a major highway and to evaluate the hypothesis that these locations are associated with features of the highway and the adjacent landscape. In order to evaluate this hypothesis, we tested the following predictions: (1) the locations of mammalian road crossing locations are significantly clustered in space, and (2) these locations are significantly associated with attributes of the highway and the surrounding landscape (Table 1). In order to test these predictions, we quantified successful and unsuccessful road crossing attempts made by non-volant mammals (through snow tracking and road-kill surveys, respectively) along a four-lane divided highway, within Adirondack Park of New York State, USA. We tested for spatial clustering of attempted road crossing locations and then tested for associations between these locations and the attributes of the highway and its surrounding landscape.

2. Methods

2.1 Study area

This study took place along a 144 km portion of Interstate 87, within Adirondack Park of New York State, USA (Fig. 1). Interstate 87 was constructed in 1965 as a four-lane, divided highway that passes north-south through the eastern portion of the Park connecting Albany (43°22' N, 73°43' W) in the south with Plattsburgh (44°33' N, 73°30' W) in the north. Within the study area, approximately 113 tunnels pass beneath I-87, serving a variety of purposes including storm drainage, vehicle passage, and pedestrian hiking trails. The highway receives approximately 30 000 vehicles per day at the southern extent of the study area, 9000 vehicles per day in the central portion, and 13 000 vehicles per day at the northern extent (Highway Data Services Bureau, 2004). The maximum speed limit is posted at 108 km per hour throughout the entire study area. The Adirondack Mountains reach their highest elevations at 1600 m, but within the study area the elevation ranges between 150 and 500 m above sea level (Jenkins, 2004).

Adirondack Park is a predominantly forested, 2.5-million ha state park located in northeastern New York State, USA. The Park is dominated by northern hardwood tree species, including yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and eastern hemlock (*Tsuga canadensis*). Approximately 51% of the land within the Park is privately owned by seasonal and permanent residents, and the public owns and manages approximately 43% of the remaining lands (Jenkins, 2004). The climate of the system is relatively moist (96 cm of rainfall per year) and characterized by cool summers with a short growing season, and cold winters producing substantial snow pack (average January and July temperature -9°C and 20°C, respectively) (Thaler, 2004). Road density within the Park is approximately 1 km of roads per km^2, 73% of which are rural (compared to 3 km of roads per km^2 throughout the remainder of the State) (Jenkins, 2004).

This study focused on non-volant, terrestrial mammal species with masses greater than 75 g known to occur in the Adirondack region (Table 2); species smaller than this were not detected during the study, presumably due to scavenging by other species. This includes twenty-six potentially detected species of mammals ranging in size from moose (*Alces alces*, 500 kg), black bear (*Ursus americanus*, 200 kg), white-tailed deer (*Odocoileus virginianus*, 100 kg), and coyote (*Canis latrans*, 20 kg), down to gray squirrel (*Sciurus carolinensis*, 550 g), red squirrel (*Tamiasciurus hudsonicus*, 200 g), eastern chipmunk (*Tamias striatus*, 100 g), and southern flying squirrel (*Glaucomys volans*, 75 g). None of these species are state protected, but twenty are game species and are considered harvestable (New York State Department of Environmental Conservation, 2003). Domestic cat (*Felis domesticus*) and domestic dog (*Canis familiaris*) were included in the analyses also.

2.2 Road crossing data collection

We documented road-kills and successful mammalian road crosses for one continuous year beginning on 31 October 2004 and ending on 22 October 2005.

Unsuccessful mammalian road crossing attempts, identified as road-kills, were documented while traveling in a vehicle along the north- and south-bound lanes of I-87. Road-kill surveys were performed weekly on Sundays, beginning at 0800 h due to above average traffic volumes that occurred on Fridays and Saturdays. Weekly traffic volume peaks were thought to increase the frequency of road-kills (see Romin and Bissonette, 1996; Clarke et al., 1998; Saeki and Macdonald 2004), thus performing the surveys immediately following these days should increase the sample size. We performed all road-kill surveys from a vehicle traveling at 66 km per hour (the minimum legal speed limit during snow-free conditions) in the right-hand lane (i.e., the lane nearest to the highway shoulder). The vehicle was stopped at all road-kill occurrences to identify the species, record the date and geographic location with a Garmin 12XL global positioning system (gps) unit (Garmin International Inc., Olathe, Kansas, USA), and to note the placement of the road-kill within the road. We only included road-kills located on the pavement in the analyses, thereby removing any biases which may be introduced by the increased relative probability of detecting larger species that fell in the unpaved, grassy roadsides.

We identified successful mammalian road crosses by conducting snow tracking surveys. We performed these surveys on four days beginning at 0800 h, between 11 February 2005 and 3 March 2005. These surveys were conducted within 24 h of a snowfall event during which at least 15 cm of snow accumulated over the entire study area. This requirement ensured that all previously recorded tracks were removed and would not be re-recorded. We located mammal tracks from a moving vehicle (50 – 55 km per hour) in the road shoulder. We conducted tracking surveys on foot along the study area, prior to data collection, to ensure the efficacy of conducting these surveys from a moving vehicle. We recorded tracks that were located within the right-of-way, which consists of the open, mowed area along the far sides of the highway (i.e., excluding the median). (We ignored tracks found within the median under the assumption that any tracks found in the median would also be detected in the right-of-way.) For each track occurrence, we recorded the date, species, direction of travel, geographic location with a gps unit, direction of traffic, and the result (i.e., successful cross, turn around, or road-kill) of the individual's attempt. We mapped sections of the right-of-way that were out of the field of view (e.g., steep banks, overpasses, etc.) during the snow tracking surveys in order to exclude these sections later during the spatial clustering analyses.

2.3 Analysis of spatial patterning

We analyzed results of successful road crossing attempts and road-kills separately. The width of the highway was constant (4-lanes) throughout the study area, therefore we treated the highway as a 1-dimensional transect along which all mammalian road crossing attempts were plotted. We tested for spatial clustering for each lane, for individual species for which we detected at least ten road crossing attempts (either successful or road-kill), and for all species combined.

We first tested for spatial clustering of road-kills over all surveys and all species combined. We measured the nearest neighbor distances between observed road-kill locations, calculated the median nearest neighbor distance (MNND), and then compared this value to the MNND calculated for an equal number of randomly distributed locations using macros created within Microsoft Excel (Microsoft Corporation, 2001, macros available upon request). We repeated this routine 1000 times, comparing each randomly generated MNND to the observed MNND after each run. Reported p-values for this analysis represent the number of times out of the 1000 runs that the randomly generated MNND was smaller than the observed MNND (i.e., observed crossing locations were farther apart than expected by chance). The median nearest neighbor distance was selected over the mean nearest neighbor distance after inspection of the histogram for nearest neighbor distances revealed that the data were heavily skewed. Successful crossing locations from snow tracking surveys were analyzed similarly, except that we excluded randomly generated locations that fell within areas that were out of view from the road (see above).

This MNND, randomization approach was chosen over alternative spatial analysis techniques for several reasons. The approach that we selected (MNND) produced a simple, quantitative method for determining whether the observed crossing locations were closer or farther from each other than what you would expect if they were randomly located. For the purposes of this study, it was not necessary to define and locate road mortality "hotspots" (i.e., variable distances within which significantly more road-kills occur than found in control sites) as other studies have done with the use of Ripley's K-function (Ripley, 1976) or K-means clustering (MacQueen, 1967) (see Clevenger et al., 2003; Ramp et al., 2005). Rather, we used MNND to determine if mammal road crossing locations were spatially nonrandom, which would suggest that the landscape is influencing these crossing locations. Further, Ripley's K-function and K-means clustering are dependent on user-defined scales and/or a desired number of clusters, producing results dependent upon the initial parameters.

2.4 Explanatory factors for crossing patterns

We tested for associations between mammalian road crossing locations (both successful and road-kills) and characteristics of the highway and the surrounding landscape by selecting eight continuous variables that may influence mammalian movements (Table 1). The study area was partitioned into 48, 3 km long segments. Partitioning the study area into segments of 3 km produced 48 sampling units which provided two things: (1) a post-hoc power analyses suggested that a sample size of 48 would provide a statistical power level of 0.811 to detect a correlation of 0.4, and (2) it captured a sufficient level of variation within key variables, such as the number of under-road passageways per segment (mean = 2.458, c.v. = 0.707, s.d. = 1.738).

We calculated values for each variable within a 1 km wide buffer created around each segment, producing observation units of 3 km^2 area. We believe this 1 km buffer appropriately characterized the extent at which the surrounding landscape influenced the movements of resident mammals, and captured a sufficient level of variability in the target environmental variables. To do this, we used the tabulate area function within the spatial analyst toolset of ArcGIS 9 (Environmental Systems Research Institute, 2004) to calculate the total area for the raster data layers (i.e., open and forested habitat, from the National Land Cover Data set available from the United States Geological Survey [1993]) within each segment. Next, we calculated the area of the right-of-way by digitizing ortho-images obtained from the New York State GIS Clearinghouse (2003 and 2004). We then used the hydrography data layer available from the Adirondack Park Agency (2001) to measure the total surface area of standing water within the study area. We used the road data set available from the Accident Location Information System

(2005) and the stream data set available from the New York State Department of Environmental Conservation (2001) to generate polyline layers specific for the study area. We calculated the area of the polygon layers that we created (i.e., right-of-way) with the polygon-return-area function within EasyCalculate 5.0 (Tchoukanski, 2004). We calculated the polyline layers that we created (i.e., road length and stream length) with the return-shape-length function within EasyCalculate 5.0 (Tchoukanski, 2004). Traffic volume values were reported by the Highway Data Services Bureau (2003), and we located and recorded the number of under-road passageways from field surveys of the study area.

All data analysis for this portion of the study was conducted within SYSTAT 10.2 (2002). We used Pearson's and Spearman's rank correlations to test for associations among independent variables, and between mammalian road crossing locations and these independent variables. When necessary, we transformed the data (either $\log_{10}$ or square root) in order to increase the normality and decrease the skewness and kurtosis of the data. We visually inspected the data, complemented with Anderson-Darling normality tests, to select the most appropriate transformation. Variables that were not satisfactorily transformed (i.e., area of forested habitat, length of streams, traffic volume, and area of the right-of-way) were analyzed separately with Spearman's rank correlations. Because independent variables were often correlated with each other (Table 3), we used Principal Component Analyses (PCA) to assess the combined influence of these variables on road crossing locations. We chose PCA over regression for two reasons: (1) PCA is not influenced by multi-collinearity among independent variables, and (2) PCA provides a better visualization of the relationships between all variables entered into the analyses.

3. Results

3.1 Frequency and species composition

Forty-six road-kill surveys, covering a total of 6624 km of I-87 surveyed yielded a total of 220 individuals of 19 identifiable species (0.033 road-kills per km surveyed; 4.78 road-kills per survey) (Table 4). The most frequently recorded species included striped skunk (*Mephitis mephitis*), northern raccoon (*Procyon lotor*), porcupine (*Erethizon dorsatum*), and white-tailed deer (Table 4). No road-kills for bat or small mammal species were recorded during this study, and we failed to detect any road-kills during three surveys (between 5 December 2004 and 16 January 2005). Also, river otter (*Lontra canadensis*), weasels (*Mustela erminea* and *M. frenata*), bobcat (*Felis rufus*), and black bear are known to occur in the study area, but were not recorded during road-kill surveys (Table 4).

The number of road-kills recorded per survey ranged between 0 and 15 (mean = 4.8). Road-kills were most frequently detected (n = 80) during the summer months (June –August), and least frequently detected (n = 11) during the winter months (December – February) (Fig. 2).

Four snow tracking surveys (576 km) yielded 116 successful mammalian road crossings (0.201 crosses per km surveyed, 29 crosses per survey) made by seven species between 11 February 2005 and 3 March 2005 (Table 5). The number of successful crosses by all mammal species combined, per survey, ranged between 15 and 38 (mean =

29; Fig. 3). Coyote were responsible for the majority of the successful crosses and white-tailed deer was the second most frequently recorded species (Table 5). Both the absolute and relative frequencies of movements by these two species, however, differed substantially among the four snow tracking surveys, with white-tailed deer movements dominating the first survey but not detected in either of the latter two surveys (Fig. 3).

3.2 Spatial patterning of mammalian road crossing locations

Mammalian road crossing locations, both unsuccessful and successful (as revealed by road-kills and snow tracking surveys, respectively), were spatially clustered ($p < 0.001$, randomization test), albeit along different regions of the highway (Table 6). Segments at the southern and northern edges of the study area experienced higher road-kill frequencies than the more centrally located segments (Fig. 4). Conversely, snow tracking surveys indicated that successful crossings tended to be clustered in the central portion of the study area (Fig. 4).

Analyses at the species level revealed that locations of road-kills were spatially clustered for seven of the eight species analyzed (Table 6). These results did not change regardless of whether we conducted separate analyses for the north- or south-bound lanes, or for the three seasons with adequate data (Table 6). Woodchuck (*Marmota monax*), gray squirrel, and white-tailed deer road-kills were more common in the southern sections of the highway, while porcupine and snowshoe hare road-kills were more common in the central and northern sections (Fig. 5). Striped skunk and northern raccoon road-kills were more common in the southern and northern extents of the highway (where human populations are highest), but were nearly absent from the central portions of the highway (Fig. 5).

Similarly, successful road crossing locations for the two species most commonly detected during snow tracking surveys (coyote and white-tailed deer), were also spatially clustered, albeit along different portions of the highway (Fig. 6; Table 6). Most crossings made by coyote occurred over central sections of the highway, while those of white-tailed deer were clustered within the central and northern sections of the highway (Fig. 6).

In addition to documenting successful crosses, snow tracking surveys also indicated that mammals often avoided particular portions of the highway, by either turning to travel parallel to the highway for substantial distances, or by turning back away from the highway to return to the adjacent habitat (Table 5). Mammals approached I-87 at 175 locations, 116 (66%) of these resulting in a successful cross (Table 5). Twenty-three (13%) of these approaches were followed by parallel movements and twenty-seven (15%) resulted in returns to the adjacent habitat (Table 5). On fourteen of the occasions where an individual moved parallel to the highway, it eventually crossed the highway at a point at least 100 m from the initial point of detection (Table 5). Interestingly, coyote was the most active species along the highway and was also more prone to cross the road after approaching I-87 (Table 5).

3.3 Characteristics of the highway and adjacent landscape

Locations of mammalian road-kills were positively correlated with the length of roads and the area of open (non-forested) habitat in the adjacent landscape, and negatively correlated with the number of under-road passageways per 3 km segment of the highway (Fig. 7; Table 7). Conversely, snow tracking surveys indicated that successful mammalian road crossing locations were positively associated with under-road passageways (Fig. 7; Table 7).

Principal Component Analysis produced three components (factors) which together explained 76% of the overall variance of the independent variables. Factor 1 explained 39% of the total overall variance and was a direct measure of the amount of open habitat and the length of roads, and an inverse measure of the amount of forested habitat and the number of under-road passageways (Table 8). Factor 2 explained 21% of the overall variance and was a direct measure of the area of the right-of-way and an inverse measure of traffic volume (Table 8). Factor 3 explained 17% of the overall variance and was a direct measure of the length of streams and an inverse measure of standing water surface area (Table 8).

Pearson's correlations of the factor scores and the dependent variables suggested that road-kills were positively associated with Factor 1, while successful crosses during winter were positively associated with Factor 2 and were negatively, but marginally ($p = 0.055$), associated with Factor 1 (Fig. 8, Table 9). The ordination plot in Figure 9 more clearly illustrates the combined influence of environmental factors on the locations of road-kills and successful crossings (Fig. 9). Road-kills tended to be clustered in areas that are characterized by relatively high traffic volumes, large expanses of open habitat, and a paucity of forested habitat and under-road passageways. In contrast, successful crosses tended to occur most often in areas near forested habitat and under-road passageways, but with relatively low traffic volumes and fewer roads in the surrounding landscape (Fig. 9).

4 Discussion

4.1 Species composition of road-kill and successful crossing frequencies and locations

Variation in frequency and distribution of road-kills was high, but predictable based on differences in the natural histories of the species. Road-kill locations for striped skunk, northern raccoon, and gray squirrel were more abundant in areas with higher road densities, demonstrating these species' association with residential areas in this region. High frequencies of striped skunk, northern raccoon, and porcupine road-kills could also be explained by the slow moving nature of each species, especially considering that the majority of the road-kills for these species were located in areas with higher traffic volumes. Similarly, Inbar and Mayer's (1999) study in Florida found road-kill locations of another slow moving species, nine-banded armadillo, to be highly correlated with traffic volume. Other species such as white-tailed deer and woodchuck may experience relatively high frequencies of road-kills due to their foraging behavior and habitat preferences, with both species commonly seen foraging within the grassy roadsides during this study. Puglisi et al.'s (1974) and Hubbard et al.'s (2000) studies in Pennsylvania and Iowa, respectively, also found that greater amounts of grassy roadside vegetation were related to higher frequencies of white-tailed deer road-kills.

Snow tracking suggested that coyote and white-tailed deer were the most active species along the highway during winter (Table 5). Snow tracking also suggested that white-tailed deer were usually foraging within the highway right-of-way, most likely in search of grass or salts from road de-icing activities (see Carbaugh et al., 1975; Fraser and Thomas, 1982). Coyote activity patterns along the highway may be explained, in part, by the species' opportunistic foraging behavior which may bring individuals to the highway in search of road-killed prey, or to hunt for prey in these open habitats. Snow tracking results support this conclusion as coyote were regularly documented traveling parallel to the highway, usually remaining within the bordering forested habitat, but often approaching the highway shoulder. Also, road-killed white-tailed deer carcasses found at two locations within the right-of-way were heavily fed upon by coyote (LaPoint, personal observation).

Comparisons of results for road-kill and snow tracking surveys revealed that despite mortalities, most crossing attempts by coyote and white-tailed deer were successful. During four simultaneous road-kill and snow tracking surveys, only one coyote and one white-tailed deer road-kill were detected, whereas 98 and 12 successful crosses were documented for these species, respectively. These high success rates may be attributed to the relatively large size and/or agility of these species, which may reduce the barrier effect of the highway to a less significant level than it might be for a smaller or less agile species.

4.2 Spatial patterns and associations

The locations of mammalian road-kills and successful crosses along the highway were spatially clustered ($p < 0.001$). This suggests that individuals are not approaching the highway at random locations. Rather, mammalian road crossing locations may be associated with particular features of the landscape. Finder et al.'s (1999) study in Illinois, found that white-tailed deer road-kills tended to occur where a riparian corridor crossed the highway. Clevenger et al. (2003) also found roadside topography within the Bow River Valley of Alberta, Canada to significantly influence the locations of small mammal road-kills. Understanding where mammalian road crossing locations are clustered is a necessary first step in order to identify the landscape and highway characteristics that influence these movements.

