The Journal of Wildlife Management 76(6):1215–1224; 2012; DOI: 10.1002/jwmg.358

Management and Conservation

Integrated Risk Factors for Vertebrate Roadkill in Southern Ontario

ROBERT G. FARMER,[1,2] *Department of Biology, University of Guelph, 50 Stone Road East, Guelph, Ontario, Canada N1G 2W1*
RON J. BROOKS, *Department of Biology, University of Guelph, 50 Stone Road East, Guelph, Ontario, Canada N1G 2W1*

ABSTRACT Road mortality of animals (roadkill) threatens public safety and wildlife populations. As mitigation tools, predictive models of roadkill are becoming more common in the published literature; however, few models generalize across multiple taxa, and thus are less useful for management scenarios that account for multiple target species. Using a dataset of 653 vertebrate roadkills collected from 2 parks in southern Ontario, we constructed generalized linear mixed models to determine the simultaneous risk factors for bird, frog, mammal, five-lined skink (*Eumeces fasciatus*), snake, toad, and turtle hatchling roadkills from among a set of 8 potential predictor variables. Posted road speed limit was the dominant roadkill predictor (positive coefficient), followed by maximum daily temperature (positive), habitat diversity (positive), and distance from wetlands (negative). All else being equal, as road speed limits increase from 20 km/hr to 50 km/hr, the model predicted the season's mean roadkill probability for a given location to increase from less than 0.1 to 0.75. Conversely, roadkill probability declined from 0.55 to 0.29 as distance from wetland edges increases from 0 km to 1 km. Model diagnostics calculated from randomly resampled cross-validation datasets indicated that the best model formulation had an averaged predictive accuracy of 67.5% and an area under the curve (AUC) of 0.867. The best model also reflected seasonal patterns of animal behavior, including late-summer frog movements and fall turtle hatching events. The best model also compared favorably to single-taxon equivalent models. To reduce the incidence of vertebrate roadkill, we recommend that managers lower road speed limits, especially on roads near diverse habitats and near wetlands, and on warmer days if temporary signage is used. © 2012 The Wildlife Society.

KEY WORDS amphibians, birds, generalized linear mixed models, mammals, reptiles, roadkill, road mortality. southern Ontario.

Ecological studies have shown that roads affect wildlife populations in many ways, often negatively (Fahrig and Rytwinski 2009). One effect of roads is wildlife-vehicle collisions resulting in animal mortality (roadkill), a phenomenon that can have substantial negative impacts on a variety of taxa, especially reptiles and amphibians (Ashley and Robinson 1996, Steen et al. 2006, Row et al. 2007, Fahrig and Rytwinski 2009). In addition to direct population effects, roadkill can also visibly tarnish the image of protected areas, and among large animals, it can have human safety consequences (Nielsen et al. 2003, Malo et al. 2004, Seiler 2005).

Recognizing that roadkill is a multispecies problem, roadkill mitigation should ideally involve strategies that capitalize on shared risk factors among multiple taxonomic groups, assuming these risk factors are sufficiently informative for all taxa and that the plight of a single species (or taxonomic group) is not an urgent management concern. Identifying generalized risk factors would help to balance the needs of multiple taxonomic groups and limited management resources, and would be consistent with ecosystem management strategies preferred by many jurisdictions (e.g., Grumbine 1994, Zorn et al. 2001).

Unfortunately, most published predictive models for roadkill have targeted specific taxonomic groups, rather than generalizing across taxa. For example, published research identified predictors of roadkill for mammals (Clevenger et al. 2003, Malo et al. 2004, Seiler 2005, Ramp et al. 2006), birds (Clevenger et al. 2003, Ramp et al. 2006), or reptiles and amphibians (Orlowski et al. 2008, Langen et al. 2009) using models derived independently for each taxonomic group. If roadkill probability shares common risk factors across taxonomic groups, we argue that for generalized roadkill management, information is needlessly lost in single-taxon models. This information loss can be avoided by using statistical techniques such as mixed-effects modeling, which generalizes effects across all groups (i.e., as fixed effects) while providing simultaneous corrections for group-specific deviations from an overall mean (as random intercepts) and group-specific deviations from an overall trend (as random slopes; Pinheiro and Bates 2004,

Received: 5 August 2010; Accepted: 6 December 2011;
Published: 6 March 2012

Additional supporting information may be found in the online version of this article.

