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Identifying road mortality threat at multiple spatial scales for semi-aquatic turtles

Frederic Beaudry^{a,*}, Phillip G. deMaynadier^b, Malcolm L. Hunter Jr.^a

^aDepartment of Wildlife Ecology, University of Maine, Orono, ME 04469, United States

^bWildlife Resource Assessment Section, Maine Department of Inland Fisheries and Wildlife, Bangor, ME 04401, United States

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ABSTRACT

Prioritizing sites for localized mitigation measures, and forecasting the effect of interventions on an endangered population, requires an understanding of the spatial scales at which threat processes operate. Road mortality is among the greatest threats to semi-terrestrial freshwater turtles due to the group's life-history traits. Declining throughout much of their range, spotted (*Clemmys guttata*) and Blanding's turtles (*Emydoidea blandingii*) are exposed to high road densities and traffic volumes in the northeastern United States. We examine the distribution of roadkill risk for spotted and Blanding's turtles at three spatial scales. Tortuosity during upland movements was used to predict road-crossing locations at the single-movement scale. A gravity model of wetland-to-wetland interactions was then developed to identify road mortality hot spots at a broader road segment scale. Finally, road-crossing risk was assessed at the scale of focal areas that support distinct populations, using a population viability analysis to evaluate the consequences of road mortality on resident populations. The observed spatial variability of road mortality risk was high for single road crossing movements, limiting the effectiveness of static mitigation measures conducted at this scale. At the broader road segment scale, road mortality hotspots were evident. The demographic risk associated with roads varied widely among discrete populations, with probabilities of extinction over 100-year projections reaching 5.1% for spotted turtles, and 58.8% for Blanding's turtles. We conclude that conservation interventions are most likely to be effective in mitigating the effects of road mortality when implemented at the road segment and population scales.

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1. Introduction

Endangered species conservation often requires identifying specific threats to populations, and designing and implementing mitigation measures. These measures can be spatially generalized and applied to entire jurisdictions, or they can be spatially targeted to areas where the threat process

occurs at a higher rate than in surrounding areas (threat hot spots). For many wide-ranging species conservation strategies are most successful and cost-effective when tailored to local conditions (Wittingham et al., 2007; Stahl et al., 2001). Examples of spatially specific measures include poaching control, habitat enhancement and restoration, or population reintroductions. To select the best possible site for localized

* Corresponding author. Present address: Department of Forest and Wildlife Ecology, 1630 Linden Dr., University of Wisconsin-Madison, Madison, WI 53690, USA. Tel.: +1 608 265 2228; fax: +1 608 9922.

E-mail addresses: frederic.beaudry@umit.maine.edu (F. Beaudry), phillip.demaynadier@maine.gov (P.G. deMaynadier), hunter@umenfa.maine.edu (M.L. Hunter).

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mitigation measures, and to forecast the effect of those measures on the population as a whole, specific threat processes need to be understood at all relevant spatial scales.

Roads are increasingly recognized as a widespread ecological threat (Forman and Alexander, 1998; Trombulak and Frisell, 2000), and road mortality has been shown to have significant effects on certain wildlife populations (Dalrymple and Reicheinbach, 1984; Kushlan, 1988; Fahrig et al., 1995; Lodé, 2000; Hels and Buchwald, 2001; Gibbs and Shriver, 2002). Mitigating road mortality requires knowledge of species movement patterns and other processes at various spatial scales (Malo et al., 2004). At the finest scale, a roadkill event is the result of an individual's movement coinciding with a moving vehicle at a specific site. At a coarser scale, local population behavior patterns, along with road segment characteristics, may determine the presence of road mortality hot spots. Finally, at the broader geographic scale a species' life-history traits may increase the inherent vulnerability of entire populations, or even the species, to regional road networks.

Spotted turtles (*Clemmys guttata*) and Blanding's turtles (*Emydoidea blandingii*) approach the northeastern edge of their range in northern New England, USA (Ernst et al., 1994). State listed as threatened and endangered, respectively, they occupy southern Maine where human population density and growth are high and rates of exurban sprawl are among the fastest in the region (Plantinga et al., 1999). The area's high rate of habitat loss and fragmentation endangers turtle populations that are inherently limited by delayed sexual maturity, low annual fecundity, and low recruitment rates (DePari et al., 1987; Congdon and van Loben Sels, 1993; Congdon et al., 1993, 2000; Litzgus and Brooks, 1998a,b). For populations to persist, these characteristic freshwater turtle life-history traits need to be offset by high adult survivorship and longevity (Heppell, 1998; Litzgus, 2006). Road mortality, as a relatively new source of chronic adult mortality, can lead turtle populations to negative growth rates and local extirpation (Brooks et al., 1991; Congdon et al., 1993; Doak et al., 1994). Additionally, the complex movement ecology and habitat requirements of spotted and Blanding's turtles make their populations especially vulnerable to road mortality: over the course of a year, they typically visit multiple wetlands to forage, mate, thermoregulate, and overwinter (Rowe and Moll, 1991; Joyal et al., 2001;

Grgurovic and Sievert, 2005), requiring frequent overland migrations and road crossings.

At road mortality's finest spatial scale, individual behavior determines the location of a turtle's crossing site. For some species, crossing site selection is repeated by multiple individuals, blurring the distinction between single movement and road segment scales (e.g. crossings that follow riparian areas, or ridgelines), but for other species the physical crossing location is variable and difficult to predict. Road crossing events by spotted and Blanding's turtles are rarely witnessed by researchers and thus their road crossing behavior is poorly understood.

At the road segment scale, previous research on other taxa has detected road-crossing patterns, usually by correlating roadkill locations with environmental factors (e.g. Clevenger et al., 2003; Taylor and Goldingay, 2004). However, the processes regulating the distribution of road mortality hot spots at this scale are rarely determined (but see Clevenger et al., 2002). We introduce the use of a gravity model to represent road-crossing behavior by semi-aquatic turtles. Gravity models allow one to estimate the interaction, or flow, between two points, based on their characteristics and proximity (Isard, 1975). Such models are commonly used in geographic applications such as human migration and epidemiology (e.g. Plane, 1984; Xia et al., 2004), and recently in ecology to predict the dispersal of invasive species and pathogens (Bossenbroek et al., 2001; Ferrari et al., 2006; Muirhead et al., 2006).