Road-kill locations for all species combined were more frequent in areas with more open habitat, higher road densities in the adjacent landscape, and fewer under-road passageways. The amount of open habitat and road density were highly correlated, most likely because open habitat was a measure of agricultural, pastoral, and residential land covers, and therefore their influence on road-kill locations can be considered simultaneously. Six of the eight most frequently road-killed species (striped skunk, northern raccoon, white-tailed deer, eastern gray squirrel, coyote, and woodchuck; Table 4) are known to prefer open or heterogeneous habitats in this region, which would increase their abundances in these areas (Kays and Wilson, 2002). It should not be a surprise to find higher road-kill frequencies in areas where species are more abundant. Also, residential areas may force dispersing individuals to travel farther distances, either in search of resources or mates, thereby increasing their chances of crossing the highway.

Encouragingly, the number of under-road passageways per 3 km of highway was negatively correlated with the number of road-kills, but positively correlated with the number of successful crosses. Monitoring of nineteen under-road passageways during a concurrent study yielded 823 detections of 19 species of mammals (see Chapter 3). Thus under-road passageways may reduce mortalities and enhance cross-road movements. Other studies also have documented mammalian utilization of under-road passageways along a variety of transportation corridors (e.g., Reed et al., 1975; Foster and Humphrey, 1995; Yanes et al., 1995; Rodriguez et al., 1996; Forman et al., 2003; Taylor and Goldingay, 2003; Ng et al., 2004; Mata et al., 2005). Similar to our findings, Clevenger et al. (2003) determined that small vertebrate road-kills occurred farther away from under-road passageways than would be expected by chance. Our results, however, may be the first to document that successful mammalian road crossings are also influenced by their proximity to under-road passageways.

Interestingly, road-kills were not significantly associated with the traffic volume, despite many reports of such an association detected by other studies (Romin and Bissonette, 1996; Inbar and Mayer, 1999; Saeki and Macdonald, 2004). There are however, numerous exceptions to this association in addition to our study (Case, 1978; Clevenger et al., 2003; Ramp et al., 2005). Considering the traffic volume along I-87, road-kill rates (0.016 per km) during this study were surprisingly low, especially compared to other studies (e.g., Hell et al. [2005] and Ashley and Robinson [1996] which reported rates of 0.042 and 0.041 road-kills per km, respectively, despite having lower traffic volumes). The relatively low road-kill rates reported here may be attributed, in part, to an artifact: snow removal activities by transportation crews, which occurred on several occasions between 5 December 2004 and 26 March 2005. However, we believe the influence of this potential artifact was minimal, partly due to the infrequency of these activities during this study and because very few road-kills were detected even when no snow removal activities had occurred since the previous survey. Snow tracking suggested that individuals were more likely to turn away from the highway and re-enter the adjacent habitat in areas along I-87 that experienced relatively higher traffic volumes. This suggests that, paradoxically, more heavily traveled highways may experience lower reported road-kill rates due to an apparent reluctance to cross the highway, thereby reducing the probability for a road-kill occurrence (see Clarke et al. 1998; Clevenger et al. 2003).

In contrast to our results for road-kills, successful crosses were inversely correlated with traffic volume and directly correlated with the area of the right-of-way (Fig. 8; Table 8 and 9). That is, these mammals were more likely to cross the highway in areas where there was less traffic, and where motorists most likely had greater visibility of the road shoulder.

4.3 Conclusions

Features of the highway and the adjacent landscape significantly influence both the attempts and success of cross-highway movements by mammals. Both attempted and successful road crosses are significantly clustered in space, each being associated with particular, albeit different, features of the highway and the adjacent landscape.

A special feature of this research is that we were able to document spatial patterning of mammalian road crossing locations using exact geographic locations, over a large extent of a major highway (144 km). While still informative, most other studies have been conducted over more limited areas and relied on less precise spatial data, often only specific to road names or townships (Puglisi et al., 1974; Reilly and Green, 1974, Carbaugh et al., 1975; Case, 1978; Ashley and Robinson, 1996; Romin and Bissonette, 1996; Finder et al., 1999; Hubbard et al., 2000; Saeki and Macdonald, 2004; Hell et al., 2005). Also, unlike many of the previously mentioned studies, this study was conducted over one continuous year, thus avoiding any seasonal biases regarding the location of mammalian road crossing attempts.

These results also highlight the importance of understanding not only where road-kills occur, but also knowing where mammals successfully cross roads and the characteristics of the highway and adjacent habitat at these locations. Further, understanding that successful road crossing locations are indeed associated with characteristics of the highway and surrounding landscape, and that these associations are different from those which are associated with relatively high road-kill frequencies, provides extremely valuable information for efforts designed to mitigate the effects of roads on mammalian species.

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Fig. 1 – Map depicting the 144 km portion of Interstate 87 within Adirondack Park of New York State, USA, along which mammalian road crossing locations were mapped between October 2004 and 2005.

Fig. 2 – Frequency of mammalian road-kill occurrences (N = 220) documented during 46 surveys along 144 km of Interstate 87 within Adirondack Park, New York State, between October 2004 – 2005.

Fig. 3 – Species composition of successful mammalian road crossing attempts (N = 116) detected during four winter tracking surveys along 144 km of Interstate 87 within Adirondack Park, New York State, during February and March 2005. Number of successful crosses indicated above each bar.

Fig. 4 – Locations of mammalian road-kills and successful crosses varied spatially and were significantly clustered ($P < 0.001$, randomization test) along 144 km of Interstate 87 within Adirondack Park, New York State, between October 2004 and 2005. Shading is proportional to the frequency of road-kills or successful crosses during winter, which varied from 0 to 16 and 0 to 14 per 3 km segment, respectively.

Fig. 5 – Road-kill locations of seven mammalian species commonly detected ($n \geq 10$) demonstrated significant spatial patterning ($P < 0.05$, randomization test) after 46 surveys along 144 km of I-87 within Adirondack Park, New York State, between October 2004 and 2005. Sample sizes and spatial clustering analysis results are presented in Table 6.

Fig. 6 – Successful road crossing locations of coyote and white-tailed deer demonstrated significant spatial patterning ($P < 0.001$, randomization test) after 4 snow tracking surveys along 144 km of I-87 within Adirondack Park, New York State, during February and March 2005. For sample sizes and spatial clustering analysis results see Table 4.

Fig. 7 – The frequency of mammalian road-kills and successful road crossings per 3 km segment (N = 48) of Interstate 87 (I-87) were significantly correlated with three of the eight landscape and highway variables measured along 144 km of I-87 within Adirondack Park, New York State, between October 2004 and 2005.

Fig. 8 – Relationships between factors generated by Principal Component Analyses on the landscape and highway variables, and the frequency of mammalian road-kills and successful road crossings per 3 km segment (N = 48) of Interstate 87 (I-87) within Adirondack Park, New York State between October 2004 and 2005. See Table 7 for factor loading scores.

Fig. 9 – Principal Component Analysis factor loading plot demonstrating the relationships between mammalian road-kills and successful crosses and the landscape and highway variables measured for each 3 km segment (N = 48) along Interstate 87 within Adirondack Park, New York State, between October 2004 and 2005. See Table 7 for variable descriptions, weight values, and factor components.

Table 1 - Landscape and highway characteristics analyzed to explain mammalian road crossing patterns along 144 km of Interstate 87 within Adirondack Park, New York State, between October 2004 and 2005. Each variable was measured within a 1 km wide buffer along 3 km segments of the highway.

Variable name	Description	Source (Date)
Landscape		
Road Length	Length (m) of public roads (excluding I-87) within this segment	ALIS[1] (2005)
Stream	Length (m) of streams within this segment	NYSDEC[2] (2001)
Water	Surface area (m^2) of standing water within this segment	APA[3] (2001)
Forest	Surface area (m^2) of forested habitat within this segment	USGS[4] (1993)
Open	Surface area (m^2) of open habitat within this segment	USGS[4] (1993)
Highway		
Traffic Volume	Number of vehicles on I-87 per day within this segment	NYSDOT[5] (2003)
Under-road Passageways	Number of under-road passageways in this segment	Field survey[6] (2004)
Right-of-way	Surface area (m^2) of open area (maintained by the DOT)	NYSDOP[7] (2003-2004)

[1] Accident Location Information System

[2] New York State Department of Environmental Conservation

[3] Adirondack Park Agency

[4] United States Geological Survey

[5] New York State Department of Transportation

[6] Located by the author during field surveys

[7] New York State Digital Orthoimagery Program

Table 2 – Non-volant, terrestrial mammalian species (mass > 75 g) considered residents of Adirondack Park, New York State, USA.

Common name	Latin name	Habitat	Body size (kg)
Virginia opossum	*Didelphis virginiana*	Forest / Open	2.8
Coyote	*Canis latrans*	Forest / Open	18.0
Red fox	*Vulpes vulpes*	Open	5.0
Gray fox	*Urocyon cinereoargenteus*	Forest	5.5
Black bear	*Ursus americanus*	Forest	200
Northern raccoon	*Procyon lotor*	Forest / Open	9.9
American marten	*Martes americana*	Forest	0.7
Fisher	*Martes pennanti*	Forest	3.4
Ermine	*Mustela erminea*	Forest / Open	0.1
Long-tailed weasel	*Mustela frenata*	Forest / Open	0.4
Mink	*Mustela vison*	Forest / Water	1.7
Striped skunk	*Mephitis mephitis*	Forest / Open	3.8
River otter	*Lontra canadensis*	Forest / Water	17.6
Bobcat	*Lynx rufus*	Forest	8.6
White-tailed deer	*Odocoileus virginianus*	Open	81.0
Moose	*Alces alces*	Forest	410
Eastern chipmunk	*Tamias striatus*	Forest	0.09
Woodchuck	*Marmota monax*	Open	23.0
Gray squirrel	*Sciurus carolinensis*	Forest / Open	0.57
Red squirrel	*Tamiasciurus hudsonicus*	Forest	0.2
Southern flying squirrel	*Glaucomys volans*	Forest	0.06
Beaver	*Castor canadensis*	Water	20.4
Muskrat	*Ondatra zibethicus*	Water	1.2
Porcupine	*Erethizon dorsatum*	Forest	6.8
Eastern cottontail	*Sylvilagus floridanus*	Open	1.1
Snowshoe hare	*Lepus americanus*	Forest	1.6

Table 3 – Correlation coefficient matrix between landscape and highway variables used as explanatory factors for mammalian road crossing locations along 144 km of Interstate 87 within Adirondack Park, New York State, between October 2004 and 2005 (Pearson's correlation test, except where indicated when Spearman's rank correlation test was used).

Variable	Roads[1]	Water[2]	Forest[3a]	Open[4]	Streams[5a]	Traffic Volume[6a]	U-R P[7]
Roads[1]							
Water[2]	0.030						
Forest[3a]	-0.719**	-0.139					
Open[4]	0.562***	0.081	-0.684**				
Streams[5a]	-0.315*	-0.352*	0.383**	-0.283			
Traffic Volume[6a]	0.598**	0.080	-0.368**	0.108	-0.233		
U-R P[7]	-0.426**	0.144	0.308**	-0.382	0.070	-0.430**	
Right-of-way[8a]	0.111	-0.047	-0.348*	0.414**	-0.125	-0.247	-0.049

[a] Spearman's rank correlation test was used on non-normally distributed variables (based on visual inspection and Anderson-Darling's normality test).

[1] Length of roads (excluding I-87).

[2] Surface area of standing water.

[3] Area of forested habitat.

[4] Area of open habitat.

[5] Length of streams.

[6] Traffic volume.

[7] Number of under-road passageways.

[8] Area of I-87 right-of-way.

* p-value is < 0.05; ** p-value is < 0.01; *** p-value is < 0.001

Table 4 – Occurrences of mammalian road-kills during 46 surveys along 144 km of Interstate 87 within Adirondack Park, New York State, between October 2004 and 2005.

Common name	Scientific name	Road-kills (%)	Number of surveys detected (%)
Striped skunk	*Mephitis mephitis*	40 (18)	18 (39)
Northern raccoon	*Procyon lotor*	38 (17)	21 (46)
Porcupine	*Erethizon dorsatum*	23 (10)	15 (33)
White-tailed deer	*Odocoileus virginianus*	22 (10)	15 (33)
Eastern gray squirrel	*Sciurus carolinensis*	17 (8)	11 (24)
Coyote	*Canis latrans*	13 (6)	11 (24)
Snowshoe hare	*Lepus americanus*	10 (5)	7 (15)
Woodchuck	*Marmota monax*	10 (5)	8 (17)
Red fox	*Vulpes vulpes*	8 (4)	7 (15)
Virginia opossum	*Didelphis virginiana*	7 (3)	6 (13)
Gray fox	*Urocyon cinereoargenteus*	7 (3)	5 (11)
Mink	*Mustela vison*	5 (2)	4 (9)
Eastern cottontail	*Sylvilagus floridanus*	5 (2)	5 (11)
Beaver	*Castor canadensis*	4 (2)	3 (7)
Domestic cat	*Felis domesticus*	3 (1)	3 (7)
Red squirrel	*Tamiasciurus hudsonicus*	3 (1)	3 (7)
Fisher	*Martes pennanti*	2 (1)	1 (2)
Muskrat	*Ondatra zibethicus*	2 (1)	1 (2)
Domestic dog	*Canis familiaris*	1 (<1)	1 (2)
Totals		220	46

Table 5 – Description and frequency of mammalian movements detected during four winter snow tracking surveys conducted along 144 km of Interstate 87 within Adirondack Park, New York State, during February and March 2005.

Common name	Latin name	Number of surveys detected	Approaches	Crosses	Parallel movements[a]	Turn-backs
Coyote	*Canis latrans*	4	141	98	18	17
White-tailed deer	*Odocoileus virginianus*	3	20	12	4	4
Mink	*Mustela vison*	3	4	2	0	1
Domestic cat	*Felis domesticus*	1	1	1	0	0
Fox	Fox spp.	2	2	1	1	0
American marten	*Martes americana*	1	1	1	0	0
Red fox	*Vulpes vulpes*	1	1	1	0	0
Red squirrel	*Tamiasciurus hudsonicus*	1	1	0	0	1
Weasel	*Mustela* spp.	2	4	0	0	4
Totals		4	175	116	23	27

[a] Indicates the frequency at which individuals traveled along the side of (parallel to) Interstate 87 before either crossing or turning around and thus failing to cross.

Table 6 – The locations of road-kills, and those of successful crossing attempts during winter were both significantly spatially clustered for most mammal species, for both lanes of travel, and during all seasons except winter. N = sample size; EMNND = expected median nearest neighbor distances; MNND = observed median nearest neighbor distance (both measured in meters); p = p-value based on randomization tests. Clustering analyses were limited to species with ten or more occurrences (see Methods).

	Unsuccessful			Successful		
Variable	N	EMNND	MNND (p)	N	EMNND	MNND (p)
Species						
All mammal species	220	233.8	160.9 (<0.001)	116	369.6	89.4 (<0.001)
Striped skunk	40	1303.9	482.8 (0.001)			
Northern raccoon	38	1368.9	482.8 (0.001)			
Porcupine	23	2318.7	885.1 (0.006)			
White-tailed deer	22	2398.8	804.7 (0.014)	12	4390.3	160.9 (<0.001)
Gray squirrel	17	3156.3	885.1 (0.012)			
Coyote	13	4117.1	2413.9 (0.162)	98	443.2	160.9 (<0.001)
Woodchuck	10	5581.5	482.8 (0.002)			
Snowshoe hare	10	5565.4	321.9 (0.001)			
Lane						
North Lane	133	385.3	160.9 (<0.001)	72	631.4	42.3 (<0.001)
South Lane	87	588.4	321.9 (0.002)	44	1071.6	353.7 (<0.001)
Season						
Spring	77	671.9	321.9 (0.001)			
Summer	74	688.0	482.8 (0.046)			
Fall	56	914.9	321.9 (<0.001)			
Winter	13	4172.3	1770.2 (0.520)			

Table 7 – Correlation matrix (Pearson's correlation test or Spearman's rank correlation test when indicated) for landscape and highway variables associated with the locations of mammalian road-kills and successful road crosses during winter, along 144 km of Interstate 87 (I-87) within Adirondack Park, New York State, between October 2004 and 2005. Each variable was measured within a 1 km wide buffer along each 3 km segment of I-87.

Variable	Road-kill[1]	Successful Cross[2]	Roads[3]	Water[4]	Forest[5a]	Open[6]	Streams[7a]	Traffic Volume[8a]	U-R P[9]	Right-of-way[10a]
Road-kill[1]		-0.161	0.506**	-0.144	-0.529	0.500**	-0.232	0.191	-0.327*	0.223
Successful Cross[2]	-0.161		-0.274	-0.027	0.191	-0.127	-0.023	-0.283	0.343*	0.064

[a] Spearman's rank correlation test was used for non-normally distributed variables (based on visual inspection and Anderson-Darling's normality test).

[1] Number of mammalian road-kills per 3 km segment of I-87.

[2] Number of successful mammalian road crosses per 3 km segment of I-87.

[3] Length of roads (excluding I-87).

[4] Surface area of standing water.

[5] Area of forested habitat.

[6] Area of open habitat.

[7] Length of streams.

[8] Traffic volume.

[9] Number of under-road passageways.

[10] Area of I-87 right-of-way.

* p-value is < 0.05; ** p-value is < 0.001

Table 8 – Loading weights from Principal Component Analysis for each landscape and highway variable measured per 3 km segment (N = 48) of Interstate 87 (I-87) within Adirondack Park, New York State.

Variable	Factor 1	Factor 2	Factor 3
Forest[1]	-0.866	-0.195	0.079
Open[2]	0.830	0.394	0.191
Roads[3]	0.815	-0.324	-0.104
Under-road Passageways[4]	-0.612	0.374	-0.278
Traffic Volume[5]	0.503	-0.782	-0.030
Right-of-way[6]	0.459	0.704	0.414
Water[7]	0.132	0.338	-0.779
Streams[8]	-0.370	-0.061	0.672
% Variance explained	38.7	20.7	17.0

[1] Area of forested habitat.

[2] Area of open habitat.

[3] Length of roads (excluding I-87).

[4] Number of under-road passageways.

[5] Traffic volume.

[6] Area of I-87 right-of-way.

[7] Surface area of standing water.

[8] Length of streams.

Table 9 – Pearson correlations between the first three factors generated by Principal Component Analyses and the frequency of mammalian road-kills and successful road crosses per 3 km segment (N = 48) along Interstate 87 (I-87) within Adirondack Park, New York State between October 2004 and 2005.

Variable	Factor 1	Factor 2	Factor 3
Road-kill[1]	0.589**	-0.058	0.112
Successful Cross[2]	-0.279~	0.331*	0.026

[1] Number of mammalian road-kills per 3 km segment of I-87.