[1] *E-mail: farmerb@dal.ca*

[2] *Present address: Department of Biology, Dalhousie University, 1355 Oxford Street, Halifax, Nova Scotia, Canada B3H 4R2.*

Gelman and Hill 2007). We used generalized linear mixed modeling to integrate roadkill risk factors using information from 7 vertebrate taxa. In doing so, we capitalize on the increased information available from a sample-rich, multi-taxon roadkill dataset, while simultaneously accounting for and measuring independent, taxon-specific patterns in the form of random-effects coefficients.

Most roadkill events probably involve a combination of several converging ecological and anthropogenic processes which include 1) processes contributing to high animal abundance near and on roadways; 2) processes contributing to high vehicle traffic on roadways; and 3) processes leading to reduced driver avoidance of collisions (Jaeger et al. 2005, Ramp et al. 2006, Fahrig and Rytwinski 2009, but see Seiler 2005). Accordingly, to mitigate roadkill incidence, managers can act upon any or all of these processes and their associated risk factors. In our research, we consider 8 possible predictor variables representing each of these 3 processes, and incorporate information from roadkills of 7 vertebrate groups—birds, frogs, skinks (*Eumeces fasciatus*), mammals, snakes, turtle hatchlings, and toads—to generalize about predictor effects. Our predictors of interest included local building density, road curves, distance from water, distance from wetlands, habitat diversity, maximum daily temperature, rain, and posted road speed limit.

Local building density may correspond to more small mammal and bird roadkills (Clevenger et al. 2003) and reduced abundance of herpetofauna, potentially translating to fewer roadkills of reptiles and amphibians (Knutson et al. 1999). The presence of curves in a road contributes to reduced forward visibility, leading to reduced driver reaction times. Curves are also positively associated with mammal-vehicle collision locations (Klocker et al. 2006). Road locations closer to water tend to feature more mammal (Eurasian otter, *Lutra lutra*; Philcox et al. 1999), amphibian (Langen et al. 2009), and reptile (Ashley and Robinson 1996) roadkills, a clear consequence of animal habitat preferences (Marchand and Litvaitis 2004). Road locations nearer to wetlands are similarly associated with roadkill (Ashley and Robinson 1996, Langen et al. 2009). Additionally, more diverse habitats are associated with more mammal roadkills (Malo et al. 2004) and in some cases, greater anuran abundance, and diversity (Knutson et al. 1999), potentially translating to greater anuran roadkill risk.

Ectotherms such as snakes and turtles are more active on hot days in northeastern North America (our study location); hence, higher temperatures can translate to increased roadkill counts of these taxa (Shepard et al. 2008*a*). Similarly, reptile (turtle; Shepard et al. 2008*a*) and amphibian (Clevenger et al. 2003, Mazerolle 2004) roadkills occur more frequently during summer rain events. Rain can also decrease driver visibility and stopping distance. Posted road speed limits, often inferred by measures of traffic volume (Clevenger et al. 2003, Seiler 2005), may have a linear (snakes, turtles; Gibbs and Shriver 2002; Andrews and Gibbons 2005) or quadratic (mammals; Clarke et al. 1998, Seiler 2005) relationship with roadkills for some taxa. In the lower range of road speeds and traffic volumes (i.e., secondary highways and smaller roads), increased posted road speed limits and traffic volumes tend to predict a linear increase in roadkill counts (Jones 2000, Seiler 2005).

Our goal was to identify the most informative environmental predictors of multi-taxon vertebrate roadkill for our study region. Accordingly, we modeled the relationship between roadkill incidence and the previously mentioned environmental covariates, determining the most informative and parsimonious subset. To test the robustness of our result and, more broadly, our use of a multi-taxon approach in general, we subsequently measured the predictive success of the best model and compared it to identically specified models built using fewer (usually 1) taxonomic groups.