Finally, demographic modeling has been used to evaluate the effects of road mortality at the broader population scale: using population abundance estimates (Carr and Fahrig, 2001; Brock and Kelt, 2004), investigations of survivorship and reproduction (Mumme et al., 2000), and population viability analysis (van der Grift et al., 2003; Row et al., 2007). Models based on the probability of being killed while crossing a road have been used to evaluate consequences to amphibian and reptile populations (Hels and Buchwald, 2001; Gibbs and Shriver, 2002).

Recognizing the potential importance of road mortality to the population viability of spotted and Blanding's turtles, we examined the distribution of roadkill risk at three spatial scales (Table 1). We first used individual behavior, specifically upland path tortuosity, in order to predict road-crossing

Table 1 – Major factors considered when quantifying the spatial distribution of roadkill risk for spotted and Blanding's turtles in southern Maine, including scale-specific data sources and analyses employed

Scale (spatial extent):	Single movement (<0.5 km)	Road segment (up to 5 km)	Population (>5 km)
Roadkill risk factors:	Interwetland movement tortuosity	Wetland type Wetland proximity Road locations	Interwetland movement Wetland arrangement Road locations Vehicle traffic rates
Data sources:	Thread tracking	Radio telemetry NWI and road layers	Radio-telemetry Traffic rates Road layers Population parameters
Data treatment:	Residuals analysis GIS analysis	Habitat selection analysis GIS analysis Gravity model	GIS analysis Road-crossing model Spatially explicit PVA

locations at the scale of individual movements. We then integrated habitat selection into a gravity model of wetland-to-wetland interactions in order to identify road mortality hot spots at the road segment scale. Finally, we scaled up individual road-crossing risk estimates for distinct focal areas and assessed the consequences on resident turtle populations by conducting a spatially explicit population viability analysis. By evaluating road mortality risk at multiple scales, we hope to assist in developing both local and regional conservation measures for minimizing the effects of road mortality on rare turtles and similarly vulnerable taxa.

2. Study area

Fieldwork was conducted in York County, southern Maine, USA (43°N, 70°W). The low-elevation (<100 m) terrain is characterized by shallow soils, rocky outcrops, and mixed second or third-growth forest. The post-glacial landscape supports a high density of pocket wetlands consisting mainly of vernal pools, red maple (*Acer rubrum*) swamps, and scrub-shrub swamps dominated by high-bush blueberry (*Vaccinium corymbosum*), buttonbush (*Cephalanthus occidentalis*), and winterberry (*Ilex verticillata*). Predominant land uses include rural and suburban residential areas, low-intensity forest management, active and abandoned agricultural fields and pastures, and conservation lands. Work was conducted in five focal areas for both turtle species, and a sixth occupied only by Blanding's turtles. Continuous survey effort by the Maine Department of Inland Fisheries and Wildlife since 1990, along with survey and trapping effort concurrent with this study, identified these focal areas as hosting the majority of the state's spotted and Blanding's turtle populations. Focal areas were renamed A through F to prevent location disclosure and minimize the risk of illegal collection.

3. Methods

3.1. Field methods

Radio-telemetry was conducted between April and November in 2004, 2005, and 2006. Turtles were captured by hand or with baited hoop-net traps starting at spring thaw in early April. Sex was determined by plastron shape and chin color for spotted turtles, and by plastron shape, preanal tail length, and upper jaw pigmentation for Blanding's turtles (Graham and Doyle, 1979; Ernst et al., 1994). Age was estimated by averaging three counts of separate plastral growth rings, up to approximately 20 years. Beyond that age the annuli are difficult to read accurately and the turtle was recorded as >20 years of age. Thirty-nine adult spotted turtles (23 females, 16 males) and fifty adult Blanding's turtles (23 females, 27 males) were fitted with a radio-transmitter positioned near the posterior carapace margin. Lotek MBFT (Lotek Wireless, Newmarket, Ontario, Canada), and RI-2B (Holohil Systems, Carp, Ontario, Canada) transmitters were affixed with Biocryl® rapid-curing dental acrylic (Great Lakes Orthodontics, Tonawanda, New York, USA). Expected battery life was 242–448 days, and average transmitter package weight was between 3% and 6% of body weight. Turtles were released at the site of capture the same day.

Each radio-tagged turtle was relocated with a hand-held, 64-cm two-element antenna (Telonics, Mesa, Arizona, USA) and a digital receiver (Communication Specialists, Orange, California, USA). Relocation frequency varied from daily for nesting females to weekly in the fall in an attempt to keep the number of inter-wetland movements between relocations at no more than one (70% of all relocations showed no inter-wetland movement). Locations were recorded with a hand-held Global Positioning System (GPS; Garmin International, Olathe Kansas, USA), or on a digital orthoquadrangle image acquired in April–May 2003 (Maine Office of GIS, data available online [apollo.ogis.state.me.us]). Each radio-tagged individual was tracked for a single annual activity season.

3.2. Single movement scale

To check the assumption that turtles move in a straight line, the tortuosity of terrestrial movements was evaluated using thread tracking. When adult turtles were encountered upland, a 400-m spool-less thread bobbin (Komar Thread Inc., Chicago, IL) was positioned on the posterior central scutes using conduit tape (Wilson, 1994). The thread was located the next day and the turtle's path was mapped using a pole (1.5 m for spotted, 2 m for Blanding's turtles) and compass. All paths were then digitized, and for each location point the distance to the straight line between destination and origin (the x , y residual) was calculated. Each path's straight line was standardized to a common origin and destination point, and all the residuals were standardized (hereafter referred to as positional residuals) by dividing their absolute value by the net movement length and plotted on a common x -axis. At 20 intervals along this axis, the 75th and 95th percentiles of the positional residuals were identified, and generalized curves were fitted to these values using the two-parameter function

$$Y(x) = a(1 - e^{b(|x-0.5|-0.5)})$$

where a determines the height of the curve, and b dictates the rate at which it rises and falls. A regression was completed to determine the relationship between the positional residuals and movement length, allowing the subsequent proper scaling of the generalized curves to any inter-wetland distance. The curves were then used to represent the areas encompassing 75% and 95% of the positional residuals closest to the straight line. Once overlain on wetland and road GIS layers, these curves identified potential crossing areas over a road section, with the assumptions that both the generalized curves and the scaling function represent most of the variation in inter-wetland turtle movements.