[2] Number of successful mammalian road crosses per 3 km segment of I-87.

~ p-value is < 0.10; * p-value is < 0.05; ** p-value is < 0.001

Fig. 1 – Map depicting the 144 km portion of Interstate 87 (I-87) within Adirondack Park of New York State, USA, along which mammalian road crossing locations were mapped between October 2004 and 2005.

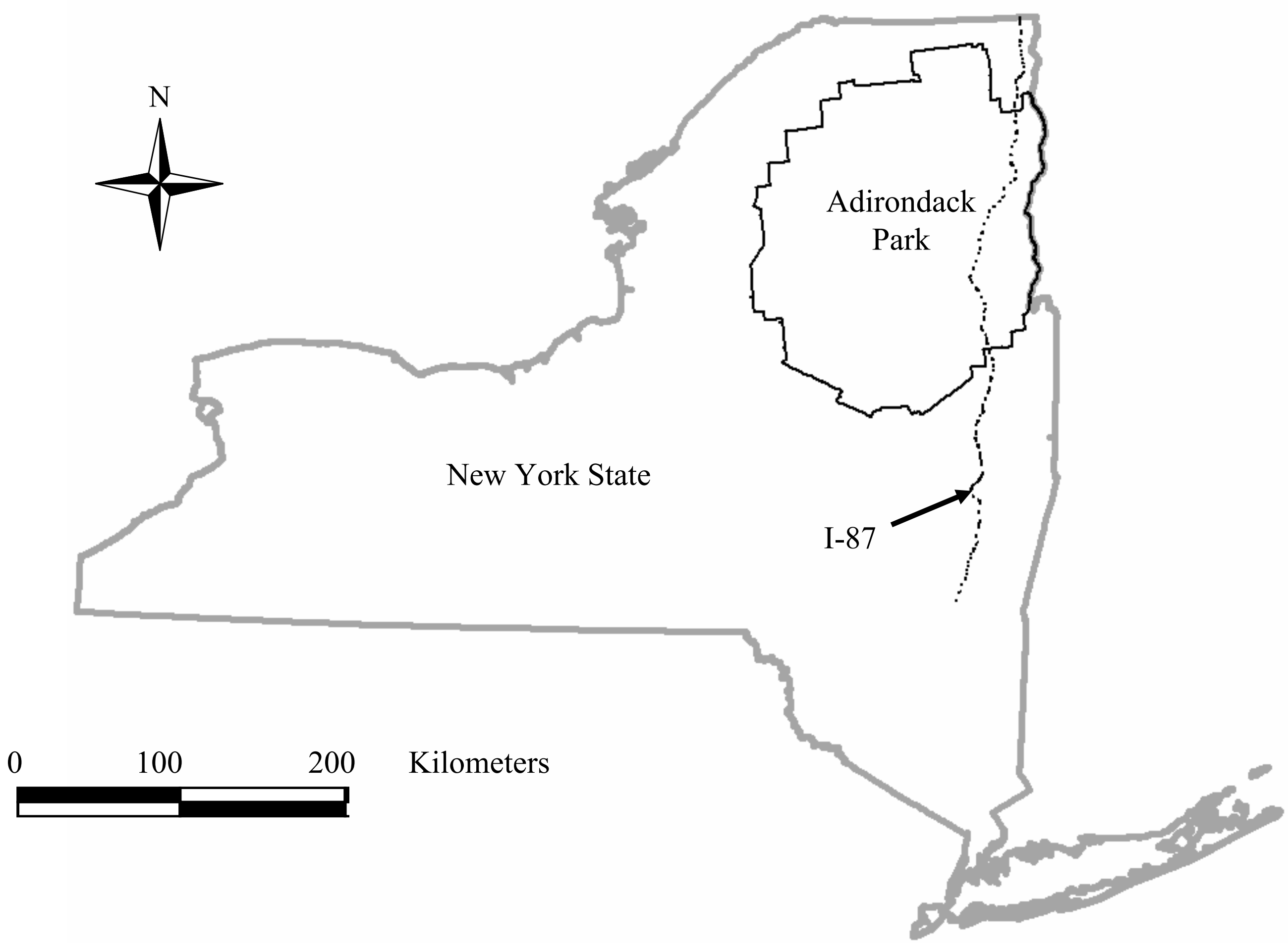


Fig. 2 – Frequency of mammalian road-kill occurrences (N = 220) documented during 46 surveys along 144 km of Interstate 87 within Adirondack Park, New York State, between October 2004 – 2005.

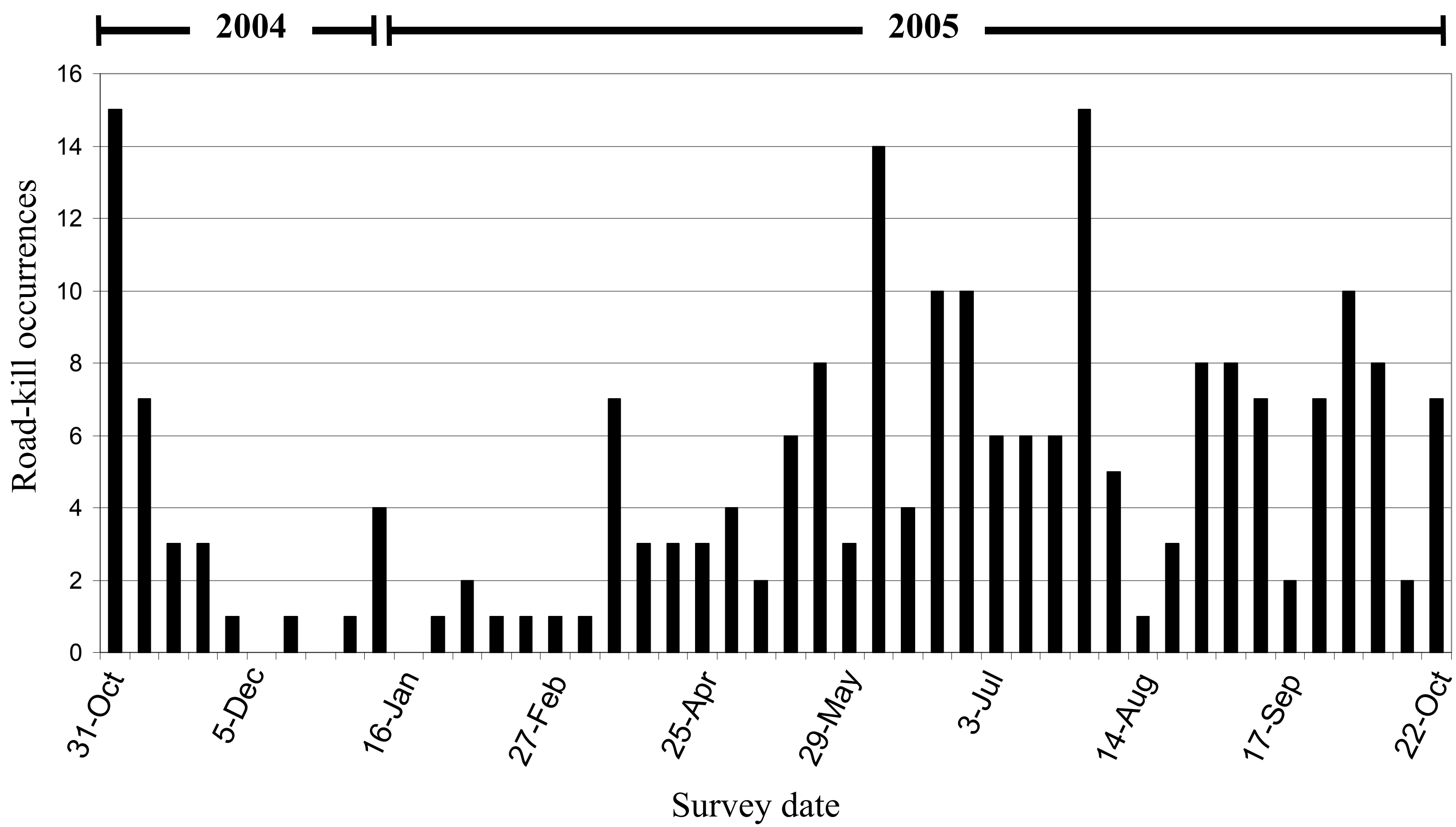
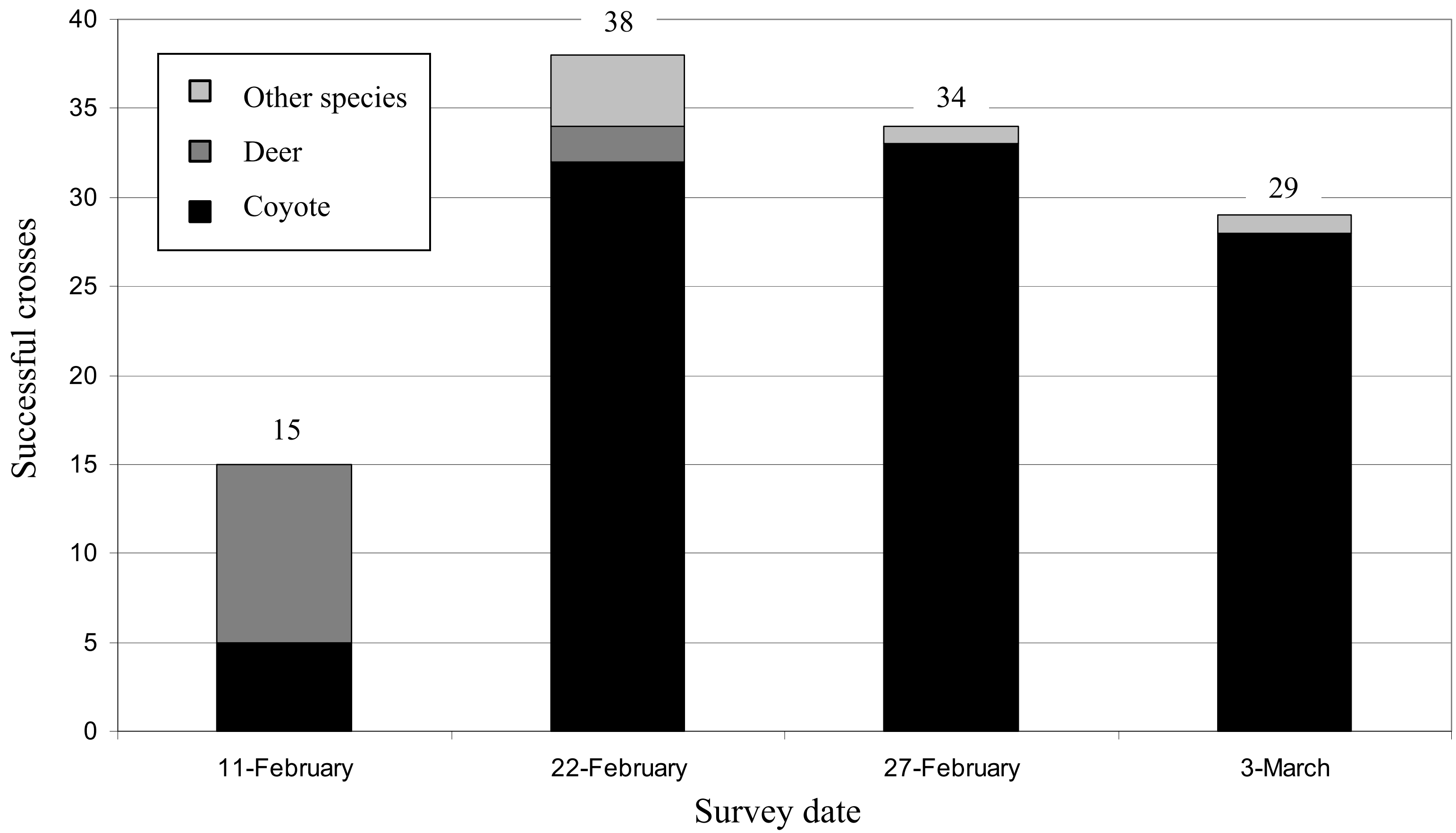


Fig. 3 – Species composition of successful mammalian road crossing attempts (N = 116) detected during four winter tracking surveys along 144 km of Interstate 87 within Adirondack Park, New York State, during February and March 2005. Number of successful crosses indicated above each bar.



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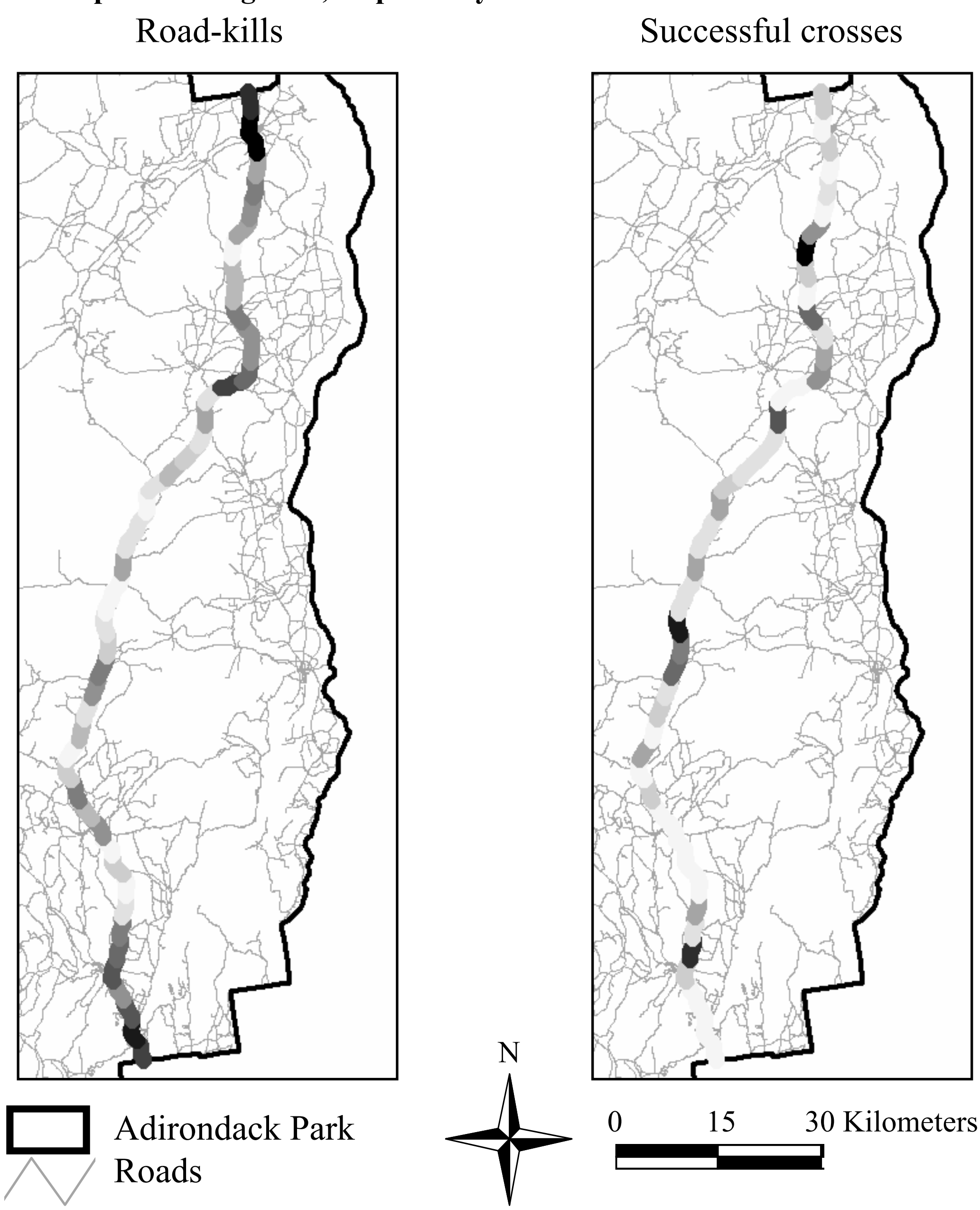


Fig. 5 – Road-kill locations of seven mammalian species (n ≥ 10) demonstrated significant spatial patterning ($p < 0.05$, randomization test) after 46 surveys along 144 km of I-87 within Adirondack Park, New York State, between October 2004 and 2005. Sample sizes and spatial clustering analysis results are presented in Table 6.

Fig. 6 – Successful road crossing locations of coyote and white-tailed deer demonstrated significant spatial patterning ($p < 0.001$, randomization test) after 4 snow tracking surveys along 144 km of I-87 within Adirondack Park, New York State, during February and March 2005. For sample sizes and spatial clustering analysis results see Table 4.