STUDY AREA

We conducted our study in 2 government-run parks (Point Pelee National Park and Rondeau Provincial Park) in southern Ontario, Canada (Fig. 1). Southern Ontario is a region of extensive agriculture and urbanization; our study parks constituted small patches of deciduous forest in a heavily modified landscape and contained a variety of endangered species (Kerr and Cihlar 2004, Kerr and Deguise 2004), which were susceptible to road mortality. Species protection in these areas was mainly accomplished through perpetual land-use restrictions; most human activities were concentrated in small regions of each park, and the destruction of habitat and wildlife was forbidden or else highly regulated in rare cases (e.g., cottage maintenance, controlled burns by park staff). Public road and trail networks were found throughout each park.

Point Pelee National Park was a 20 km^2 area of deciduous forest, wetland, and sand beach on western Lake Erie, situated at the southernmost tip of mainland Canada (41° 58′ N, 82° 31′ W; Fig. 1). Surrounded by cropland and cottage development, the day-use park contained approximately 11.2 km of roads with speed limits ranging from 20 to 50 km/hr. Rondeau Provincial Park was a 32.5 km^2 area also on western Lake Erie, located about 75 km northeast of Point Pelee (42° 19′ N, 81° 51′ W; Fig. 1). It was also composed of deciduous forest, wetland, and sand beach, and was surrounded by cropland and cottage development. Rondeau contained 262 campsites that were densely clustered near the northern boundary, and much of the park's eastern and northwestern shores were lined with cottages on land leased from the park by private individuals. Interior park roads, with an approximate total length of 17.2 km, had speed limits 20–50 km/hr (in most cases, 40–50 km/hr). Approximate road widths in all cases were 7.5 m or less.

METHODS

Field Methods

We collected roadkill incidence data during an approximately 6-month bicycle survey at the 2 study sites, regularly surveying a road transect in each park between 7 May and 26 October 2005. We conducted 118 standardized roadkill surveys ($n_{\mathrm{PointPelee}} = 62$, $n_{\mathrm{Rondeau}} = 56$), 5 days/week, sampling each park on alternate weeks. At Point Pelee, we