3.3. Road segment scale

An analysis of the arrangement and composition of wetlands across the landscape was conducted to identify road mortality risk at the scale of a road segment. First, a third-order (Johnson, 1980), within home range habitat selection analysis was performed to obtain selection indices for each of the wetland types used as assigned on National Wetland Inventory (NWI) maps (Cowardin et al., 1979). Available wetlands were identified as those within a buffer around each radiolocation point. Buffer size (spotted: 211 m, Blanding's: 364 m)

corresponded to the mean length of wetland-to-wetland movements recorded for each species during three seasons of radiotelemetry (F. Beaudry, unpublished data). Wetlands with multiple type classes (e.g. PEM/SS) were assigned to all classes represented. An estimator for the selection ratio was then calculated for each class as

$$\hat{w}_i = u_{i+} / \sum_{j=1}^n \pi_{ij} u_{+j}$$

where u_{i+} is the total number of wetlands of category i used, π_{ij} is the known proportion of wetlands of category i available to each individual j , and u_{+j} corresponds to the total number of wetlands used by each individual (Manly et al., 2002). The selection ratios were standardized into selection indices where the classes add up to 1.

A gravity model was used to estimate the relative frequency of turtles moving between wetlands. Given that inter-wetland movements for freshwater turtles have been shown to be dependent on both distance and wetland quality (Bowne et al., 2006), a gravity model integrating these two parameters should provide useful estimates of the relative frequency of turtle movements between individual wetlands. Furthermore, since roadkills occasionally interrupt these movements, this approach permits the identification of potential turtle crossing and road mortality hot spots. The interaction between two wetlands, T_{ij} , was estimated as

$$T_{ij} = \frac{k w_i w_j}{d^2}$$

where k is a scaling factor held constant, w_i and w_j are attractiveness values for the origin and destination wetlands, here the standardized selection index for each wetland, and d is the wetland center-to-center distance.

To demonstrate the approach used at this scale, a road segment was selected for its high traffic volume and proximity to spotted and Blanding's turtle habitat. Each wetland on one side of the road was paired with every wetland across

the road, provided it was within the observed range of each species' wetland-to-wetland movement distances (95th percentile). Each across-road pair was linked by a straight line, and at each intersection of that line with the road segment (represented by a single line, as width of the road was ignored), a point was created and given the T_{ij} value associated with the wetland pair. Finally, a 20-m cell raster layer was created, and each cell was attributed the sum of the T_{ij} values for all the points within a two-cell (40 m) radius. The cells were color-coded to help illustrate areas where the estimated relative frequency of turtle movement, and thus road mortality risk, were highest.

3.4. Population scale

For this analysis focal area boundaries were defined by aggregated buffers placed around each radiolocation point. The buffer radius corresponded to the mean inter-wetland movement length observed (spotted turtles: 211 m, Blanding's turtles: 364 m). The population in each of these focal areas was then simulated in a spatially explicit, age-structured, meta-population viability model developed using program RAMAS GIS v.5 (Akçakaya, 2005).

Parameters used in the simulations were empirically derived, obtained from other studies, or were derived from expert opinion (Table 2). For Blanding's turtles, age at first reproduction averaged 17.5 years in Michigan (Congdon et al., 1993), thus we defined 18 years old turtles as sexually mature. Sexual maturity for spotted turtles was set at 12 years after an Ontario study (Litzgus and Brooks, 1998a). An estimated 82.6% of Maine's sexually mature female Blanding's bred each year ($n = 21$), close to the 80% observed in Michigan (Congdon et al., 1993). All female spotted turtles radiotracked in this study were gravid prior to the nesting season ($n = 23$). For both species, the mean number of offspring is based on X-ray photography of gravid females radio-tracked during this study ($n = 12$ for spotted turtles, $n = 9$ for Blanding's; Table 2).

Table 2 – Parameters used in the population viability analysis for spotted and Blanding's turtles, using RAMAS GIS v.5

Parameters	<i>C. guttata</i>	<i>E. blandingii</i>
Replications	1000	1000
Time projection (years)	100	100
Mating system	Polygynous	Polygynous
Sexual maturity (years)	12	18
Proportion of females breeding	100%	82.6%
Mean clutch size	5.42 (0.100)	11.67 (2.74)
Fecundity	0.426 (0.106)	0.855 (0.214)
Sex ratio at birth	1:1	1:1
Survival juveniles	0.780 (0.098)	0.795 (0.100)
Baseline survival adult females	0.965 (0.057)	0.960 (0.057)
Baseline survival adult males	0.942 (0.084)	0.960 (0.086)
Demographic stochasticity	Included	Included
Environmental stochasticity distribution	Lognormal	Lognormal
Initial population	2400	2900
Extinction definition	$N < 10$	$N < 10$
Correlation of fecundity and survival	Uncorrelated	Uncorrelated
Initial age distribution	Stable	Stable
Number of populations	5	6
Values in parentheses are standard deviations.		

Fecundity estimates corresponded to the number of female offspring produced surviving to the next spring. Fecundity was estimated by multiplying the average clutch size obtained from X-ray photography with the percent of females breeding (this study), then by a hatchling survivorship estimate obtained from Blanding's turtles in Michigan (Congdon et al., 1993), applied to both species.

No long-term mark-recapture dataset exists for either spotted or Blanding's turtles in Maine, so mortality rates were derived from the literature (Table 2). Blanding's estimates were obtained from a 34-year study of a stable population in Michigan (Congdon et al., 1993, and Congdon et al., 2000). Published adult spotted turtle survival estimates were available from an Ontario study (Litzgus, 2006), and juvenile survival was adjusted to allow for a stable population. In the absence of known estimates of the yearly variation around survival rates for both spotted and Blanding's turtles, standard deviations were obtained from a relatively undisturbed population of another long-lived species, ornate box turtles (*Terrapene ornata ornata*). Based on an 18-year mark-recapture study, annual standard deviation of survival was 8.9% for males and 5.9% for females (Converse et al., 2005). We used these values for sub-adults and adults of both species, while standard deviation around the survival of juveniles was set at 12.5% of the mean (Table 2; cf. MacDonald and Ise, 2006).

For each focal area, the number of road crossings completed by radiotracked turtles was inferred from the location data. Each road crossing was associated with an estimate of the number of vehicles per minute for that specific road (N). This traffic rate was based on road-segment specific Maine Department of Transportation 2005 annualized average daily traffic rate estimates (AADT), and then modified as follows:

$$N = \frac{F_{\text{season}} \times 0.8 \text{AADT}}{1440}$$

where the rate was reduced by a factor of 0.8 to represent the proportion of traffic estimated to occur between 0600 and 1800 h (Festini, 1996), as nearly all of this study's observed turtle movements occurred during the morning, day, or early evening hours. Tourism increases traffic seasonally in southern Maine, so AADT was also multiplied by a seasonal traffic correction factor ($F_{\text{season}} = 1.093$) averaged for the turtles' active season, April–October, representing a 9.3% increase in traffic volume over the annual average (Maine Department of Transportation, 2006). The subsequent division by 1440 changes traffic units from vehicles/day to vehicles/min.