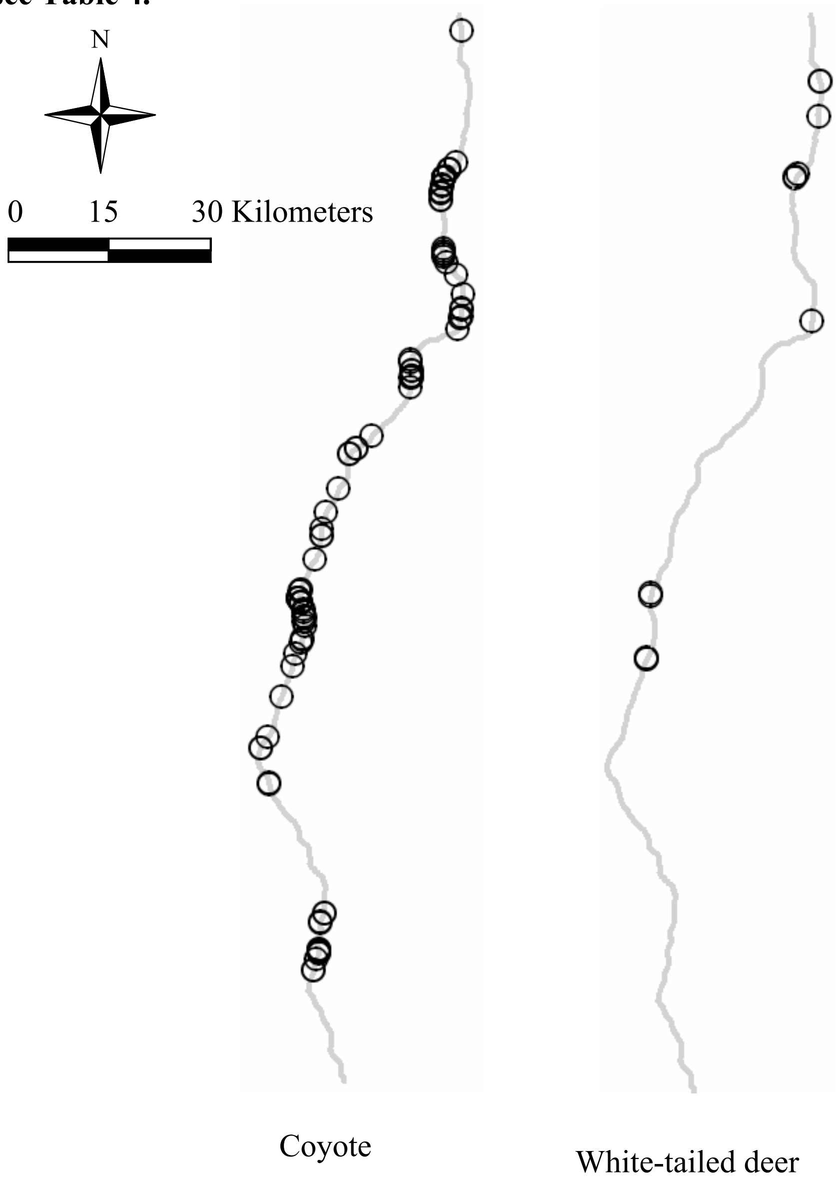
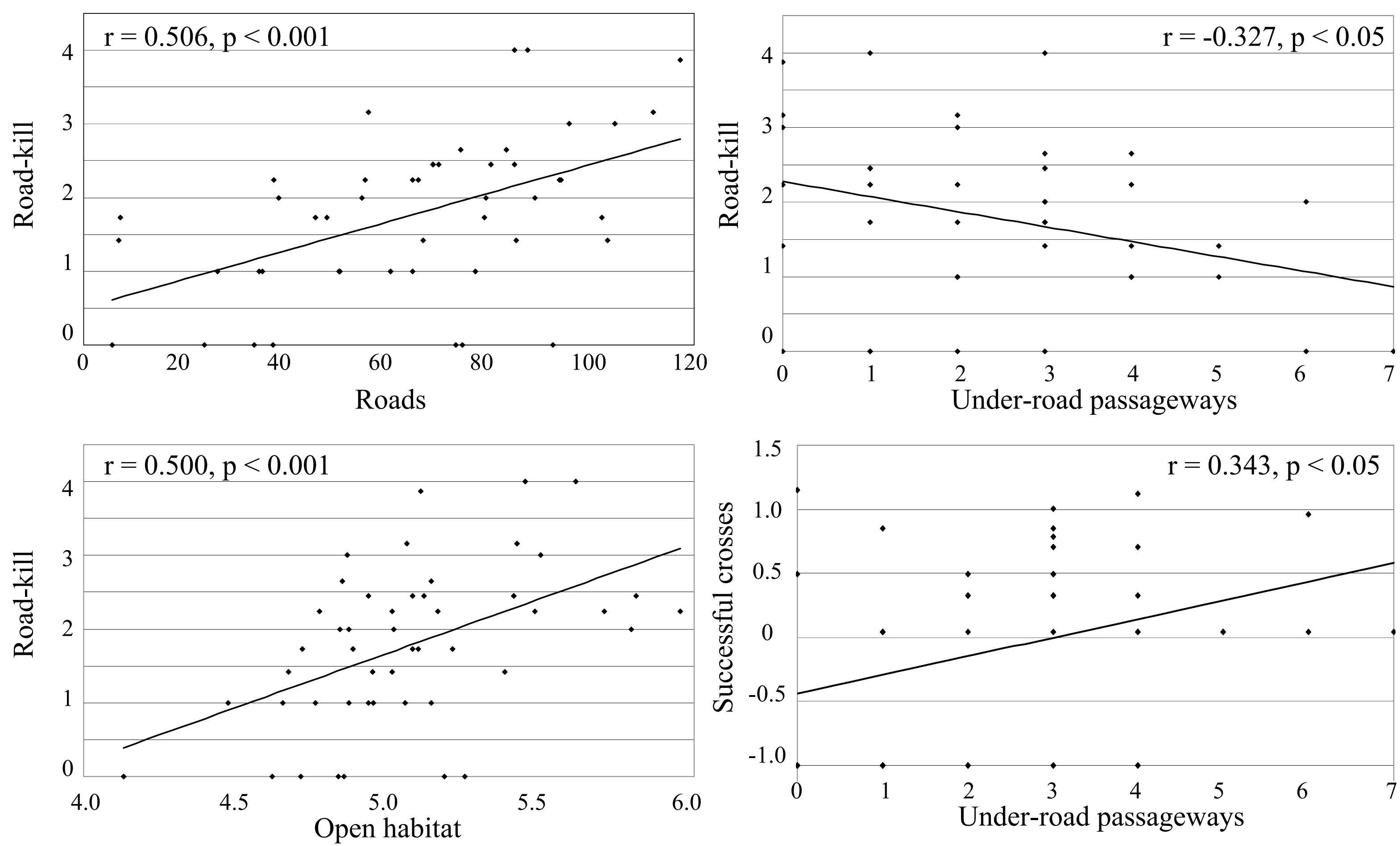


Fig. 7 – The frequency of mammalian road-kills and successful road crossings per 3 km segment (N = 48) of Interstate 87 (I-87) were significantly correlated with three of the eight landscape and highway variables measured along 144 km of I-87 within Adirondack Park, New York State, between October 2004 and 2005.



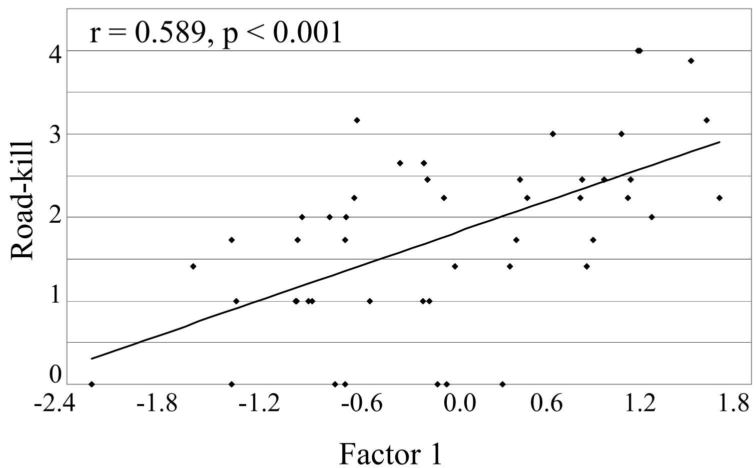


Figure 8 – Relationships between factors generated by Principal Component Analyses on the landscape and highway variables, and the frequency of mammalian road-kills and successful road crossings per 3 km segment (N = 48) of Interstate 87 (I-87) within Adirondack Park, New York State between October 2004 and 2005. See Table 7 for factor loading scores.

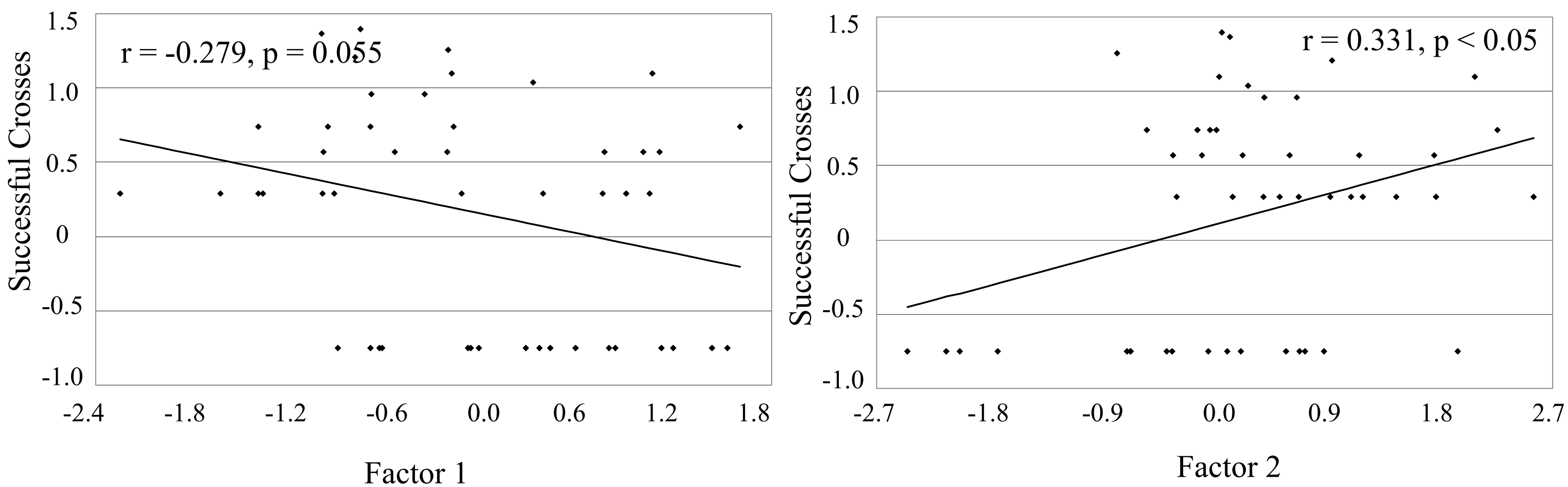
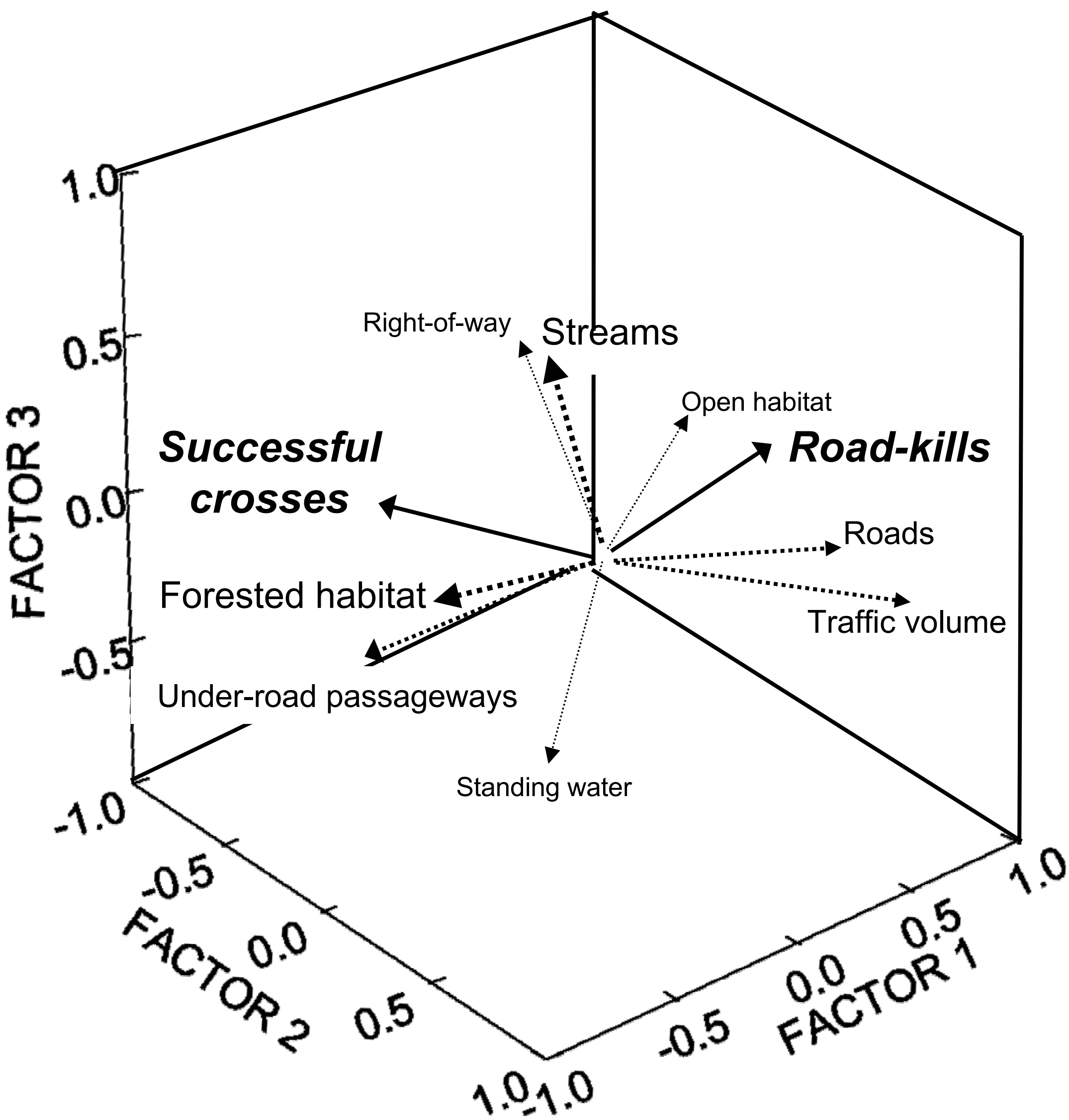


Figure 9 – Principal Component Analysis factor loading plot demonstrating the relationships between mammalian road-kills and successful crosses and the landscape and highway variables measured for each 3 km segment (N = 48) along Interstate 87 within Adirondack Park, New York State, between October 2004 and 2005. See Table 7 for variable descriptions, weight values, and factor components.



CHAPTER 3

Associations between mammalian use of underpasses and local and landscape characteristics within Adirondack Park, New York, USA

Abstract

The millions of roads bisecting the landscape are an integral component of our society, but unfortunately have numerous negative impacts on wildlife. Although mitigation strategies, such as wildlife underpasses, are being developed to help reduce some of these impacts, there is still much to learn regarding their efficacy in facilitating wildlife movements. We investigated mammalian responses to local and landscape characteristics of underpasses along Interstate 87 (I-87) within Adirondack Park of New York State, USA. We used track-plates and infra-red triggered cameras to detect mammalian movements within 19 passageways beneath I-87 from 17 October 2004 to 15 October 2005. We recorded 823 detections, including those from 19 species. Detection rates of mammals were higher at passageways which were farther from the nearest forest edge and had more open canopies within the immediate vicinity, but also had more forested habitat within the adjacent landscape (500 m radius). Species richness of detections increased toward the north, and was higher for passageways with more open canopies and with lower costs of moving through the adjacent landscape. Different species exhibited individualistic responses to characteristics of the local habitat and adjacent landscape. Thus, passageways in this region were frequently used for mammalian movements, and their potential for mitigating the impacts of roads can be enhanced for focal mammal species by managing the local habitat and considering the adjacent landscape.

1. Introduction

The rate of habitat fragmentation is increasing as human populations expand our infrastructure across the globe. Fragmentation influences wildlife in two principal manners: (1) by reducing the amount of suitable habitat, and (2) by serving as a barrier to wildlife movements, thus reducing interpatch movements (Wilcox and Murphy, 1985; Saunders et al., 1991). Conservation biologists have targeted habitat fragmentation's "barrier effect" with many mitigation strategies, including managing for biological corridors. Corridors are designed to connect separate habitat patches by facilitating the movement of individuals from one habitat patch to the other(s) (Simpson, 1940; Saunders and Hobbs, 1991; Beier, 1993; Noss et al., 1996; Rosenberg et al., 1997).

The 6.2 million km of roadways within the United States alone are a major source of habitat fragmentation (Forman and Alexander, 1998; Trombulak and Frissell, 2000; Forman et al., 2003). The barrier effects of roads are numerous and well documented for many species of mammals in particular (Oxley et al., 1974; Mader, 1984; Swihart and Slade, 1984; Brody and Pelton, 1989; Alexander and Waters, 2000; Dyer et al., 2002; Rondinini and Doncaster, 2002; McDonald and St. Clair, 2004; Riley et al., 2006). Vehicle-animal collisions, or "road-kills", are the leading mortality source for some populations (Gallagher and Nelson, 1979; Bangs et al., 1989; Jones, 2000; Schmidt-Posthaus et al., 2002; Taylor et al., 2002).

A few mitigation strategies have been developed to reduce the negative effects of roads on mammals, including barrier fencing, warning signage, and wildlife underpasses. Of these, however, only wildlife underpasses are, by definition, designed to facilitate wildlife movements across roads, (i.e., to serve as a corridor between two habitats on opposite sides of the road), while simultaneously reducing the number of road-kills. Wildlife underpasses come in a variety of designs, depending on the target species. Unfortunately, not all species respond similarly to the same wildlife underpass design parameters, with some species responding more strongly to structural attributes (Yanes et al., 1995; McDonald and St. Clair, 2004; Ng et al., 2004; Clevenger and Waltho, 2005; Mata et al., 2005), level of human activity (Clevenger and Waltho, 2000), or location relative to the surrounding landscape (Foster and Humphrey, 1995; Rodriguez et al., 1996; Gloyne and Clevenger, 2001). As a result of these differences, larger, but fewer wildlife underpasses are built under the assumption that their large size will accommodate the highest diversity of species.

Despite the negative impacts of roads on mammals, and the fact that there are no doubt millions of underpasses beneath our roads, (either designed for wildlife or for drainage and other purposes), there are still many issues that need to be addressed by scientifically rigorous studies (Forman et al., 2003). For example, studies are often conducted at small spatial or short temporal scales, often only collecting data seasonally (Hunt et al., 1987; Clevenger et al., 2001; Taylor and Goldingay, 2003; McDonald and St. Clair, 2004; Mata et al., 2005), thus providing little information on geographic or seasonal variation in underpass usage. Also, monitoring studies are often conducted shortly after road construction, thus limiting the opportunities to assess the influence of successional habitats and adjacent landscapes on mammalian movements (Rodriguez et al., 1996; Ng et al., 2004).

An earlier study on mammal movements through non-wildlife underpasses along a highway within Adirondack Park, New York State, USA, suggested that underpasses such as these, which were not designed specifically for wildlife, may not facilitate mammalian movements (LaPoint et al., 2003). However, this study was preliminary, of relatively short duration (1.5 months), and did not assess the influence of environmental characteristics, which differ substantially among underpasses. Therefore, the purpose of the current study is to expand on these preliminary studies, to evaluate the hypothesis that underpasses facilitate mammalian movements, and to investigate the local-to-landscape-scale environmental factors influencing these movements. To evaluate this hypothesis, we tested the predictions that the geographic location, adjacent landscape, and local habitat characteristics of an underpass influence it's usage by mammals.

2. Methods

2.1. Study Area

We conducted this study along a 144 km section of Interstate 87 (I-87) which is located within Adirondack Park of New York State, USA (Fig. 1). Interstate 87 was completed and opened to the public in 1965 as a four-lane, divided highway that cuts north-south through the eastern portion of the Park. This section of the highway continues beyond the Park, connecting Albany (43°22' N, 73°43' W) in the south with Plattsburgh (44°33' N, 73°30' W) in the north. Within the study area, we located 170 underpasses (herein referred to as "passageways" in reference to their non-wildlife design intentions at the time of their construction and placement) which serve a variety of purposes (i.e., pedestrian access, vehicle passage, and storm drainage). The majority of these passageways experienced moving or standing water at some point during the course of this study. The study area receives approximately 30 000, 9000, and 13 000 vehicles per day in its southern, central, and northern extents, respectively (Highway Data Services Bureau, 2004). The maximum posted speed limit is 108 km/hr throughout the entire study area.