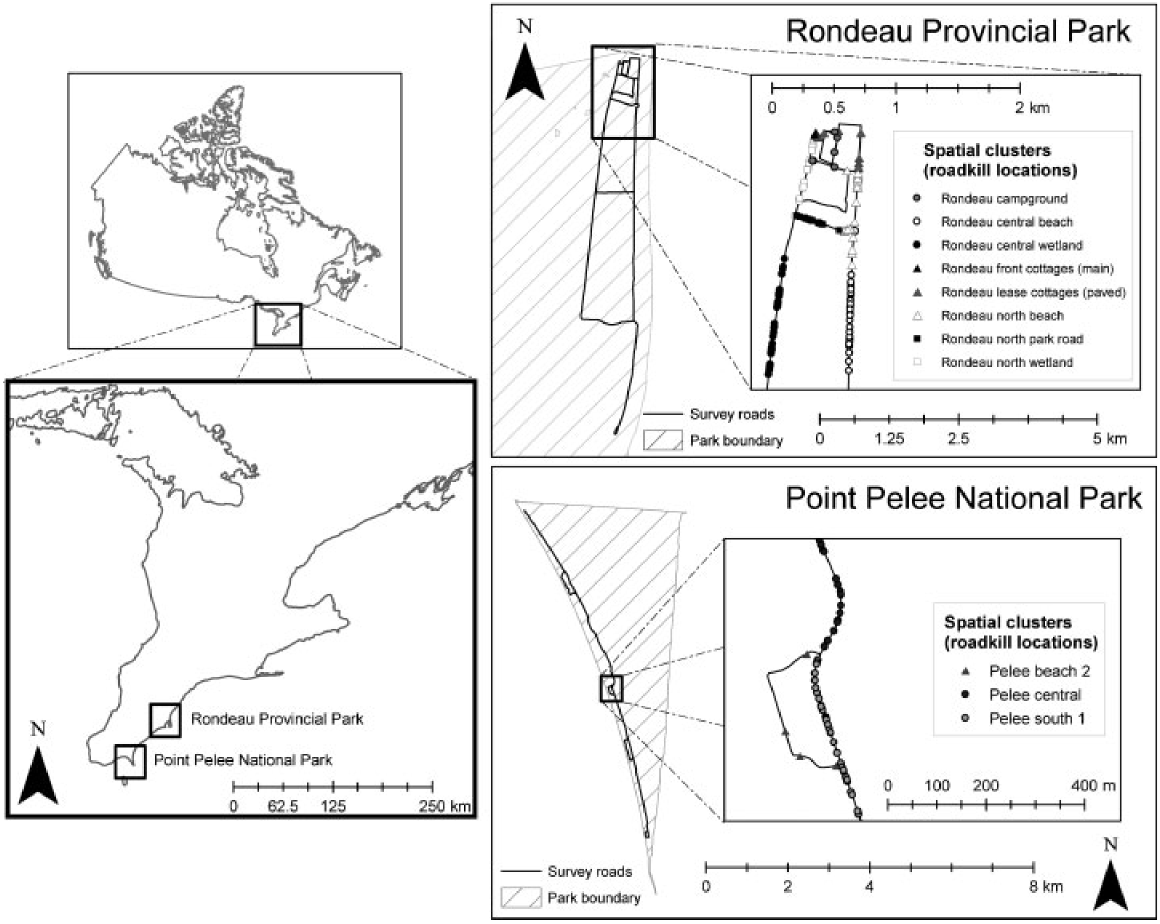

Figure 1. Study areas (Rondeau Provincial Park and Point Pelee National Park, Ontario, Canada) and roadkill survey roads, showing selected spatial cluster subregions.

surveyed all 11.2 km of the park's roads per survey, whereas at Rondeau, we surveyed 16.5 km (80%) of the park's approximately 20.6 km of public roads per survey. Although we also surveyed 4.7 km and 4.6 km of roads outside of Point Pelee and Rondeau, respectively, we did not model roadkill incidence information from these areas because habitat diversity information was unavailable; data from these sections of road were used in summary statistics (total roadkill counts; Table 1) only.

Within each week, start times of surveys were kept within 24 hours of the previous survey ($\mu = 23.3$ hr, $\sigma = 1.74$ hr), with surveys usually starting in mid-morning. During each survey, a single observer rode a bicycle at a slow speed (averaging 14 km/hr) and stopped to examine and remove any dead vertebrate found on the road surface. We chose bicycling over driving because it increased our ability to detect small taxa such as frogs (Langen et al. 2007); we consequently assumed perfect detection probability. Where feasible, depending upon carcass integrity, we identified the carcass, noted its location with a global positioning system (±10 m), and discarded it off the roadway to prevent double-counting. Owing to the large number of

Table 1. Sample sizes and incidence of roadkills collected in Point Pelee and Rondeau parks, southern Ontario, Canada, 2005. The number of modeled datapoints (i.e., those datapoints with complete information on every predictor variable) appear first; total collected datapoints, some of which were not modeled, are in parentheses for reference. Roadkill incidence and maximum roadkill incidence are measured as modeled roadkills per 10 km per day among both parks collectively.

	Sample size (Point Pelee)	Sample size (Rondeau)	Sample size (both parks)	Roadkill incidence (mean roadkills/10 km/day)	Maximum roadkill incidence (roadkills/10 km/day)
Amphibian (species unknown)	24 (103)	3 (19)	27 (122)	0.90 ± 3.83	29.5
Bird	17 (137)	24 (69)	41 (206)	1.43 ± 2.27	11.6
Frog	123 (235)	49 (135)	172 (370)	2.53 ± 7.11	58.04
Mammal	8 (22)	32 (90)	40 (112)	0.65 ± 0.86	3.64
Skink	13 (16)	14 (18)	27 (34)	0.22 ± 0.72	6.25
Snake	48 (77)	84 (171)	132 (248)	1.50 ± 1.98	10.30
Toad	164 (246)	33 (122)	197 (368)	2.55 ± 3.89	21.43
Turtle (hatchling)	3 (12)	14 (24)	17 (36)	0.22 ± 0.58	3.64
All roadkills	400 (848)	253 (648)	653 (1496)	10.0 ± 12.67	88.39

unidentifiable amphibian carcasses, we added a generic category of the same name (amphibian) to our list of taxa, and recorded these carcasses as such. We categorized roadkills by age group; we considered all amphibians, frogs, snakes and toads part of a single age group (adult-juvenile), birds to be adults unless pin feathers were present (fledgling), and all mammals and skinks to be adults. We considered turtles to be adults unless their carapace length was <4.5 cm, in which case we recorded them as hatchlings. In our roadkill models, we assumed that dead animals found on the road were killed by vehicles, and did not die as a result of other stressors (e.g., predation) before being run over. We excluded live animals and carcasses that appeared unusually dried or old, suggestive of a missed detection from an earlier survey, from the modeling dataset.