For each crossing, the probability of being killed by a vehicle (P_{killed}) was defined as

$$P_{\text{killed}} = 1 - e^{-Na/v}$$

where a is the "kill zone" on the road (twice a tire's width plus twice the shell length), and v is the turtle walking speed in m/min (modified slightly from Gibbs and Shriver, 2002). For shell length, the median carapace length of adults from this study was used (spotted turtles, 12.3 cm; Blanding's turtles, 21.4 cm), and tire width was set at 25 cm. Turtle velocity estimates were estimated based upon field observation and published values from other turtle species (Muegel and Claussen, 1994; Marvin and Lutterschmidt, 1997; Wren et al., 1998) as

follows: 4.1 m/min for spotted and 7.5 m/min for Blanding's turtles.

The probabilities of being killed by a vehicle for each crossing were totaled for each focal area, and subtracted from the baseline survival rate obtained from stable populations. These new survival rates, along with recalculated standard deviations, were used for each population to create a spatially explicit metapopulation model.

4. Results

4.1. Single movement scale

Thread-tracking turtles moving upland between wetlands revealed paths with some tortuosity, evident as positional residuals arcing away from the x-axis representing total net movements (Fig. 1). Spotted turtles diverged less from a straight line than Blanding's turtles, both in absolute terms and proportionally, given that spotted turtles' thread-tracked movements were shorter (mean: 102 m, s.d.: 80 m, range: 18–251 m) than Blanding's (mean: 163 m, s.d.: 98 m, range: 16–430 m). The two-parameter functions used to describe the 75th and 95th percentile positional residuals also varied between spotted (75th: $a = 0.14$, $b = 6$; 95th: $a = 0.19$, $b = 7$) and Blanding's turtles (75th: $a = 0.18$, $b = 7$; 95th: $a = 0.29$, $b = 9$). As an example, the 75th percentile curve should be interpreted as comprising 75% of the locations where a turtle would be if it was going from point 0 to point 1. The relationship between the net movement length and the size of the positional residuals was adequately described by linear functions with each species (Fig. 2), suggesting that relative tortuosity was directly proportional to total distances moved. Proportional linear scaling was therefore used to map potential turtle path deviations from the straight-line shortest route between two wetlands. When this turtle path area is overlain on a GIS layer of Focal Area D's busiest road, the segment of road intersected (i.e. area of potential road–turtle intersection) is more than 100-m long for spotted turtles, and greater than 600-m long for Blanding's turtles (Fig. 3). The length of the road–turtle intersection zone is positively correlated with the distance of the wetlands to the road, the distance between the origin and destination wetlands, and the angle between the path and the road.

4.2. Road segment scale

The habitat selection analysis was based on the use of 78 wetlands by spotted turtles, and 175 wetlands by Blanding's turtles. Each spotted turtle visited on average 3.4 unique wetlands per year (range: 1–9), compared to 6.5 wetlands per year (range: 1–20) for Blanding's turtle, with no difference between sexes within species. Both spotted and Blanding's turtles showed the strongest selection for emergent wetlands and scrub-shrub swamps (Table 3). The wetland type most available to both species was forested-deciduous wetlands, typically red-maple swamps, for which selection was far below availability.

In Area D, the gravity model clearly identified hot spots where road mortality risk is potentially highest for rare turtles

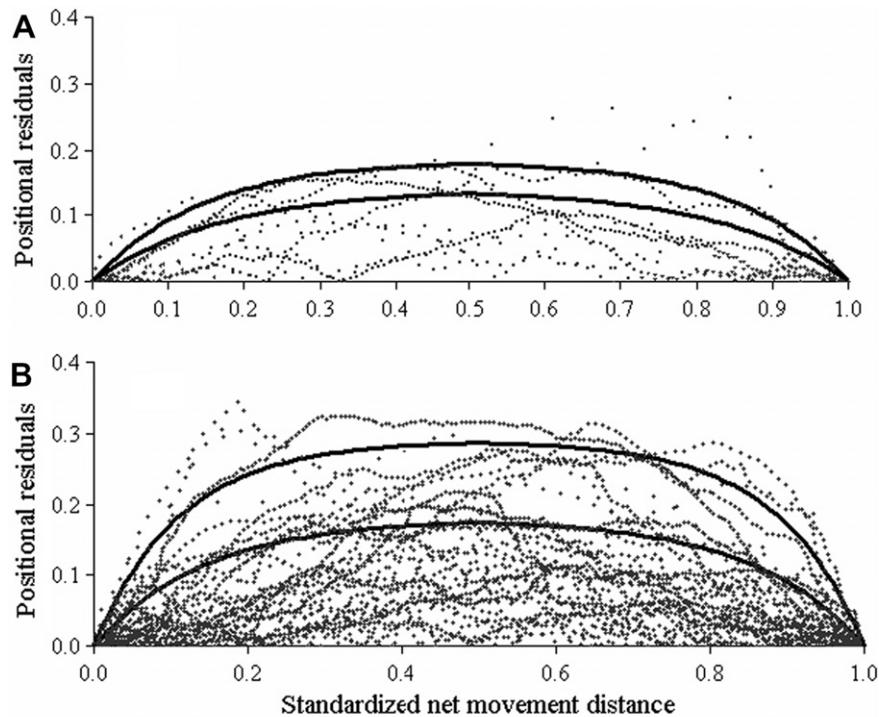


Fig. 1 – Standardized representations of upland paths from turtles completing wetland-to-wetland movements, tracked using thread bobbins. Spotted turtle (A) sample is from 11 tracks obtained from 9 individuals; Blanding's turtle (B) is from 52 tracks and 27 individuals. Inner and outer solid lines represent approximately 75% and 95% of the positional residuals closest to the straight line. The path of a turtle traveling in a perfectly straight line would lie on the x-axis.