Adirondack Park is a 2.5-million ha, predominately forested state park. Although the Adirondack Mountains attain heights of 1600 m, the elevation within the study area ranges between 150 and 500 m above sea level (Jenkins, 2004). Northern hardwood species such as yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccharum*), and American beech (*Fagus grandifolia*) typically dominate the Park, with eastern hemlock (*Tsuga canadensis*) and quaking aspen (*Populus tremuloides*) being abundant as well. The Park represents a unique management situation, as 51% of the Park is owned by private citizens and 43% of the remaining is owned and managed by the State of New York (Jenkins, 2004). The climate of the Adirondack region is relatively moist (96 cm of rainfall per year), with cold winters producing a substantial snow pack, and relatively cool summers with a short growing season (average January and July temperature -9°C and 20°C, respectively) (Thaler, 2004). Road density within the Park is relatively low - just 1 km of roads per km^2, 73% of which are rural (compared to 3 km of roads per km^2 throughout the remainder of the State) (Jenkins, 2004).

Our studies focused on the non-volant, terrestrial mammal species known to occur within the study area (Saunders, 1989; Kays and Wilson, 2002). This includes forty-five species, none of which are of official conservation value within the State. These forty-five species range in size from the small mammals (at 5 – 75 g) up to black bear (*Ursus americanus*, 200 kg) and moose (*Alces alces*, 500 kg) (Table 1). Canada lynx (*Lynx canadensis*), gray wolf (*Canis lupus*), and cougar (*Puma concolor*), which are considered extirpated from the State, were not detected during these studies.

2.2. Passageway monitoring

We monitored mammalian use of 19 passageways beneath I-87 on a weekly basis from 17 October 2004 through 15 October 2005. In addition to the 19 passageways we monitored, we originally selected two others, however, consistent vandalism and theft forced us to exclude them from this study. Selected passageways were located beneath the two north-bound lanes of traffic only, and were composed entirely of either cement or steel. These selected passageways depicted a representative sample of the total variation in geographic position, adjacent landscape characteristics, and local habitat characteristics. Although some locations along the highway experienced higher levels of human activity during this study, human activity at the selected passageways was rare.

We monitored each passageway with an infra-red triggered camera and a specially designed track-plate. We placed Olympia® Trip AF S-2 35mm cameras mounted in TrailTimer Plus® infra-red sensors approximately 0.25 m above the ground at the entrance of each passageway. At the smaller passageways, we placed the camera and sensor near the eastern opening of the passageway and angled it so that the infra-red beam would be broken if a mammal passed though the passageway. Within larger passageways, we placed the camera and sensor near the track-plate, facing across the passageway at a 45º angle over the track-plate.

The track-plate structures consisted of two designs, depending on whether the passageway experienced flooding. At dry passageways, the track-plate consisted of a sheet of aluminum roofing flashing measuring 1 m in length and varying in width as needed in order to cover the base of the passageway. For wet passageways, the track-plate also used aluminum roofing flashing which was mounted to a wooden base. The wooden base provided a secure tracking surface and allowed us to elevate the track-plate surface (by resting it on the sides of the passageway or on cement cinder blocks) above varying water levels. We fastened steel hardware cloth (mesh size = 0.635 cm) to the up- and down-stream sides of the track-plate in order to prevent mammals from passing beneath the track-plate surface while simultaneously allowing for water flow. In order to confirm that this raised track-plate design did not bias our detection results, we ran an off-site trial run where we released several small vertebrates within a passageway to determine if the track-plate inhibits their movements. Our results later confirmed that the raised track-plate design did not impede movements as the three highest detection rates were recorded by raised track-plates. We mixed carpenter’s chalk with ethyl alcohol and sprayed it over the tracking surface. The alcohol dried quickly leaving a consistently smooth and thin tracking medium. In all but the narrowest passageways, those $\leq$ 1 m wide, we placed the track-plate midway through the passageway. In the narrower passageways, we placed the track-plate approximately 2 m from the eastern opening inside the passageway.

We checked the passageways weekly and avoided creating any paths between the highway shoulder and the entrances to the passageway in order to minimize disturbance at the site. During each visit, we recorded the number of exposures on the camera and ensured its functionality. We surveyed the track-plate extensively for any animal sign. We photographed each animal track with a digital camera, identified it to species, and recorded the direction of the individual's path. Finally, we cleaned and re-chalked the track-plate before we left the site.

2.3. Geographic, landscape and local habitat characteristics

We investigated the relationships between detection rates of mammals within passageways and nine continuous variables characterizing the geographic location, adjacent landscape, and local habitat (Table 2). The geographic location of each passageway was measured in universal transverse mercator northing and easting with a global positioning system.

We characterized the adjacent landscape by measuring four variables: surface area of forested habitat, distance to nearest forest edge, proximity, and cost of movement (Table 2). We characterized the local habitat by measuring the size of the opening to the passageway, canopy closure at both openings of the passageway, and the proportion of monitoring days during which there was water within the passageway (Table 2). We performed all spatial analyses within ArcGIS 9.0 (Environmental Systems Research Institute, 2004).

We calculated a proximity index to estimate the degree of isolation for each monitored passageway from all other passageways within the study area using the formula below:

$$P_i = \sum_{i=1}^{n} \frac{1}{D_i^2}$$

We only included passageways located along the north-bound side of the highway, with D_i representing the distance from the target passageway to another passageway (i) along the highway. The amount of forested habitat within 500 m of each passageway and the distance to the nearest forested edge were significantly, but positively correlated (Table 5). While this seems counterintuitive, close inspection of each site confirms this trend, which likely reflects the different scales (landscape versus local) of these two measures of forest cover.

We estimated the relative energetic cost of a mammal moving through the adjacent landscape by performing a cost-distance analysis. A cost-distance analysis calculates the Euclidean distance between a source and destination point, but weighs this distance with the resistance value of the surrounding matrix. These resistance values (i.e., “cost”) are assigned to different habitat types to represent how easily a species can move through that habitat (see Chardon et al., 2003). We used this analysis to estimate the degree to which the surrounding topography might redirect, or “funnel”, mammalian movements across the landscape. To perform the analysis, we created two parallel lines, each with 1000 random starting points, located 2 km to the west and east of the study area. This designated the spatial extent for our cost analysis as a 4 km buffer around the highway. As a measure of resistance, we considered the landscape’s slope (calculated from a 10 m resolution, digital elevation map from the New York State Department of Environmental Conservation [1999]) and surface water (Adirondack Park Agency, 2001) within this 4 km buffer around the study area to affect mammalian movements, with relatively steep slopes and surface water hindering movements. By extracting the cost values at the passageways, we were able to compare the relative cost to a mammal of moving to each passageway.

We tested for relationships between these nine independent variables and two dependent variables – detection rate and species richness, both standardized for the number of functional monitoring days at each passageway. Because some of the variables were not normally distributed, we used both Pearson's product moment correlations and Spearman's rank correlations to test for associations between the dependent and independent variables. In order to investigate how individual species responded to geographic, landscape, and local characteristics, we conducted canonical correspondence analysis using XLSTAT (Addinsoft, 2007). Canonical correspondence analysis is a unimodal ordination method which generates linear combinations of the environmental variables along two axes in order to maximize separation between species abundances (Gotelli and Ellison, 2004). Permutation tests are then used to evaluate the statistical significance of the separation of species across the environmental space defined by the canonical variables.

3. Results

3.1. Under-road passageway usage by nonvolant mammals

We recorded 823 detections of 19 species of nonvolant mammals moving through the 19 passageways. The detection rate for all species combined was 0.282 detections per functional monitoring day (Table 4). Detection rates varied substantially among the different passageways, ranging from 3 to 127 detections per 100 days ($\bar{x}$ = 29, sd = 28) (Table 4). Detection rates also varied substantially over time, peaking in August, September, and December, and declining in January through April when ice and flooding may have prevented mammals from entering the passageways (Fig. 2).

Muskrat (*Ondatra zibethicus*) was the most frequently detected species (n = 309, 37.5% of all detections) and occurred at nearly half (42.1%) of the passageways (Table 4). Northern raccoon (*Procyon lotor*) was the second most frequently detected species (n = 200, 24.3% of all detections), but was the most broadly distributed species occurring at all but two of the passageways (89.5%). Red squirrel (*Tamiasciurus hudsonicus*) and mink (*Mustela vison*) were also frequently detected, albeit at a more limited number of passageways (11) (n = 104, 12.6% of all detections; n = 62, 7.5% of all detections, respectively). The three largest species known to occur in the study area (moose [*Alces alces*], black bear [*Ursus americanus*], and white-tailed deer [*Odocoileus virginianus*]) were not detected during this study, despite the fact that nearly one third (31%) of the passageways are large enough for these species to move through. Interestingly, white-tailed deer were active at some of the passageways (as evidenced from snow tracking during the winter months), but never actually entered any of the passageways.

3.2. Correlations with environmental variables

Mammalian detection rates (for all species combined) were higher at passageways with more open canopies within the immediate vicinity (Pearson's product moment, $r_p = -0.629$, $p < 0.01$), with more forested habitat within a 500 m radius of the passageway ($r_p = 0.530$, $p < 0.05$), and those which were farther from the nearest forest edge ($r_p = 0.872$, $p < 0.001$) (Table 5; Fig. 3a-c). Species richness of mammals detected at the passageways increased toward the north (Spearman's rank correlation, $r_s = 0.554$, $p < 0.05$) and was higher at passageways with more open canopies in the immediate vicinity ($r_s = -0.539$, $p < 0.05$), but decreased with increased cost of moving to the passageways ($r_s = -0.557$, $p < 0.05$) (Table 5; Fig. 3d-e).

3.3. Mammalian species composition at under-road passageways

Canonical correspondence analysis (CCA) produced two axes which, combined, explained 70% of the variance in environmental variables, and indicated that variation in species composition among the passageways was significantly and linearly related ($p = 0.027$) to their environmental characteristics. The first principal axis described a northeastern gradient (from left to right in Fig. 4) of decreasing canopy closure, increasing cost of moving through the adjacent landscape, more forested habitat, higher distances to the nearest forest edge, and, to a lesser degree, more water within the passageway. The second principal axis described a gradient (from top to bottom in Fig. 4) of increasing size of passageways, increasing proximity values (i.e., other passageways are relatively close by), and to a lesser degree, less water within the passageways.

These axes separated mammal species into three functional groups based on their associations with different characteristics of the local habitat and adjacent landscape. The first group, comprised of the two most aquatic species, muskrat (*Ondatra zibethicus*) and river otter (*Lontra canadensis*), were, as expected, more frequently detected at wetter passageways located in the northeast, including those with higher costs of reaching the passageways, and with more forested habitat and farther from the nearest forest edge. The remaining groups were both comprised of more terrestrial species with strong affinities for drier passageways with more canopy closure. One group, comprised of weasels (*Mustela* spp.), fisher (*Martes pennanti*), red squirrel (*Tamiasciurus hudsonicus*), eastern chipmunk (*Tamias striatus*), deer mice (*Peromyscus* spp.), and unidentifiable small mammal species, were more often detected within drier and larger passageways. The last group, comprised of coyote (*Canis latrans*), northern raccoon (*Procyon lotor*), mink (*Mustela vison*), and jumping mice (Zapodinae spp.) were detected more frequently at smaller, more isolated passageways (i.e., those of lower proximity to other passageways) (Fig. 4).

Partialing out the geographic variables (i.e., removing the influence of northing and easting on the separation of species) increased the amount of environmental variance explained to 78.5%, and revealed a stronger relationship between species composition and the environmental variables ($p = 0.003$) (Fig. 5). The two new principal axes are similar to those from the original CCA, except size and proximity contribute more strongly to the first principal axis, and cost now contributes more strongly on the second principal axis (Fig. 5).

Muskrat were again the most distinct species, being most frequently detected at passageways with more water, higher landscape cost, more open canopies, more forested habitat, and farther from the nearest forest edge (Fig. 5). The eleven remaining species were separated into three functional groups. Coyote and northern raccoon were more frequently detected at smaller, wetter passageways. Mink, weasels, river otter, and jumping mice were detected more often at larger, wetter passageways. The final group, (fisher, red squirrel, eastern chipmunk, deer mice, and unidentified small mammals), were more frequently detected in drier and less isolated passageways (Fig. 5).

4 Discussion

The detections of mammals within the passageways suggest that these passageways do in fact facilitate mammalian movements across this highway. The number of detections and species richness of mammals within the passageways were each significantly associated with the geographic location, and the characteristics of the adjacent landscape and local habitat of the passageways. Individual species of mammals also responded significantly to characteristics measured at these three different scales (geographic, landscape, and local), highlighting the importance of considering passageway use at multiple spatial scales.

4.1 Mammalian responses to environmental characteristics

Mammals responded to several of the environmental variables that we measured. Northern passageways received higher species richness levels, possibly in response to lower human disturbances and the overall lower human population densities in these areas. The diversity (richness) of species utilizing a passageway decreased with increased cost of moving through the adjacent landscape, suggesting that topography may funnel movements of mammals through the landscape, and consequently to different locations along the highway (see also Foster and Humphrey, 1995; Rodriguez et al., 1996; Gloyne and Clevenger, 2001; Ng et al., 2004).

Some of our results were unexpected and even contrary to those of other published studies. For example, although numerous studies suggest that passageway size is correlated with both overall use and diversity (Yanes et al., 1995; Clevenger et al., 2001; Gloyne and Clevenger, 2001; Ng et al., 2004; Clevenger and Waltho, 2005; Mata et al., 2005), our study found no such correlation. Although we found detection rates to decrease as canopy closure (i.e., forested cover in the immediate vicinity of the passageway) increased, this association was scale-dependent, with detections being positively associated with forested cover in the adjacent (500 m radius) landscape. Many of our passageways contained moving water and were built to allow forest streams to continue en route beneath the highway. Such passageways, by default, could have more open canopies (at a local scale) and could also facilitate movements of aquatic species. In fact, unlike most of the passageway literature, we purposefully selected a few passageways that received water regularly, and our results suggest a trend of increased detection rates and species richness at wetter passageways.

Individual species also responded differentially to the local and landscape-scale characteristics of the passageways. Most species responded in a manner consistent with their known habitat associations. For example, muskrat, the most aquatic species, was most often detected in passageways with water and with environmental characteristics of a typical stream system (i.e., open canopies, greater distances to forest edge, and higher landscape cost). All of the other rodent species tended to occur in drier passageways, possibly because their relatively small size made it difficult to pass through moving water. These same species were also more frequently detected at passageways with greater local-scale canopy closure, which may provide protection from aerial predators.

Although past studies have found it difficult to monitor passageways with moving water (Mata et al., 2005), river otter in our study, were detected more often in larger passageways with water and closed canopies. This is important information as river otter is often a species of conservation concern across its native range.

Snow tracking surveys conducted simultaneously with this study indicated that coyote approached some of these larger passageways, but failed to enter the passageways – instead crossing over the surface of the highway (LaPoint, 2007). Perhaps the most surprising result was the absence of large mammals within the passageways, despite their documented use at other locations (Reed et al., 1975; Foster and Humphrey, 1995; Clevenger and Waltho, 2000; Ng et al., 2004; Clevenger and Waltho, 2005). White-tailed deer, although active along the highway throughout the study area (LaPoint, 2007), were never detected within a passageway. Winter snow tracking revealed that deer approached several of the sufficiently large passageways, but, like coyote, crossed over the highway rather than move through the passageway. Black bear were also never detected within the passageways. This, however, may be explained by their avoidance of roads (Brody and Pelton, 1989). Finally, beaver (*Castor canadensis*), a relatively large aquatic species, was also never detected within a passageway despite what seems to be suitable habitat at many of the passageways, especially considering the frequency of muskrat detections.

4.2 Conclusions and recommendations

Environmental variables, from local to landscape-scale, influence both the frequency and diversity of passageway use by mammals. Our results also highlight the importance of a rigorous monitoring protocol that includes multiple detection techniques, and evaluates the potential influence of factors ranging from local to landscape scales. By monitoring passageways that were constructed over four decades ago, we were able to study sites where the disturbance from constructing the highway has long since been replaced by the native vegetation, and where the resident mammal species have had generations to incorporate the passageways into their regular movements. Understanding the utility of existing passageways such as these may be more useful than studying specifically designed wildlife underpasses, as there are more opportunities to retrofit existing passageways than to construct new wildlife underpasses along new roads.

These studies provide important insights for regional wildlife managers and conservation biologists; identifying the characteristics of passageways, local habitats, and adjacent landscapes that could be modified to enhance wildlife movements across fragmented ecosystems. Similar studies conducted in other regions should prove equally successful in mitigating the effects of the many millions of kilometers of roadways that threaten mammal species worldwide.

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Fig. 1 – Map depicting the 144 km portion of Interstate 87 (I-87) within Adirondack Park of New York State, USA, that we monitored for this study. We documented mammalian movements through 19 passageways (see inset) from 17 October 2004 through 15 October 2005.

Fig. 2 – Detection rates (standardized by the number of functional monitoring days) of mammals at 19 passageways located along 144 km of Interstate 87 within Adirondack Park, New York State, USA.

Fig. 3a – Detection rates (standardized for the number of functional monitoring days) of mammals at 19 passageways increased significantly as the nearest forested habitat became further from the passageway ($p < 0.001$) (a), where there was more forested habitat within the adjacent landscape ($p < 0.05$) (b), and with more open canopies within the immediate vicinity of the passageway ($p < 0.01$) (c) (see Table 5).

Fig. 3d – Species richness (standardized for the number of functional monitoring days) of mammals detected at 19 passageways increased significantly ($p < 0.05$) toward the north (d), but decreased significantly ($p < 0.05$) with increased canopy closure (e) and the cost of moving within the adjacent (2 km) landscape ($p < 0.05$) (f) (see Table 5).

Fig. 4 – Results of canonical correspondence analysis describing the significant ($p = 0.027$) separation of species detected at 19 passageways as a function of geographic variables (dashed arrows), characteristics of the adjacent landscape (thin, solid arrows), and characteristics of the local environment (bold, solid arrows). Species are labeled in bold (see Table 1 for species codes).

Fig. 5 – Results of canonical correspondence analysis (after removing the influence of the geographic variables) describing the significant ($p = 0.003$) separation of mammal species detected at 19 passageways as a function of characteristics of the adjacent landscape (thin, solid arrows) and characteristics of the local environment (bold, solid arrows). Species are labeled in bold (see Table 1 for species codes).