We used a geographic information system (GIS) and weather station data to associate several environmental covariates with each datapoint, including building density, the presence of curves, distance from water and wetlands, habitat diversity, maximum daily temperature, incidence of rain, and posted speed limit. We defined building density as the $\ln(x + 1)$ transformed kernel density value, derived from a surface of building locations generated in a GIS from aerial photos as a grid of 25 m pixels using a kernel bandwidth of 500 m. We determined curve locations subjectively from roads mapped in a GIS. We calculated distance from water and distance from wetlands as the distance from a roadkill datapoint to the nearest water or wetland edge defined in the Ontario GIS Fundamental Dataset (http://www.mnr.gov.on.ca/en/Business/LIO/index.html, accessed 30 Dec 2011). We defined habitat diversity as the number of ecozone habitat classes (as defined in the original government dataset using provincial Ecological Land Classification survey criteria; http://www.mnr.gov.on.ca/en/Business/LUEPS/Publication/264779.html, accessed 30 Dec 2011) within 25 m of a roadkill datapoint. We measured maximum daily temperature in degrees Celsius as the maximum temperature of the previous day recorded by the nearest Environment Canada weather stations (Kingsville and Erieau for Point Pelee and Rondeau parks, respectively). We derived rain incidence similarly using weather station data. Road speed limits refer to the posted road speed limits.

Because we conducted surveys at each park on alternating weeks, roadkills collected on the first survey day of every week were not representative of the previous day's weather data (temperature, rain), which by definition referred only to conditions within the past 24 hours. Our statistical models did not accommodate missing values; hence, all roadkill locations collected on the first day of a given week were excluded from the regression models, resulting in unequal collected and modeled sample sizes (Table 1). We report roadkill counts by taxon using the larger dataset (Table 1); we calculated all remaining summary statistics (Table 1) and models from the smaller dataset.

Statistical Methods

To create a dataset suitable for logistic regression, we collected a number of randomly located non-kill (null) points, equivalent to the number of roadkills recorded on a previous day, during each survey using a bicycle odometer and a random-distance generator. At the end of the season, we excluded null points found to be within 10 m of any kill point from the analysis. We randomly assigned null points to a survey day, ensuring that all time-sensitive effects were randomly distributed. To assemble the modeling dataset, we then randomly sampled with replacement an equivalent number of null points as modeled kill locations for each taxon.

We did not standardize any predictors, and instead inferred their relative influence from their corresponding model *t*-statistics. After verifying that collinearity between all variables was not present (Spearman's $\rho < 0.7$, sensu Clevenger et al. 2003; Variance Inflation Factor for continuous variables <2, Fox and Monette 1992), we built a global generalized linear mixed model (GLMM) containing all potential predictor variables using the package MASS (Venables and Ripley 2002) in R (R Version 2.12.0, http://r-project.org, accessed 17 Oct 2010), where roadkill was a Bernoulli dependent variable (presence or absence), modeled with binomial error and a logit link. Generalized linear mixed models are an extension of linear mixed models (Gelman and Hill 2007) that incorporate link functions to model the response, analogous to generalized linear models with random effects structures (Venables and Ripley 2002). We specified a nested random effects grouping structure consisting of spatial clusters within park within month within taxon, where spatial cluster groups were defined as contiguous sections of roads within a park sharing the same road substrate (e.g., paved, gravel) and shade characteristics (e.g., full canopy cover, no canopy cover; we derived cluster definitions from field observation and aerial photograph interpretation; Fig. 1). We removed most spatial autocorrelation by specifying an exponential spatial correlation structure (Pinheiro and Bates 2004, Zuur et al. 2009) using the *x*- and *y*-coordinates of each datapoint, but also included the spatial cluster grouping level as a random effect to ensure complete spatial independence (i.e., asymptotic semivariograms; Fortin and Dale 2005).