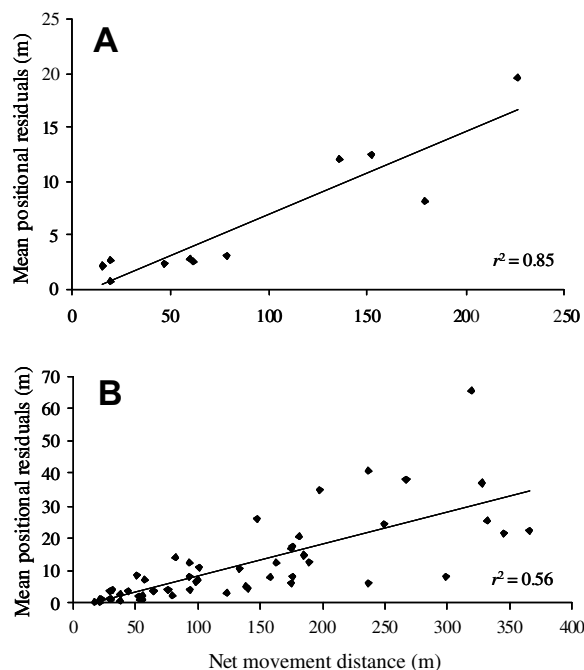


Fig. 2 – Relationship between mean x, y residuals (distance away from straight line) and net upland path length from turtles completing wetland-to-wetland movements. Spotted turtle (A) sample is from 11 tracks obtained from 9 individuals; Blanding's turtle (B) is from 52 tracks and 27 individuals.

(Fig. 4). The distance between wetlands, the selection index of each wetland, and the number of wetlands clustered together all influenced the location of hot spots. Because of their longer movement capacity, many more pairs of wetlands were within reach of wetland-to-wetland movements for Blanding's than for spotted turtles.

4.3. Population scale

Based on the best data available for both species and under current conditions, all populations are projected to decline over the next 100 years within the focal areas examined, and many show a high risk of extinction (Table 4). The spotted turtle population in Area D faces the greatest decline (98.3%) and extinction (5.1%) risks. The Blanding's turtle population in the same area has a nearly 60% chance of extinction in the next 100 years, followed by populations in areas B (11%) and E (6.9%) (Table 4). Populations in areas A, C, and F of both species, despite a low risk of extinction, show a considerable probability of decline (>30%). Interestingly, areas with the highest road density are not necessarily those with the highest risk to turtles (Fig. 5) – other factors such as road arrangement and traffic volume are not examined here.

5. Discussion

While there is increasing recognition that road mortality is among the greatest threats to the viability of semi-aquatic turtle populations, including spotted and Blanding's turtles

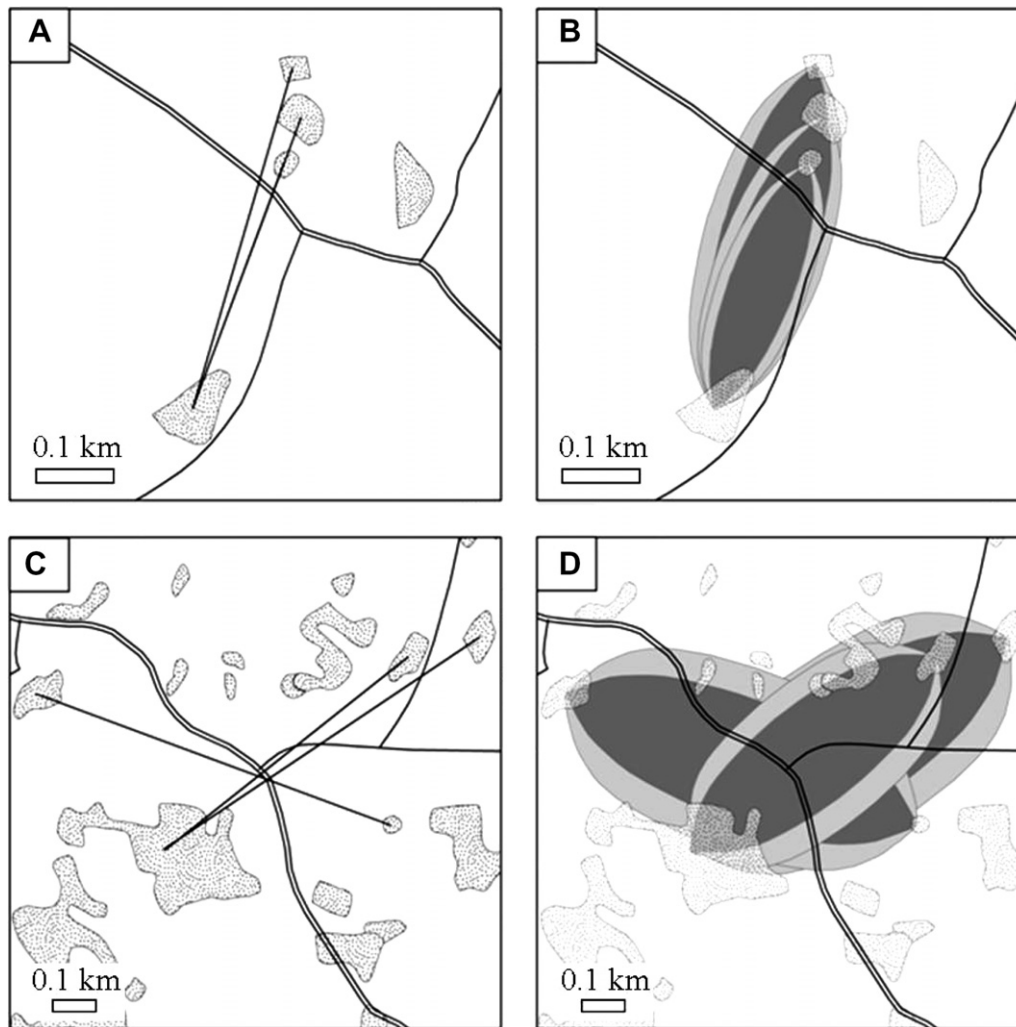


Fig. 3 – Modeled inter-wetland interactions for spotted turtles (A; $n = 3$) and Blanding's turtles (C; $n = 3$). Thread tracking data were used to predict how far upland paths deviate from the straight-line, shortest route (spotted turtles: B, Blanding's turtles: D). Shown here are areas where 75% (inner area) and 95% (outer area) of upland paths are predicted to be located for each inter-wetland interaction.

in New England, questions remain about the effectiveness of specific mitigation measures and their location on the landscape. We have identified three spatial scales where road mortality processes, their consequences for rare turtles, and possible mitigation measures can all be examined. First, at the finest scale of a single turtle inter-wetland movement, individual behavior leads to variable path sinuosity, and consequently a wide area of potential road crossing uncertainty – over 100 m and 600 m for spotted and Blanding's, respectively. At the broader road segment scale, wetland selection patterns and individual behavior can be used to predict the relative frequency of inter-wetland movements and thus the location of potential road mortality hot spots. Lastly, at the population scale, we observed that the number and arrangement of roads and associated traffic volumes in a given area can have significant effects on populations, in one case generating a probability of local extinction more than fifty-fold that of areas with little predicted road mortality. All three scales revealed spatial variations in the road mortality risk for spotted and Blanding's turtles. The nature and amplitude of variations at

each scale should inform the selection of conservation mitigation measures.