Table 1 – Non-volant, terrestrial mammalian species considered residents of Adirondack Park, New York State, USA (Saunders, 1989; Ernest, 2003).

Common name	Latin name	Species code	Habitat	Body size (kg)
Virginia opossum	*Didelphis virginianus*	Dv	Forest / Open	2.8
Insectivores	Soricidae / Talpidae	Sor/Tal	Variable	0.04
Coyote	*Canis latrans*	Cl	Forest / Open	18.0
Red fox	*Vulpes vulpes*	Vv	Open	5.0
Gray fox	*Urocyon cinereoargenteus*	Uc	Forest	5.5
Fox	Fox spp.	Fox	Variable	5.2
Black bear	*Ursus americanus*	Ua	Forest	200
Northern raccoon	*Procyon lotor*	Pl	Forest / Open	9.9
American marten	*Martes americana*	Ma	Forest	0.7
Fisher	*Martes pennanti*	Mp	Forest	3.4
Ermine	*Mustela erminea*	Me	Forest / Open	0.1
Long-tailed weasel	*Mustela frenata*	Mf	Forest / Open	0.4
Mink	*Mustela vison*	Mv	Forest / Water	1.7
Weasel	*Mustela* spp.	Weasel	Various	0.7
Striped skunk	*Mephitis mephitis*	Mm	Forest / Open	3.8
River otter	*Lontra canadensis*	Lc	Forest / Water	17.6
Bobcat	*Lynx rufus*	Lr	Forest	8.6
White-tailed deer	*Odocoileus virginianus*	Ov	Open	81.0
Moose	*Alces alces*	Aa	Forest	410
Eastern chipmunk	*Tamias striatus*	Ts	Forest	0.09
Woodchuck	*Marmota monax*	Mam	Open	23.0
Gray squirrel	*Sciurus carolinensis*	Sc	Forest / Open	0.57
Red squirrel	*Tamiasciurus hudsonicus*	Th	Forest	0.2
Southern flying squirrel	*Glaucomys volans*	Gv	Forest	0.06
Beaver	*Castor canadensis*	Cc	Water	20.4
Peromyscus spp.	*Peromyscus* spp.	Pero	Forest / Open	0.02
Voles	*Microtus / Myodes*	Vole	Various	0.03
Muskrat	*Ondatra zibethicus*	Oz	Water	1.2
Southern bog lemming	*Synaptomys cooperi*	Syc	Forest / Open	0.03
Jumping mice	Zapodinae	Zap	Forest / Open	0.02
Small mammal	Rodent spp.	Small	Various	0.03
Porcupine	*Erethizon dorsatum*	Ed	Forest	6.8
Eastern cottontail	*Sylvilagus floridanus*	Sf	Open	1.1
Snowshoe hare	*Lepus americanus*	La	Forest	1.6

Table 2 – Variables measured to describe 19 passageways located along a 144 km stretch of Interstate 87 within Adirondack Park, New York State, USA (October 2004 through October 2005).

Variable name	Description	Source (Date)
Geographic variables:		
Easting	Measured in Universal Transverse Mercator (m).	This study (2004)
Northing	Measured in Universal Transverse Mercator (m).	This study (2004)
Landscape characteristics:		
Proximity	An inverse measure of relative isolation of a passageway from all of the other passageways on this highway (see Methods).	This study (2004)
Distance to edge	Combined distance (m) from both openings of the passageway to the nearest forest edge.	This study (2005)
Forest	Surface area (m^2) of forested habitat within a 500 m radius of the mid-point of the passageway.	USGS[1] (2001)
Cost	A measure of the terrain ruggedness and surface water area to be crossed, representing the "cost" of moving across the landscape (see Methods).	NYSDEC[2] (1999) & APA[3] (2001)
Local habitat characteristics:		
Size	Surface area (m^2) of the opening to the passageway.	This study (2004)
Canopy closure	Proportion of forested cover (measured with a spherical densiometer), combined for the western and eastern openings of the passageway.	This study (2005)
Water	Proportion of monitoring days when water was within the passageway.	This study (2004-2005)

[1] United States Geological Survey, [2] New York State Department of Environmental Conservation, [3] Adirondack Park Agency

Table 3 – Characteristics of the 19 passageways monitored for mammalian use located along a 144 km stretch of Interstate 87 within Adirondack Park, New York State, USA, from 17 October 2004 through 15 October 2005.

Site	Easting	Northing	Proximity	Distance to edge	Forest	Cost	Size	Canopy closure	Water
1710-1181	601573	4817721	12.555	4.7	0.522	17320	3.574	1.622	0.870
1710-1185	601567	4818391	12.304	2.2	0.388	24785	0.456	1.973	0.674
1710-1197	601880	4820248	11.206	3.1	0.582	21736	0.456	2.000	0.304
1710-1218	602218	4823344	3.500	3.9	0.482	23365	2.625	1.973	0.522
1710-1225	602667	4824511	3.230	3.4	0.631	24120	0.893	0.973	0.543
1710-1291	599608	4833690	27.113	15.7	0.496	18011	0.656	1.703	0.087
1211-1001	596441	4847053	6.035	18.9	0.613	15986	1.167	1.892	0.848
1211-1057	599102	4855518	42.910	42.6	0.388	12336	1.750	1.108	0.870
1211-1162	602434	4871525	137.518	15.0	0.496	26344	3.610	1.919	0.630
1211-1166	602526	4872160	226.195	26.6	0.467	25621	8.168	1.892	1.000
1211-1216	605466	4879163	147.018	38.8	0.521	14420	11.669	0.919	1.000
1211-1245	608417	4882372	149.027	60.4	0.757	15099	1.823	0.541	0.717
1211-1253	609361	4883238	67.968	46.5	0.845	22830	3.574	1.108	0.891
1211-1256	609724	4883652	71.502	199.9	0.790	24318	3.574	0.000	0.935
1211-1290	613062	4887757	36.522	36.0	0.628	20600	0.656	1.216	0.391
1211-1297	613276	4888841	131.091	20.6	0.677	19897	1.588	1.243	0.804
1211-1430	617152	4905861	15.695	36.2	0.469	11546	0.219	0.838	0.043
1211-1473	617032	4912625	35.884	40.8	0.601	15567	1.477	1.000	0.957
1211-1534	620034	4921550	30.228	39.5	0.526	14563	2.625	0.892	0.935

Table 4 – Detections of non-volant mammal species varied among the 19 passageways located along a 144 km stretch of Interstate 87 within Adirondack Park, New York State, USA, (monitored from 17 October 2004 through 15 October 2005). See Table 1 for species codes; MD = monitoring days, SR = species richness, TD = total detections.

Site	MD	Cl	Vv	Uc	Fox	Pl	Ma	Mp	Mf	Mv	Weasel	Mm	Lc	Ts	Sc	Th	Gv	Pero	Oz	Zap	Small	SR	TD
1710-1181	98	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	3
1710-1185	208	0	0	0	0	47	0	0	0	3	0	0	0	0	1	3	0	0	0	0	0	4	54
1710-1197	180	0	0	0	0	12	0	0	0	0	2	0	0	0	0	11	0	0	0	0	1	4	26
1710-1218	178	1	0	0	0	13	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	3	21
1710-1225	208	1	0	0	0	18	0	0	0	1	1	0	0	1	0	7	0	0	0	1	7	8	37
1710-1291	222	0	1	0	0	8	1	6	0	0	0	0	0	5	0	23	0	7	0	0	11	8	62
1211-1001	146	1	0	1	1	33	0	2	0	1	4	0	0	0	0	0	0	0	5	0	0	8	48
1211-1057	226	0	0	0	0	13	0	0	0	11	1	0	0	0	0	0	0	0	25	1	1	6	52
1211-1162	152	0	0	0	0	1	0	0	0	0	0	0	0	0	0	15	0	0	0	0	0	2	16
1211-1166	156	0	0	0	0	0	0	0	0	3	2	0	0	0	0	2	0	0	0	1	0	4	8
1211-1216	153	0	0	0	0	3	0	1	1	15	8	0	1	0	0	29	1	1	2	0	8	11	70
1211-1245	149	0	0	1	1	0	1	0	0	4	5	0	2	4	0	2	0	5	13	0	0	10	38
1211-1253	133	0	0	0	0	1	0	0	0	4	0	0	0	0	0	0	0	0	63	0	0	3	68
1211-1256	159	0	0	0	0	5	0	2	0	0	0	0	2	0	0	0	0	0	193	0	0	4	202
1211-1290	146	0	0	0	0	18	1	9	0	0	0	0	0	1	0	0	0	12	0	0	0	5	41
1211-1297	69	0	0	0	0	10	0	0	1	0	0	0	0	0	0	2	3	0	2	1	0	6	19
1211-1430	215	0	1	0	1	2	0	0	0	0	0	3	0	4	0	3	0	0	0	0	1	7	15
1211-1473	53	0	0	0	0	4	0	0	0	3	0	0	0	0	0	0	0	1	0	0	0	3	8
1211-1534	77	1	0	0	0	11	0	0	0	15	0	0	2	0	0	0	0	0	6	0	0	5	35
Total	2928	4	2	2	3	200	3	20	2	62	23	3	7	15	1	104	4	26	309	4	29	19	823
Incidence		4	2	2	3	17	3	5	2	11	7	1	4	5	1	11	2	5	8	4	6		

Table 5 – Pearson product-moment and Spearman rank correlations (above and below diagonal, respectively) between environmental variables and mammalian species richness and detection rates measured at 19 passageways located along a 144 km stretch of Interstate 87 within Adirondack Park, New York State, USA. Detection rates and species richness are both standardized for the number of functional monitoring days. See Table 2 for variable definitions.

	Dependent		*Geographic*		*Landscape*				*Local habitat*		
	Detections†	**Species †**	**Easting**	**Northing**	**Proximity†**	**Distance**	**Forest**	**Cost**	**Size†**	**Canopy†**	**Water**
Detections†	-	0.123	0.205	0.272	0.036	**0.872*****	**0.530***	0.114	0.132	**-0.629****	0.325
Species†	0.402	-	0.426	**0.488***	0.267	0.035	0.259	**-0.509***	0.183	-0.394	0.279
Easting	0.146	0.400	-	**0.845*****	0.051	0.316	0.316	-0.295	-0.077	**-0.598****	0.045
Northing	0.288	**0.554***	**0.870*****	-	0.374	0.436	0.306	-0.372	0.150	**-0.610****	0.263
Proximity†	0.118	0.232	0.330	**0.496***	-	0.191	0.138	0.183	**0.648****	-0.115	0.425
Distance	0.404	0.396	**0.509***	**0.735*****	**0.632****	-	**0.518***	0.010	0.121	**-0.764*****	0.302
Forest	0.453	0.332	0.423	0.361	0.142	0.393	-	0.152	-0.062	**-0.538***	0.211
Cost	-0.072	**-0.577***	-0.198	-0.367	-0.009	-0.439	0.046	-	0.028	0.353	0.025
Size†	0.152	0.013	0.169	0.169	**0.555***	0.417	0.214	0.133	-	-0.073	**0.523***
Canopy†	-0.321	**-0.539***	**-0.650****	**-0.665****	-0.356	**-0.778*****	-0.419	**0.499***	-0.239	-	-0.224
Water	0.260	0.262	0.183	0.303	**0.512***	**0.521***	0.137	-0.075	**0.782*****	-0.320	-

† Variable is not normally distributed.

Variables in bold are significant: * p-value is < 0.05; ** p-value is < 0.01; *** p-value is < 0.001; two-tailed test.

Fig. 1 – Map depicting the 144 km portion of Interstate 87 (I-87) within Adirondack Park of New York State, USA, that we monitored for this study. We documented mammalian movements through 19 passageways (see inset) from 17 October 2004 through 15 October 2005.

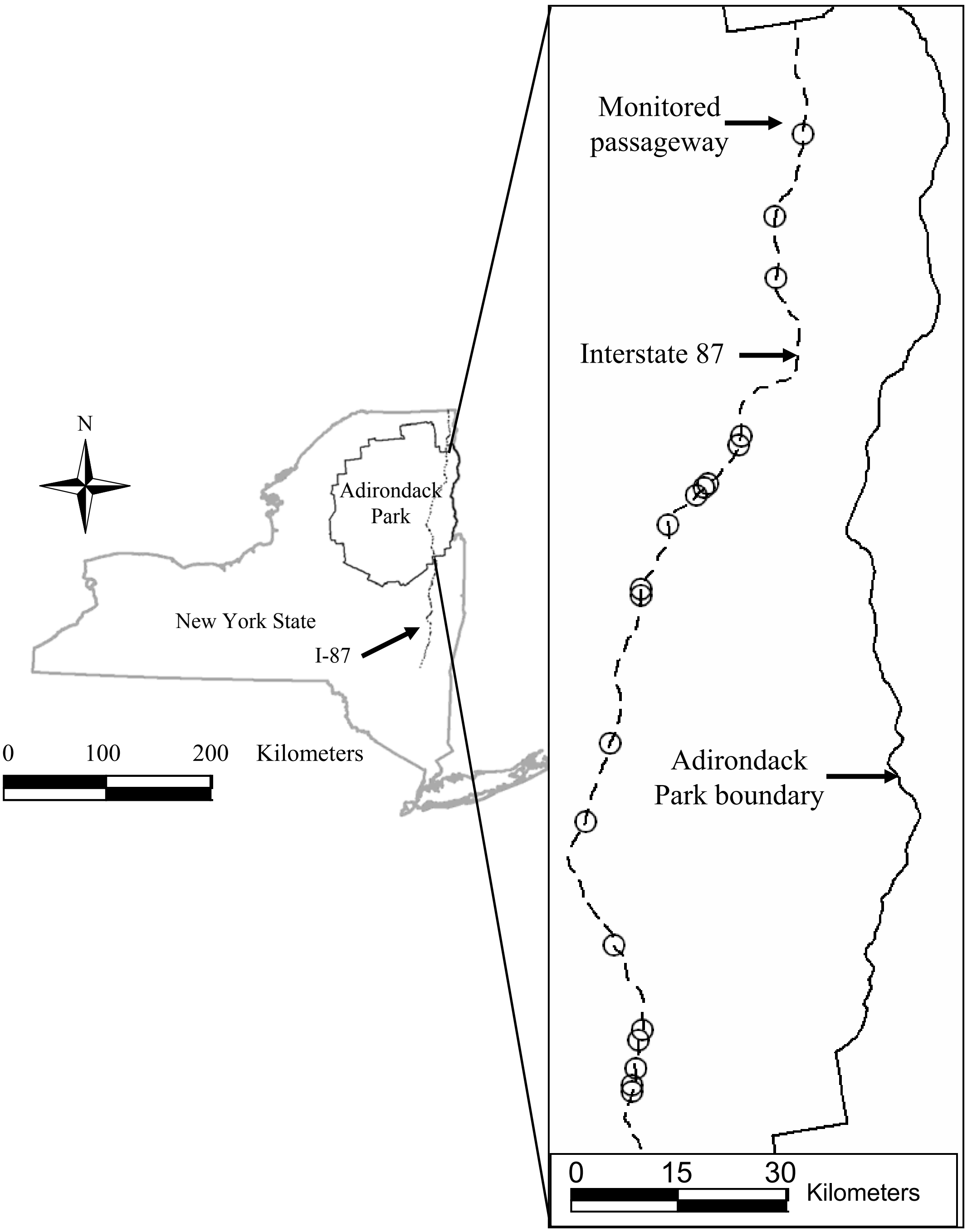


Fig. 2 – Detection rates (standardized by the number of functional monitoring days since the previous field visit) of mammals at 19 passageways located along 144 km of Interstate 87 within Adirondack Park, New York State, USA.

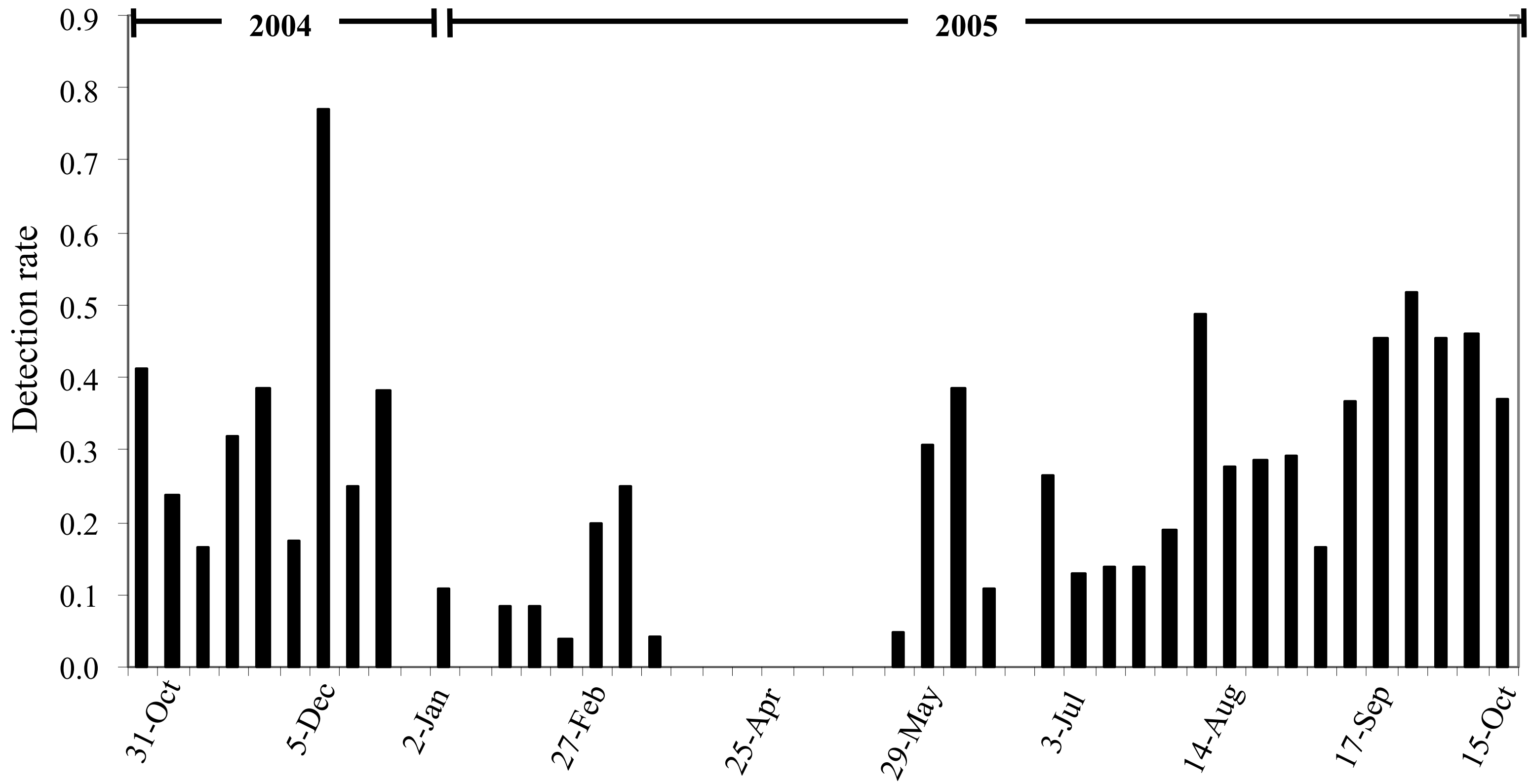


Fig. 3a – Detection rates (standardized for the number of functional monitoring days) of mammals at 19 passageways increased significantly as the nearest forested habitat became farther from the passageway ($p < 0.001$) (a), where there was more forested habitat within the adjacent landscape ($p < 0.05$) (b), and with more open canopies within the immediate vicinity of the passageway ($p < 0.01$) (c) (see Table 5).