The random effects structure included normally distributed random intercepts for each level of nesting, allowing for different mean roadkill probability values among the groups at each level. To identify terms also requiring a random slope at the taxon level (i.e., a different rate of change for a predictor variable among taxa), we built global models for each taxon in isolation, and noted those fixed-effects terms for which the effects were both significant ($P < 0.05$) and of varying signs (i.e., both positive and negative) among taxa. Random slopes (drawn from a normal distribution) to account for differences among taxa were required for building density, distance from wetlands and maximum temperature in the global model.

We used a backwards stepwise selection approach to remove variables having little influence on roadkill probability. Stepwise approaches are effective at selecting predictor variables from a large set of candidate variables (Murtaugh 2009). Here, we sequentially removed variables from the global model having a *P*-value greater than 0.1, beginning with the least significant term. The final, best model was chosen as that model for which no more steps were required (i.e., *P* for all terms was less than 0.1). Based on our inspection of binned residual plots (Gelman and Hill 2007), the normalized residuals of models from each step showed no evidence of inappropriate fit (i.e., we found no systematic patterns).

For the models produced at each variable elimination step, we compared the averaged predictive accuracies and areas under the receiver operating characteristic curves (AUCs, which give a measure of predictive specificity balanced against predictive accuracy; Eng 2005) generated using a 10-fold split-sample cross-validation procedure. In this procedure, we randomly sampled 90% of each group of park × taxon datapoints 10 times in order to create 10 training datasets from which we refit converging cross-validation models of the same formulation as the parent model. We calculated predictive accuracies and AUCs for each cross-validation model using the remaining cross-validation data (i.e., the remaining 10% of the data), and then averaged the values. This modification of standard cross-validation and bootstrapping approaches was more computationally efficient than conventional alternatives, and necessary given the complex spatial correlation structures of the models. Given the large number of events per variable (EPV) in our dataset (653 events among 8 predictor variables, which is approximately 81 EPV), we do not expect our cross-validation method to be misleading; in general, EPV values exceeding 40 tend to minimize bias among logistic regression model diagnostics (Steyerberg et al. 2001).

To evaluate the taxonomic independence of the best multi-taxon model, we first built "best" logistic mixed models (i.e., with the same formulation as the best multi-taxon model) for each taxon separately, modeling the same random effects terms (excluding taxon effects, which could not exist by definition) and spatial covariance structures as before. We then compared the directionality and significances for each single-taxon model coefficient to those of the best multi-taxon model. We also assessed the sensitivity of the best multi-taxon model to the influence of particular taxa by building leave-1-taxon-out models, which shared the same model formulation as the best multi-taxon model, but which excluded a given taxon. To ensure that the influence of anuran species—which were particularly abundant in the sample–was not overly influential, we also built a model that excluded all members of the amphibian, frog, and toad taxonomic groups simultaneously. As with the single-taxon models, we compared the directionality and significance of model coefficients from the leave-1-taxon-out models to those of the best multi-taxon model.

RESULTS

Roadkill Frequency

We modeled 653 roadkill datapoints from a larger dataset of 1,496 events recorded during the sampling season (Table 1). Of the larger dataset, we could not identify approximately 7% of anuran kills to taxon owing to degraded body condition and we thus designated these simply as amphibian. We also collected data from 847 non-kill (null) sites.

Among the modeled data subset, averaged across both parks and along the entire 6-month field season, toads and frogs were the most likely taxa to be found dead on the road on any given survey (first survey of the week and amphibian records excluded), followed by snakes, birds, and mammals (Table 1). We encountered skinks and turtles relatively rarely (Table 1).

Multi-Taxon Models

The generalized linear mixed models (GLMMs) used 653 roadkill datapoints (Table 1) matched with the same number of randomly selected null points for a sample size of 1,306. In the roadkill dataset, each taxonomic group was often dominated by a few, common species (Appendix 1, available online at www.onlinelibrary.wiley.com). All modeled turtle roadkills were of hatchlings (<4.5 cm maximum carapace length).