5.1. Single movement scale

The area representing potential spotted and Blanding's turtle trajectories between wetlands intersected with long sections of road (Fig. 3). The length of that overlap is dependent on the distance of the wetlands to the road, the distance between the origin and destination wetlands, and the angle at which the path lies in relationship to the road. The predicted possible paths between wetlands occupy an area broad enough that the precise location of road-crossing sites is difficult to pin-point, an important aspect to consider when planning road mortality mitigation measures.

The upland travel paths generally appeared as long, sweeping arcs. These non-random movements are probably directed, as previous experiments suggest that aquatic turtles possess navigational abilities (Yeomans, 1995; Caldwell and Nams, 2006). Given the longevity of both these turtle species,

Table 3 – Standardized indices of wetland selection (availability in parentheses) by NWI class for spotted and Blanding's turtles in Maine, 2004–2006

NWI class	PFO1E	PSS1E	PUBH	PEM1E	PFO4/1E	PUBF	PSS1F	L1UB
Description	Deciduous forested swamp	Shrub swamp, medium hydroperiod	Open wetland, medium hydroperiod	Emergent vegetation	Mixed forested swamp	Open wetland, short hydroperiod	Shrub swamp, long hydroperiod	Lake or reservoir
<i>C. guttata</i>	0.07 (0.44)	0.14 (0.20)	<u>0.14</u> (0.13)	<u>0.24</u> (0.11)	<u>0.09</u> (0.04)	<u>0.10</u> (0.04)	<u>0.14</u> (0.02)	Na (na)
<i>E. blandingii</i>	0.05 (0.48)	0.10 (0.18)	0.15 (0.15)	<u>0.21</u> (0.04)	0.06 (0.06)	<u>0.08</u> (0.05)	<u>0.31</u> (0.02)	<u>0.05</u> (0.01)

Underlined values are for wetland types with a selection index greater than its availability.

it is likely that they have made the same movements in previous years. Indeed turtles are known to maintain a geographic memory, possibly using landmarks and vegetation communities (Emlen, 1969; Bowne and White, 2004). An alternative hypothesis could suggest that the movements observed simply represent an effective search strategy where the locations of the resource patches are unknown. Computer simulations predicted that animals could most effectively search an inhospitable matrix for resource patches, such as wetlands, by moving in a nearly straight line through the landscape (Zollner and Lima, 1999). Predictions stemming from these simulations also positively associated the straightness of the search paths with the matrix hostility, and negatively with energy reserves and perceptual abilities (Zollner and Lima, 1999). Whether semi-aquatic turtles use navigational mechanisms or an effective search strategy in a largely unknown environment, they would benefit greatly from moving in a directed manner, as they face potential predators and chronic water loss in the upland environment (Ernst, 1968; Finkler, 2001), incur a high locomotion cost (2.64 times that of swimming, Baudinette et al., 2000), and are limited by olfactory and visual organs located a few centimeters above the ground.

The extrapolation of upland path patterns from path segments to full inter-wetland movements appears appropriate, since the relationship between the x, y residuals and the x-axis appeared linear, allowing the scaling of the thread-tracking patterns up to the wetland-to-wetland movement scale (Fig. 2). Similarly, the search paths displayed by painted turtles (*Chrysemys picta*) retained the same basic shape at two spatial scales: both small-scale (approximately 30 m) and large-scale (greater than 500 m) movements were nearly straight and had similarly small turning angles (Bowne and White, 2004).

5.2. Road segment scale

Analysis at the road segment scale located potential road mortality hot spots across the landscape, where the interactions between wetlands (T_{ij} values) were predicted to be high, or where a large number of such interactions clustered. More specifically, the gravity model estimated greater interactions when wetlands were in close proximity and when the habitat selection indices of specific wetlands were high (Fig. 4). Similarly, both distance and habitat quality have been shown to be primary factors influencing habitat connectivity, specifically inter-wetland movements, for adult painted turtles (Bowne et al., 2006).

The gravity model approach does have some potential limitations. Notably, the model assumes that the distance-decay function is constant across the landscape and for all individuals. Field observations from this study largely support this assumption for Blanding's turtles, whose movements did not appear to be affected by varying land cover types. This cannot yet be said for spotted turtles, as we observed few of their terrestrial movements. If upon further study it is found that land cover types impose differential "resistance" upon spotted turtle movements, the distance exponent of the gravity model can be changed to create a steeper distance-decay curve. Alternative approaches incorporating landscape