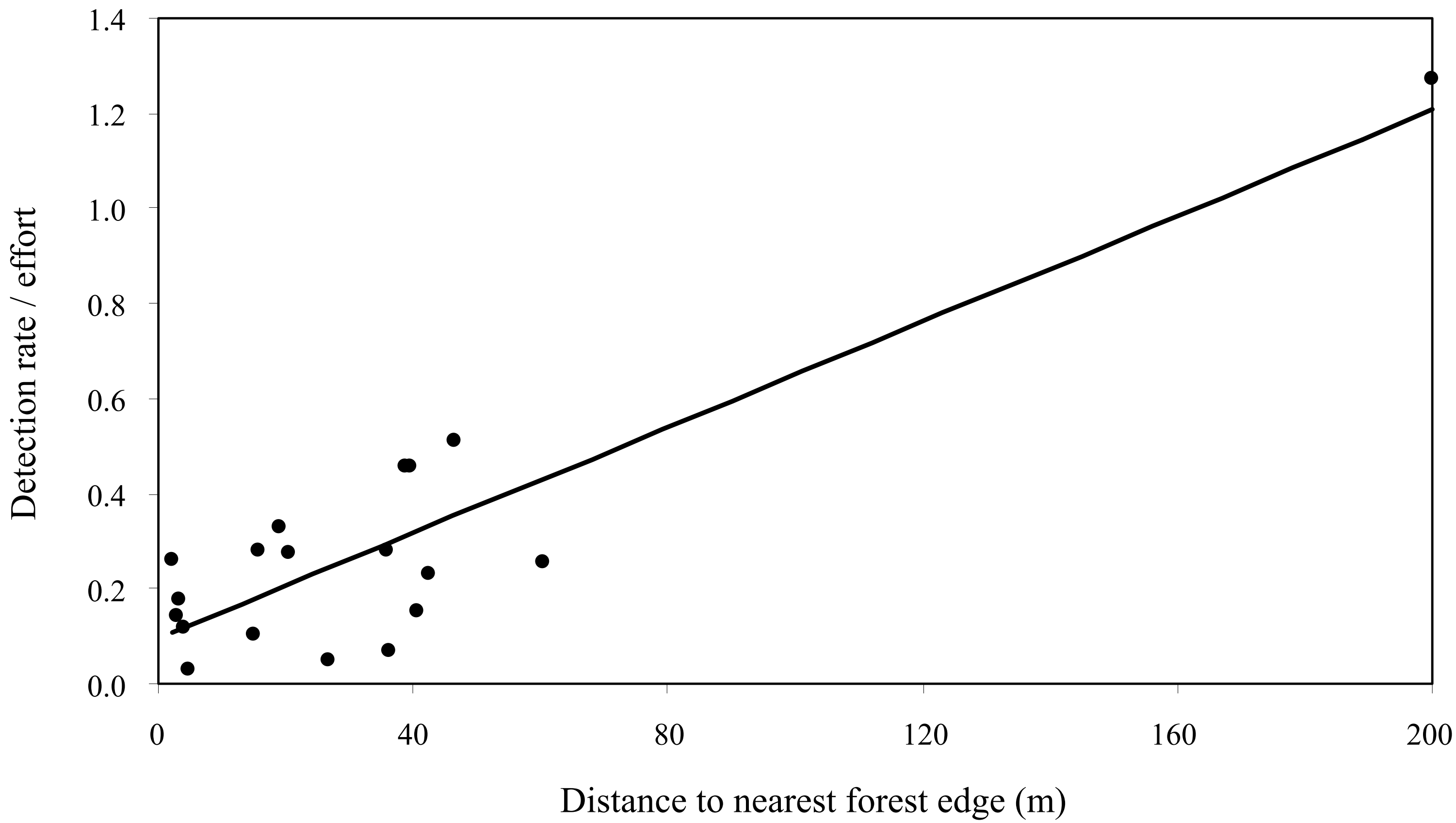


Fig. 3b

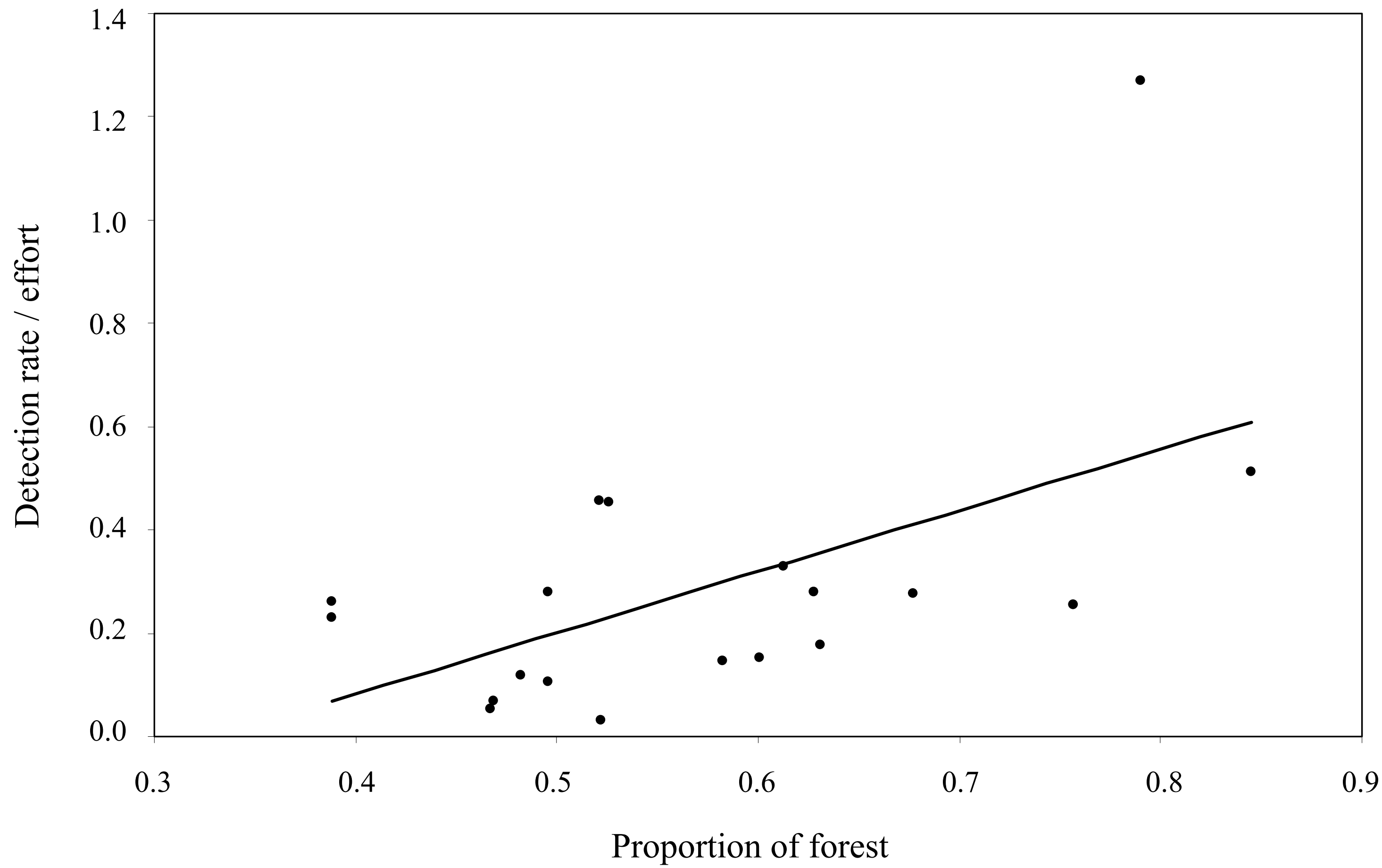
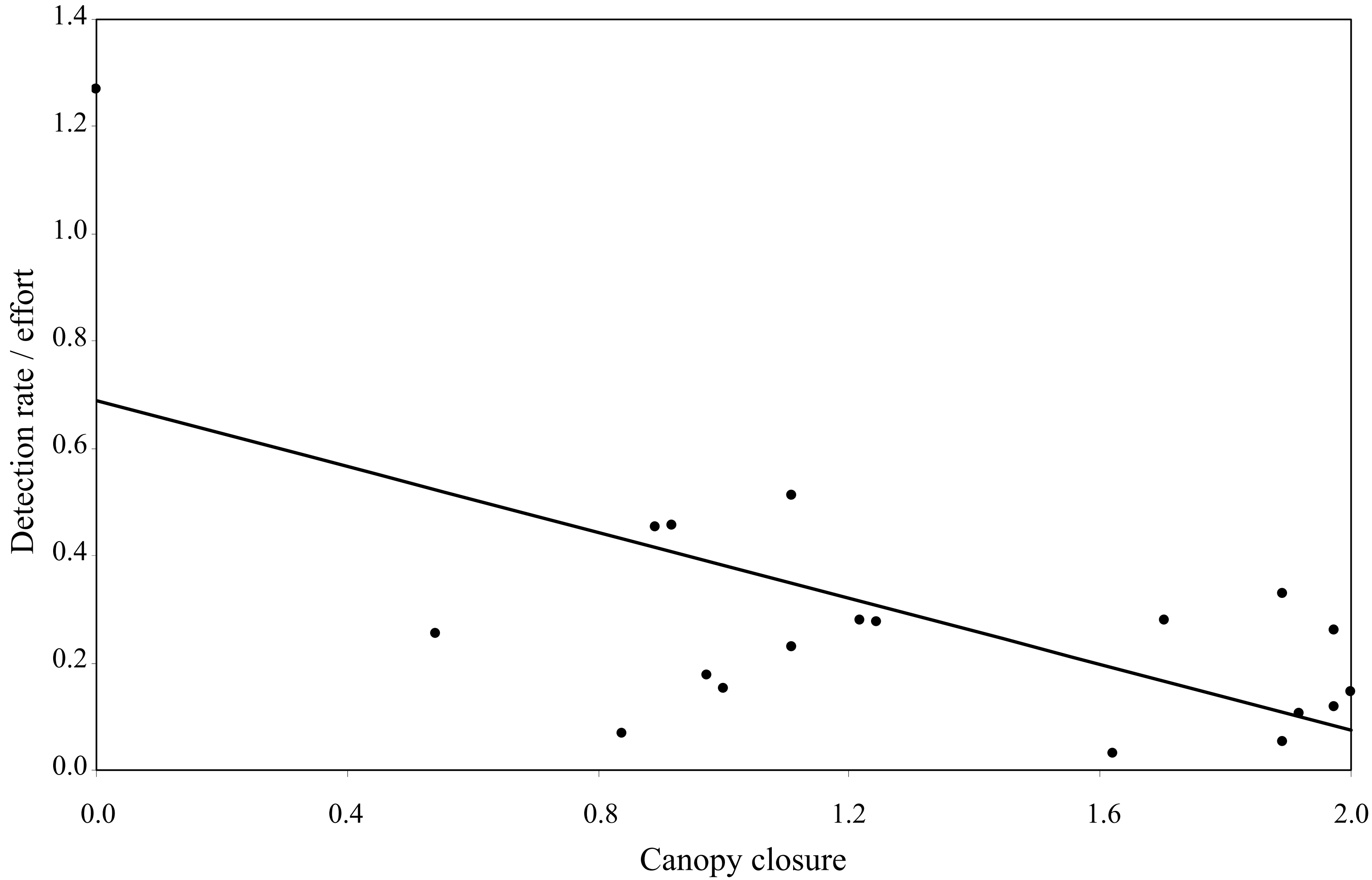

1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Detection rate / effort
0.3
0.4
0.5
0.6
0.7
0.8
0.9
Proportion of forest

Fig. 3c



Detection rate / effort
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0.0
0.4
0.8
1.2
1.6
2.0
Canopy closure

Fig. 3d – Species richness (standardized for the number of functional monitoring days) of mammals detected at 19 passageways increased significantly ($p < 0.05$) toward the north (d), but decreased significantly ($p < 0.05$) with more canopy closure (e) and higher costs of moving within the adjacent (2 km) landscape ($p < 0.05$) (f) (see Table 5).

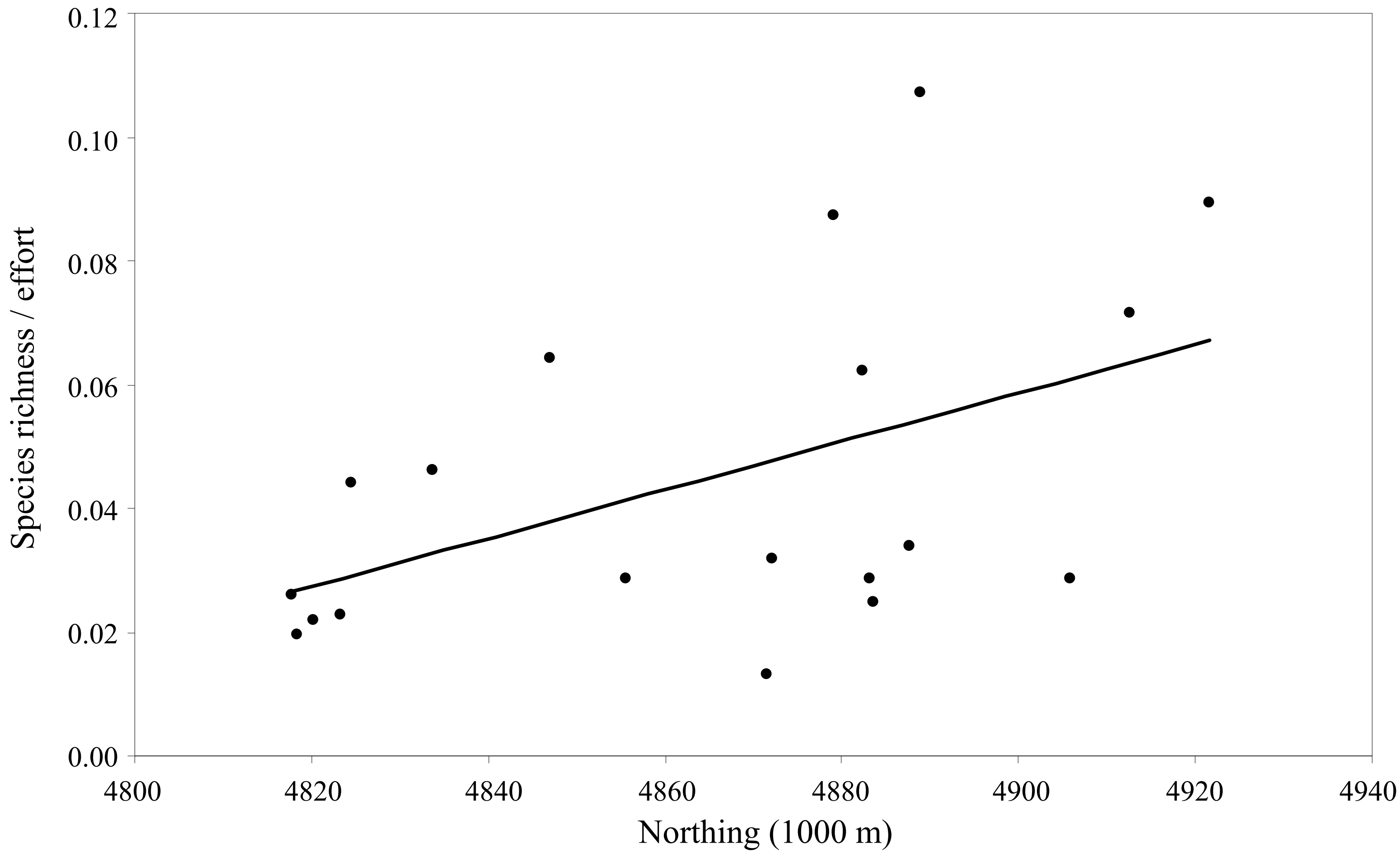
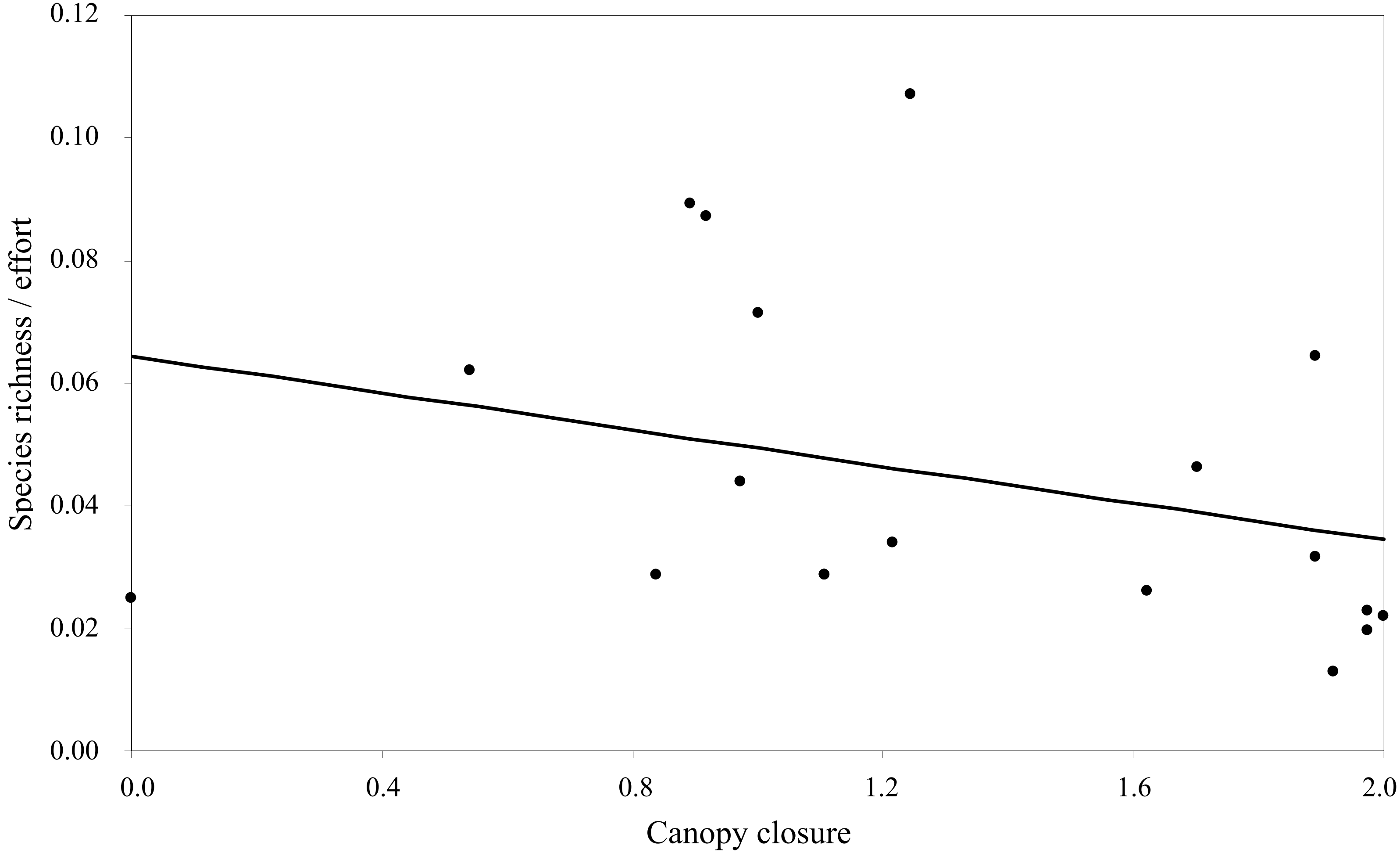