In order of increasing influence on roadkill incidence, the variables building density, rain, distance from water, and curve were sequentially excluded from the full model. All GLMMs were reasonably accurate and specific in their ability to predict roadkills, with averaged prediction accuracy and AUC values exceeding 67% and 0.86, respectively (Table 2). Needing no further stepwise elimination of predictors, the final (best) model was specified as

$$P\,(\mathrm{Roadkill}_{itm:l:k:j}) \sim \mathrm{Bern}(\mu_{itm:l:k:j})$$

$$\begin{aligned}\mathrm{logit}\,(\mu_{itm:l:k:j}) = {} & \beta_0 \\ & + (\beta_{\mathrm{DistanceToWetland}} + b_{\mathrm{DistanceToWetland}_j}) \times x_{i_{\mathrm{DistanceToWetland}}} \\ & + \beta_{\mathrm{HabitatDiversity}} \times x_{i_{\mathrm{HabitatDiversity}}} \\ & + (\beta_{\mathrm{MaxTemp}} + b_{\mathrm{MaxTemp}_j}) \times x_{t_{\mathrm{MaxTemp}}} \\ & + \beta_{\mathrm{RoadSpeed}} \times x_{i_{\mathrm{RoadSpeed}}} + b_j + b_{k:j} + b_{l:k:j} + b_{m:l:k:j}\end{aligned}$$

where βs are fixed effects, bs are random effects, i is a particular location, t is a particular date, j is a particular taxon, $k{:}j$ is a particular month-within-taxon, $l{:}k{:}j$ is a particular park-within-month-within-taxon, $m{:}l{:}k{:}j$ is a particular spatial cluster-within-park-within-month-within-taxon, assuming an exponential spatial autocorrelation structure. This model had exclusively significant ($P < 0.05$) terms (Table 3), along with no systematic patterns in the residuals and an asymptotic semivariance curve.

The directionality of significant predictors in the single-taxon best models was entirely consistent with the corresponding predictors in the best multi-taxon model (Table 4). The number of times a variable was significant among these single-taxon cases also increased with a variable's predictive influence in the multi-taxon model (i.e., with a variable's absolute *t*-statistic; Table 3).

In the leave-one-taxon-out models, all terms except distance from wetlands had the same directionality and significance as the multi-taxon best model. Exceptions in this case were models that excluded 1 of anurans (amphibians, frogs, toads), snakes, toads, or turtles, which in each case still had a negative but now non-significant distance from wetlands

Table 2. Model cross-validation statistics for models predicting vertebrate roadkills in Point Pelee and Rondeau parks, southern Ontario, Canada, 2005, including averaged predictive accuracies and areas under the receiver operating characteristic curves (AUC) for resampled, 10-fold cross-validation models among the set of global and reduced models considered ($n_{\text{dataset}} = 1,306$).

Model	Accuracy	AUC	$n_{\text{FixedTerms}}$
Full (BldDens[a] + Curve + DistWat[b] + DistWet[c] + HabitatDiversity + MaxTemp + Rain + RoadSpeed)	67.587	0.872	9
Full − BldDens[a]	67.155	0.882	8
Full − BldDens[a] − Rain	67.759	0.883	7
Full − BldDens[a] − Rain − DistWat[b]	67.329	0.861	6
Full − BldDens[a] − Rain − DistWat[b] − Curve	67.5	0.867	5

[a] Building density.

[b] Distance from water.

[c] Distance from wetlands.

coefficient. This implies that no single taxon had an overly influential or skewed effect on parameter estimates made from a multi-taxon dataset.

Within the mixed-effects framework, a model's random effects describe group-specific patterns independent of the fixed effects (which generalize across groups). In the best multi-taxon model, the random effects terms with the greatest values indicated seasonal patterns of roadkill occurrence. Specifically, the month-within-taxon modifiers ($b_{k:j}$; Fig. 2) showed roadkill peaks in September for frogs and turtle hatchlings, in June for skinks and mammals, and in October for snakes. Random slopes for each taxon were functionally irrelevant as modifiers of the fixed-effects slope estimates (i.e., with values <0.1% of the fixed-effects terms); appreciable taxon-specific differences were only present as differences in mean values (i.e., differences in random intercepts).