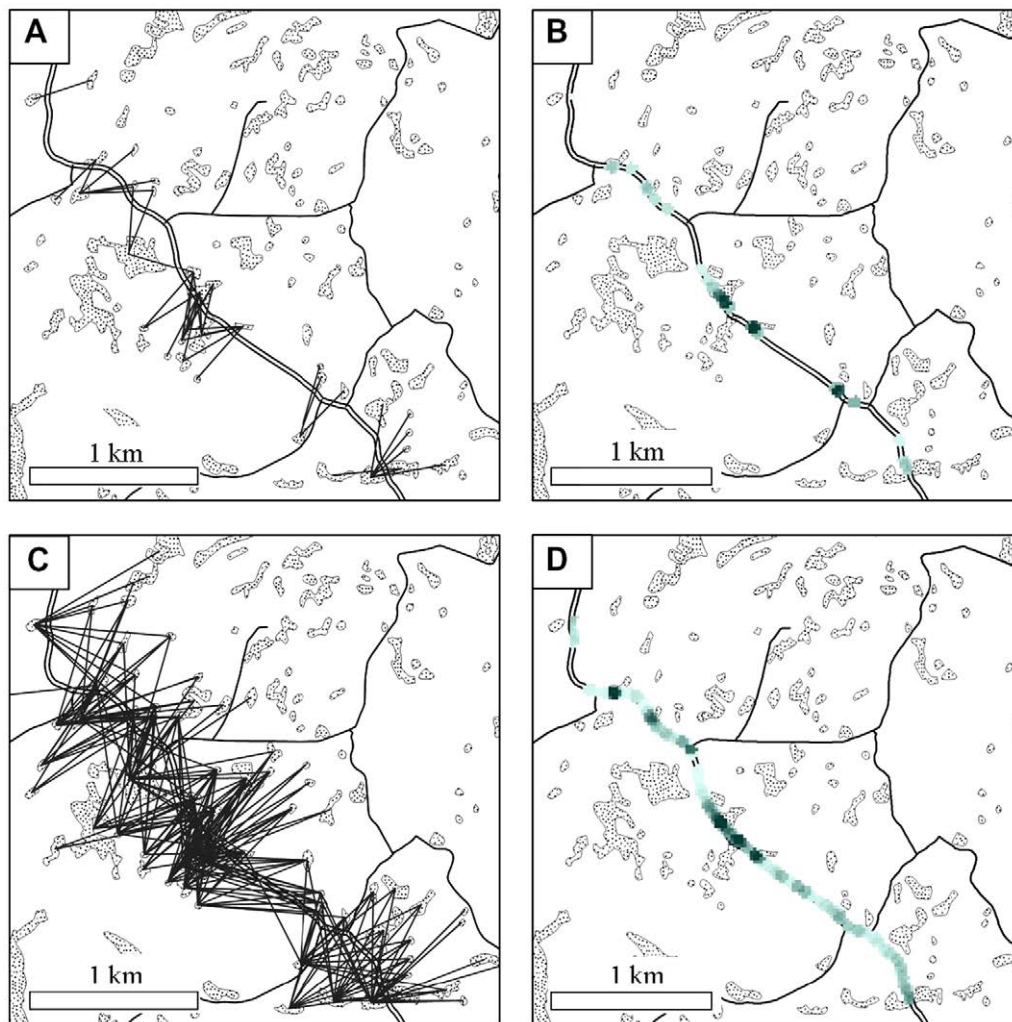


Fig. 4 – Possible inter-wetland interactions for spotted turtles (A; $n = 39$) and Blanding's turtles (C; $n = 249$) on a road segment in Area D, from a gravity model based on inter-wetland distance and wetland type selection. Potential road mortality hot spots (spotted turtles: B, Blanding's turtles: D) based on inter-wetland interaction values are represented by deeper shades of gray.

Table 4 – Spotted and Blanding's turtle population decline and extinction risk under current conditions, for six focal areas in Maine

Focal area		A	B	C	D	E	F
<i>C. guttata</i>	Number of radiotracked individuals	0	3	7	8	12	4
	Probability of a 50% decline	n/a ^b	0.421	0.413	0.983	0.299	0.319
	Probability of extinction ^a	n/a	0.013	0.005	0.051	0.004	0.014
<i>E. blandingii</i>	Number of radiotracked individuals	5	6	4	9	18	5
	Probability of a 50% decline	0.395	0.970	0.380	1.000	0.994	0.390
	Probability of extinction ^a	0.010	0.110	0.011	0.588	0.069	0.008

a Probability that the population declines below 10 individuals.

b No spotted turtles are known to occur in Area A.

friction exist for amphibians (Joly et al., 2003; Compton et al., 2007), and could be adapted for this species to more finely represent connectivity between wetlands.

Additionally, the gravity model approach to identifying road mortality hot spots ignores another level of complexity: wetlands with low selection value may be stepping-stone

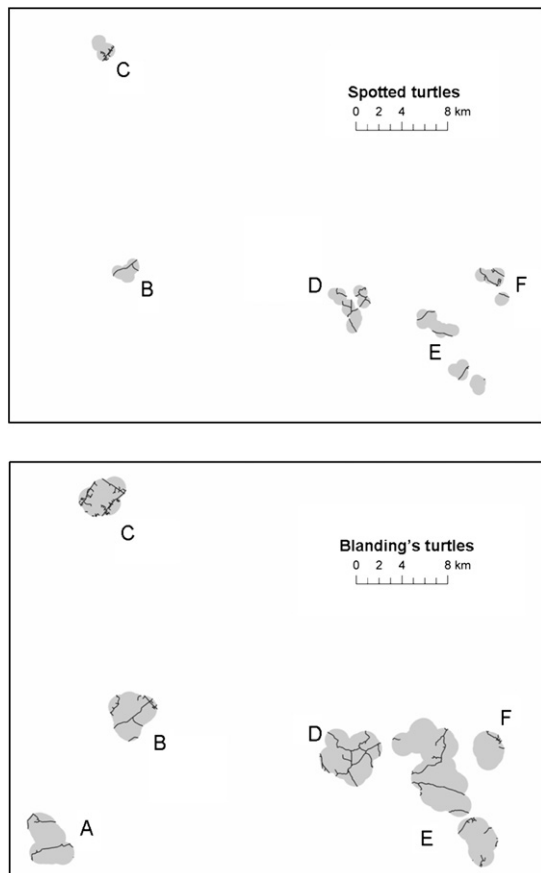


Fig. 5 – Spatial distribution of selected spotted and Blanding's turtle populations (focal areas) in Maine. Road segments overlapping the focal areas are included to help interpret differences in estimated area-specific extinction rates, but other spatial references are removed to reduce the risk of illegal collection.

wetlands between more attractive wetlands. The gravity model considers only the origin and destination wetlands, and ignores those used before or after, leading to a potential underestimation of the true interaction level. Finally, to evaluate the gravity model's effectiveness at predicting spatial variations in road mortality, our modeled hot spot road segments should be compared to independently acquired data. The Maine Department of Inland Fisheries and Wildlife collects citizen-reported turtle roadkill and road crossing observations, and as the database becomes richer for spotted and Blanding's turtles, it may be possible to conduct a model validation analysis.

5.3. Population scale

Roads appear to be a significant threat to the persistence of spotted and Blanding's turtle populations in Maine. While most spotted turtle populations examined have a small estimated extinction rate, all have a 30% or greater probability of a 50% decline in population size. Among Blanding's turtle populations, there is a 38% to nearly 100% probability of decline by at least half.

Population viability analysis (PVA) models are currently the best way to evaluate extinction risk, with the alternatives considered subjective, less rigorous, and likely to provide less accurate predictions (Brook et al., 2000; Burgman, 2000). The use of PVA models for evaluating management options by contrasting relative predictions, rather than absolute ones, is generally recommended (Beissinger and Westphal, 1998; Brook et al., 2000; Coulson et al., 2001; McCarthy et al., 2001). The predictions presented here should be interpreted with care, with the understanding that some parameter values (e.g. baseline survival) were estimates derived from other turtle populations, and that the simulations assume that the parameter values stay constant over the relatively lengthy projection period of 100 years.