Fig. 3e



0.12
0.10
0.08
0.06
0.04
0.02
0.00
Species richness / effort
0.0
0.4
0.8
1.2
1.6
2.0
Canopy closure

Fig. 3f

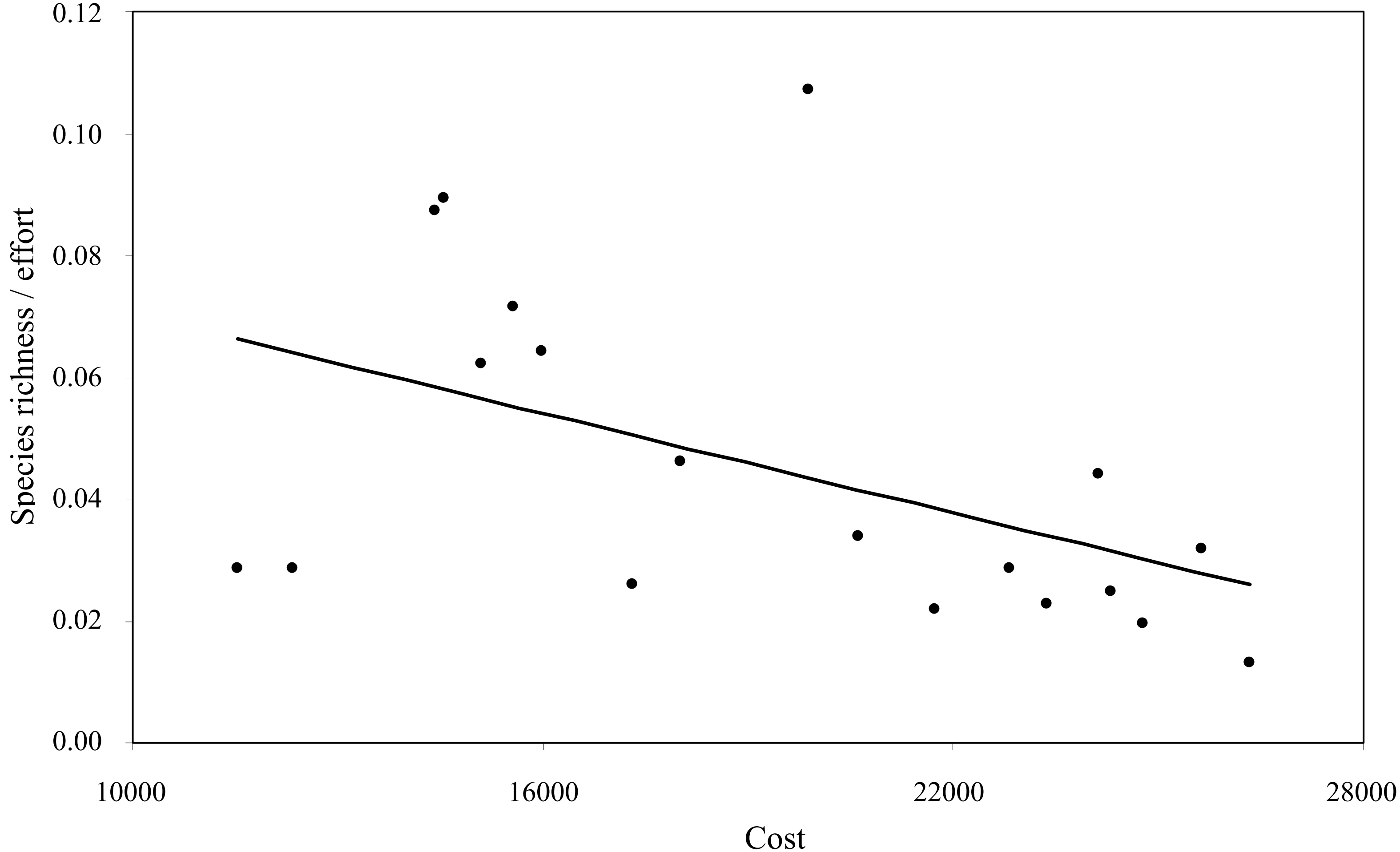

0.12
0.10
0.08
0.06
0.04
0.02
0.00
Species richness / effort
10000
16000
22000
28000
Cost

Fig. 4 – Results of canonical correspondence analysis describing the significant (p = 0.027) separation of species detected at 19 passageways as a function of geographic variables (dashed arrows), characteristics of the adjacent landscape (thin, solid arrows), and characteristics of the local environment (bold, solid arrows). Species are labeled in bold (see Table 1 for species codes).

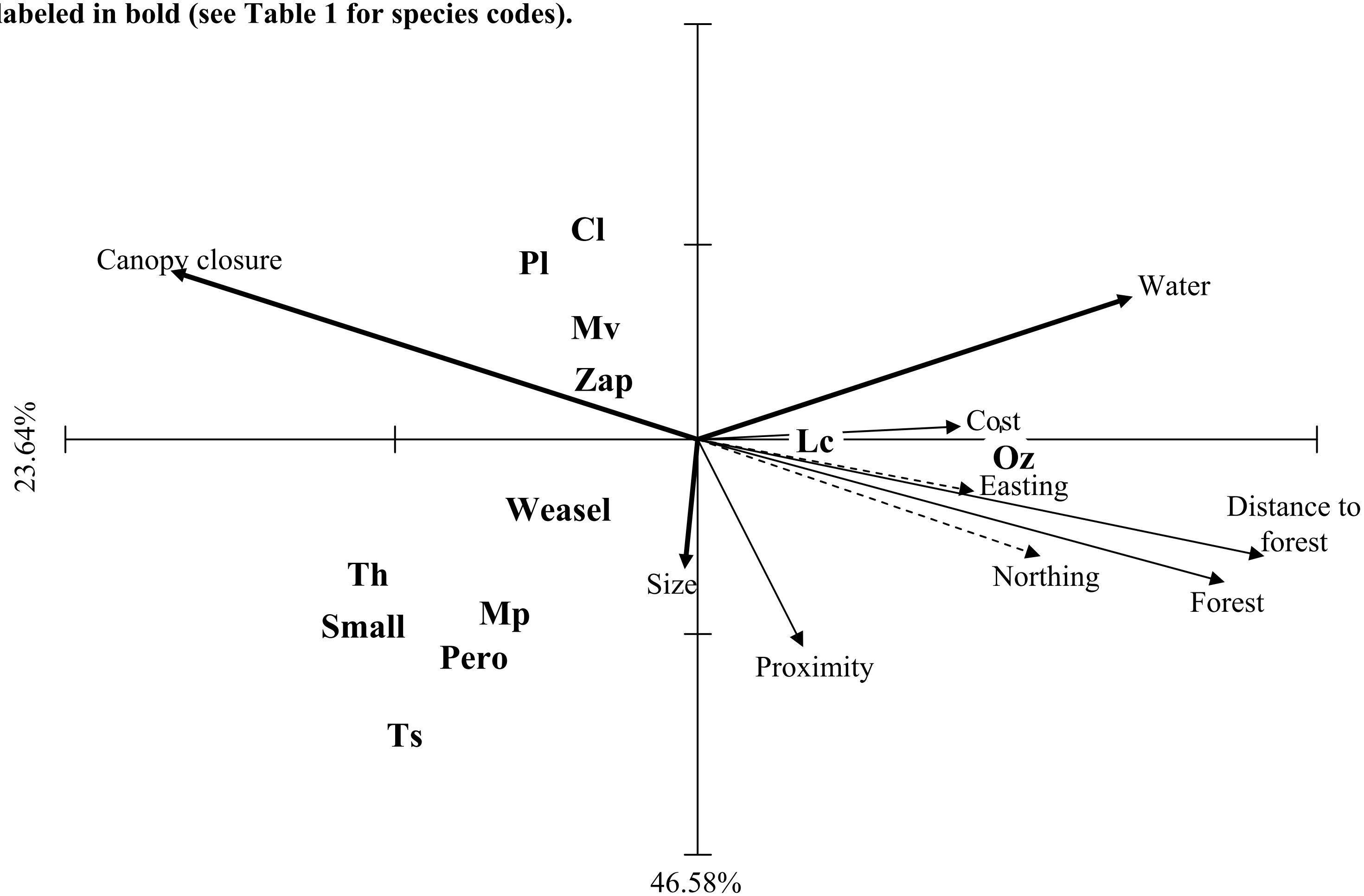
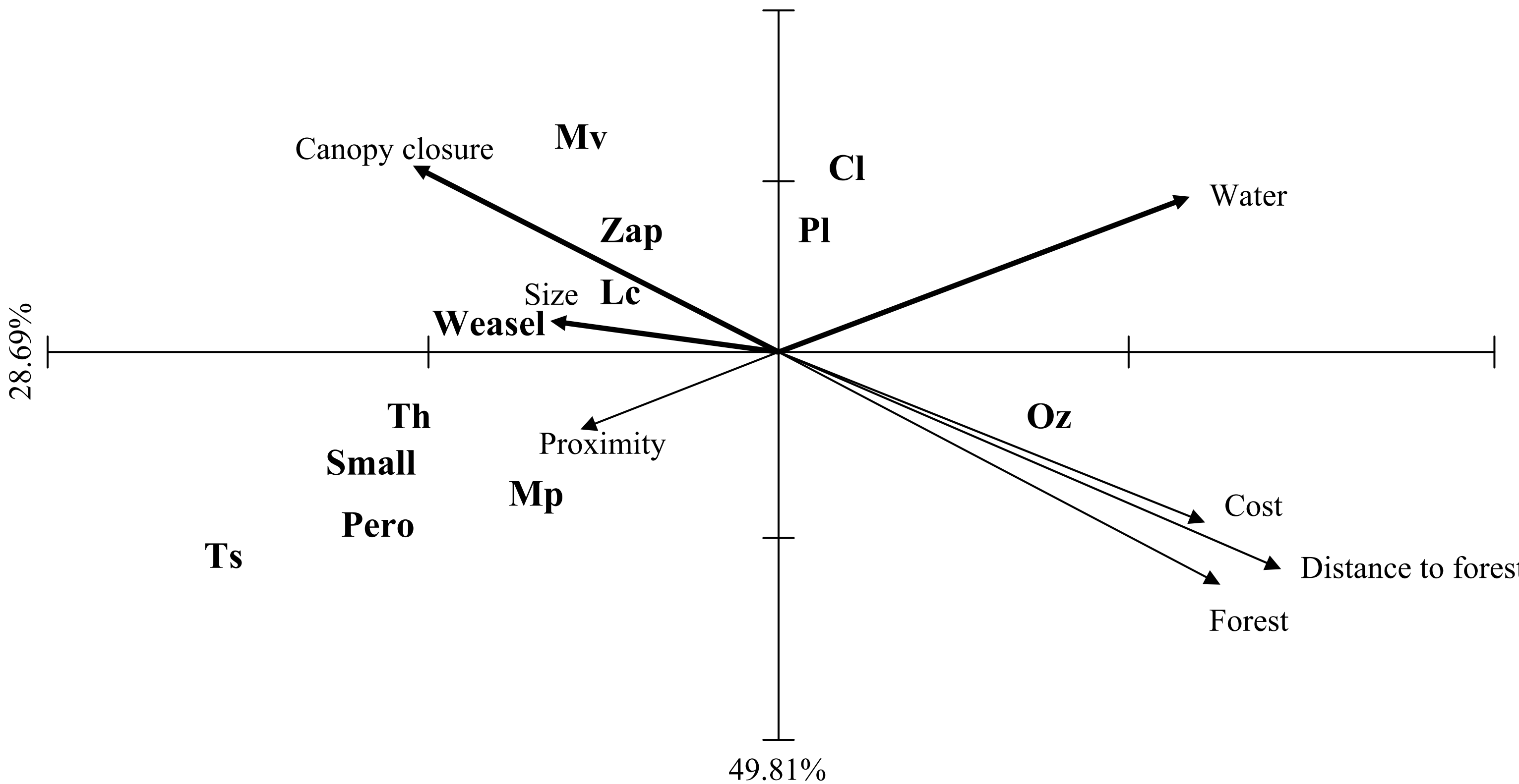


Fig. 5 – Results of partial canonical correspondence analysis (after removing the influence of the geographic variables) describing the significant (p = 0.003) separation of mammal species detected at 19 passageways as a function of characteristics of the adjacent landscape (thin, solid arrows) and characteristics of the local environment (bold, solid arrows). Species are labeled in bold (see Table 1 for species codes).



Appendix – Functional monitoring days for the 19 passageways we monitored for mammalian use. A zero ("0") represents disturbance at the passageway (i.e., flooding, ice, human disturbance, or the track-plate was missing), all other values represent the number of functional monitoring days since the previous field data collection at the passageway.

Passageway	24-Oct-04				21-Nov-04				19-Dec-04				30-Jan-05			3-Mar-05				17-Apr-05				5-May-05	
1710-1181	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17	5	0	0	0	0	0	0	0	0	0	0
1710-1185	7	7	7	7	7	7	0	0	6	0	7	13	0	6	17	0	0	0	0	0	0	0	0	0	0	7
1710-1197	7	7	7	7	7	7	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7
1710-1218	7	7	7	7	7	7	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	7
1710-1225	7	7	7	7	7	7	0	0	6	7	0	0	15	0	0	0	0	0	0	0	0	0	0	0	0	7
1710-1291	7	7	7	7	7	7	7	8	6	7	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7
1211-1001	0	7	7	7	7	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7
1211-1057	7	7	7	7	7	7	0	8	6	7	7	0	0	0	0	0	4	0	0	0	0	0	0	0	7	7
1211-1162	7	7	7	7	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7
1211-1166	0	0	0	7	7	7	0	0	0	0	0	0	15	0	17	0	0	0	0	0	0	0	0	0	0	7
1211-1216	0	7	0	0	7	7	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0	0	0	0	0	7
1211-1245	0	7	7	7	0	7	0	0	6	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	7
1211-1253	0	0	0	7	7	0	0	0	0	0	0	0	0	6	0	0	0	23	0	0	0	0	0	0	0	0
1211-1256	0	0	7	7	7	7	7	8	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1211-1290	0	0	7	7	7	7	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1211-1297	7	7	0	7	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1211-1430	0	7	7	7	7	7	7	8	6	7	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7
1211-1473	7	0	0	7	7	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0
1211-1534	0	0	0	7	7	0	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix cont. – Functional monitoring days for the 19 passageways we monitored for mammalian use. A zero ("0") represents disturbance at the passageway (i.e., flooding, ice, human disturbance, or the track-plate was missing), all other values represent the number of functional monitoring days since the previous field data collection at the passageway.

Passageway			12-Jun-05				9-Jul-05				14-Aug-05				10-Sep-05				8-Oct-05		Total
1710-1181	0	7	0	0	0	0	0	0	7	7	7	7	7	7	6	7	7	7	0	0	98
1710-1185	7	7	7	0	7	7	6	14	7	7	7	0	7	0	6	7	7	7	0	0	208
1710-1197	7	7	7	0	0	0	6	14	7	7	7	7	7	7	6	7	7	7	7	7	180
1710-1218	7	7	7	0	0	7	6	14	7	7	7	7	7	7	6	7	7	7	7	0	178
1710-1225	7	7	7	0	7	7	6	14	7	7	7	7	7	7	6	7	7	7	7	0	208
1710-1291	7	7	7	0	7	7	6	14	7	7	7	7	7	7	6	7	7	7	7	7	222
1211-1001	7	7	7	0	7	7	0	14	7	7	7	0	7	0	6	7	7	7	0	0	146
1211-1057	7	7	7	0	7	7	6	14	7	7	7	7	7	7	6	7	7	7	7	7	226
1211-1162	7	7	0	0	0	7	6	14	7	7	7	7	7	7	6	7	7	7	0	0	152
1211-1166	7	7	0	0	0	7	6	14	0	7	7	7	7	0	6	7	7	7	0	0	156
1211-1216	7	7	0	0	0	7	6	14	7	7	7	7	7	7	6	7	7	7	0	0	153
1211-1245	7	0	0	0	0	7	6	14	7	7	7	7	7	7	6	7	7	7	0	0	149
1211-1253	0	0	0	0	0	0	0	14	7	7	7	7	7	7	6	7	7	7	7	0	133
1211-1256	7	7	0	0	0	0	6	14	7	7	7	7	7	7	6	7	7	7	7	0	159
1211-1290	0	0	0	0	7	7	0	14	7	7	7	7	7	7	6	7	7	7	7	7	146
1211-1297	0	0	0	0	0	0	0	0	0	7	7	7	7	0	6	0	7	0	0	0	69
1211-1430	7	7	7	7	7	0	6	14	7	7	7	7	7	7	6	7	7	7	7	7	215
1211-1473	0	0	0	0	0	0	0	0	0	0	0	7	7	0	6	0	7	0	0	0	53
1211-1534	0	0	0	0	0	0	0	0	0	0	7	7	7	0	6	7	7	7	0	0	77

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