For both species the focal area that hosts populations at greatest risk is Area D. Every radio-tagged Blanding's turtle in this area has crossed at least one road, as several clusters of highly suitable wetlands are separated by roads. Interestingly, road density alone did not appear to correlate well with predicted population declines and extinctions. This is due in part to both the wide range in traffic volumes (10–9950 vehicles per day) and the landscape position of the existing road network in relationship to suitable wetlands. For example, Area C has the highest road density but most of the roads are located on the periphery of the area (Fig. 5), circumscribing rather than bisecting concentrations of suitable wetlands. A third confounding effect may involve individual learned or evolved behavior: some areas include relatively busy roads with wetlands on both sides, but the radio-tracked turtles have not been observed crossing these roads. It is likely that a larger sample size or tracking period may have yielded more road crossing observations. On the other hand, it is possible that the turtles that routinely crossed busier roads have been previously killed, and those that persist are relatively more sedentary, generally keeping to wetlands on one side of the road. Further research is needed to determine whether specific road characteristics (e.g. width, traffic volume) can alter or reduce the behavioral motivation to attempt crossing (deMaynadier and Hunter, 2000). Also of importance, selective mortality of certain individuals may be more damaging in the long run than a general reduction in population size. For example, it has been shown that road mortality disproportionately kills females in some turtle populations, leading to a locally skewed sex ratio (Steen and Gibbs, 2004; Aresco, 2005a; Steen et al., 2006).

Road mortality was factored into our spatially explicit PVA using the Gibbs and Shriver (2002) roadkill model, which itself carries several assumptions. Among those, two critical ones are that turtles are assumed to cross roads perpendicularly and at a constant speed without stopping. If instead turtles stopped on the roadway, maybe after a near collision with a vehicle, the risk would be substantially higher. Further studies of turtle behavior when approaching and crossing roads are needed in both experimental and semi-natural settings. Driver behavior is also ignored in the roadkill model; for example, a bias may exist if drivers actively try to avoid or run over turtles. In Ontario, 4.4% of drivers confronted with a juvenile snapping turtle decoy deliberately hit it, while 3.2% stopped to “rescue” the model (Ashley et al., 2007). The incidence of intentional killing probably varies regionally,

and in some areas may be substantial enough to warrant inclusion in a roadkill model.

Long-distance migration and dispersal have been shown to increase some vertebrates' exposure to additional mortality (Ferrerías et al., 2004; Yoder et al., 2004), and it is likely that widely dispersing reptiles are at an increased risk of roadkill, but no such data exist for freshwater turtles. We observed exceptional mobility of spotted and Blanding's turtles, including a series of movements by an adult male Blanding's turtle amounting to 17-km round-trip over a four-month period (F. Beaudry, unpublished data), illustrating the species' capability of long dispersal movements. However, in the absence of additional information on dispersal patterns, no such events or their associated mortality risks were integrated into the PVA, potentially resulting in an underestimated risk. Finally, road mortality of juveniles has been ignored in this analysis due to a lack of data on juvenile movement and habitat selection for these species. Juvenile survival is not as critical a parameter as adult survival for long-lived turtle species (Heppell, 1998), but nevertheless juvenile roadkill may further weaken overall population viability.

5.4. Management implications

The life history traits and movement ecology of many freshwater turtles make them especially sensitive to the demographic effects of road mortality. A comprehensive understanding of road mortality risk requires an investigation of its effects on populations at multiple scales – from the crossing behavior of individual turtles, to landscape-scale patterns of movement and habitat selection.

The results obtained here can assist in selecting appropriate spatial scales to intervene with conservation mitigation. First, the wide distribution of road mortality risk at even the finest scale of individual movements challenges the notion that management interventions operating at a single point location, such as undergrade passages, can be effective for wide-ranging turtle species. While the effective width of an underground tunnel or adapted culvert could be increased along a road segment by adding funneling walls on either side (Dodd et al., 2004; Aresco, 2005b), such devices would need to extend up to hundreds of meters long to intercept the full range of potential turtle road crossing variability that we observed, making them expensive to build and maintain. Also, the use of cautionary road signs indicating specific turtle crossing locations are less likely to be effective where extensive road frontage intercepts inter-wetland migration routes.

At the larger road segment scale, the gravity model clearly identified hot spots, providing guidance for spatially explicit mitigation planning, provided the methods used are appropriately scaled. Possible conservation measures appropriate for this scale of road segment vulnerability include seasonally reduced speed limits, exclusionary fencing, or zonal signage, where road crossing sign placement is designed to warn motorists that they are entering a high-risk area (versus specific crossing locales). For periods during which road mortality risk is highest (e.g. June and July for Blanding's turtles, F. Beaudry, P.G. deMaynadier, and M.L. Hunter, Jr., unpublished manuscript), volunteers could patrol these hot spots in order to assist road-crossing turtles. Given the sensitivity of rare

turtles to chronic sources of adult mortality (Heppell, 1998; Litzgus, 2006), these localized interventions can be critical for reducing risk to local populations.

A comprehensive approach to conservation mitigation should also consider spatial variations at the population level. Discrete geographic areas identified as having high roadkill rates could be targeted for population-wide interventions including public outreach and education using wide-ranging media sources, or traffic calming, a traffic engineering method that involves channeling of commuter traffic to roads that are safer to the public and to wildlife (Jaarsma and Willems, 2002). Conversely, rare turtle populations identified as least affected by roadkill could be prioritized for protection from future road frontage development and associated traffic increases through targeted land protection.

Unfortunately, the effects of roads on wildlife populations are not limited to roadkill. In addition, roads may limit specific life-history movements, including both migration and dispersal (Edwards et al., 2004; deMaynadier and Hunter, 2000), excluding individuals from high-quality habitat (Gibeau et al., 2002), generating genetic differentiation (Riley et al., 2006; Kuehn et al., 2007), reducing genetic diversity (Keller and Largiadèr, 2003; Epps et al., 2005), and ultimately affecting population persistence. A thorough analysis of the effects of roads on wildlife populations needs to consider both the direct effects of roadkill and the indirect effects of population fragmentation if a comprehensive road mitigation strategy is to be successfully implemented for multiple taxa of conservation concern.

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