Among the fixed effects coefficients of the best multi-taxon model, in decreasing order of influence (based upon absolute t-statistics), roadkill probability increased with 1) posted road speed limits (maximum road speed limits considered in this dataset were 50 km/hr), 2) at higher temperatures, 3) in areas with greater habitat diversity, and 4) in areas closer to wetlands. Posted road speed limits were by far the best roadkill predictors ($t_{\text{RoadSpeed}} = 11.453$ vs. $t_{\text{AllOtherPredictors}} \leq 4.104$). Under this model, at a speed limit of 20 km/hr, the season's mean roadkill probability at a given site for all taxa was less than 0.1 ($\hat{\mu} = 0.08$, 95% CI: 0.05–0.11), but it reached 0.75 ($\hat{\mu} = 0.75$, 95% CI: 0.68–0.82) along roads with speed limits of 50 km/hr, all other variables being set at their median, with no random effects (Fig. 3A).

Although the distance-to-wetland effect was weaker than the road-speed-limit effect ($|t_{\text{RoadSpeed}}| = 11.5$ vs. $|t_{\text{DistanceToWetland}}| = 3.5$), we highlight the relationship here because of its relevance to managers; distance to wetlands is more permanent than temperature, and more easily measured than habitat diversity. Controlling for other variables as previously described for the road speed limit effect, we found that mean roadkill probability was reduced by 0.26 at road locations 1 km from a wetland edge ($\hat{\mu} = 0.29$, 95% CI: 0.20–0.38) compared to roads directly adjacent to wetlands ($\hat{\mu} = 0.55$, 95% CI: 0.46–0.64; Fig. 3B).

DISCUSSION

Our research identified roadkill risk factors that were common to a variety of vertebrate taxa found in deciduous forest landscapes in southern Ontario. In decreasing order of influence, we found that roadkill risk was elevated in areas of greater posted road speed limits, during higher maximum daily temperatures, in areas of high habitat diversity, and close to wetlands. In developing the best model, we offer managers a robust and generalized approach to predicting and reducing roadkill incidence.

Evaluating the Multi-Taxon Modeling Approach

Our results suggest that the multi-taxon GLMM benefits from its large sample size, and hence the model detects weak but significant trends that are sometimes missed in the single-taxon and leave-1-taxon-out models. The multiple evaluation methods used also showed that all significant predictor variables in the best model formulation shared a common directionality among taxa. Hence, we have illustrated both the superior sensitivity of the mixed models to detecting significant trends in this case, and the taxonomic independence of the best multi-taxon model's predictions. Overall, our multi-taxon model is thus more informative than single-taxon approaches.

Seasonal Patterns

Seasonal patterns of frog mortality (based on the random-intercept modifiers, which are independent of the fixed-

Table 3. Coefficient statistics of the best generalized linear (logistic) mixed model predicting roadkill probability in Point Pelee and Rondeau parks, southern Ontario, Canada, 2005 ($n = 1,306$).

	β	SE	t	P
Intercept	−7.281	0.692	−10.525	<0.001
Distance from wetlands (m)	−0.001	0.0003	−3.478	<0.001
Habitat diversity (number of habitats)	0.386	0.099	3.911	<0.001
Maximum daily temperature (°C)	0.065	0.016	4.104	<0.001
Road speed limit (km/hr)	0.120	0.011	11.453	<0.001

Table 4. Sample sizes, coefficients and *P*-values of generalized linear mixed models predicting roadkills in Point Pelee and Rondeau parks, southern Ontario, Canada, 2005, constructed using data from exclusively 1 taxon. Predictors (columns) are arranged from left to right in increasing order of influence (absolute *t*-statistic) in the best multi-taxon model.

	n_{Tot}[a,b]	Intercept	Distance from wetland (m)	Habitat diversity (number of habitats)	Maximum daily temperature (°C)	Road speed limit (km/hr)
Amphibian	54	-10.904 ($P = 0.002$)	-0.0003 ($P = 0.87$)	-0.222 ($P = 0.66$)	0.204 ($P = 0.014$)	0.161 ($P = 0.005$)
Bird	82	-6.376 ($P = 0.008$)	-0.0003 ($P = 0.759$)	0.358 ($P = 0.365$)	0.043 ($P = 0.48$)	0.113 ($P = 0.006$)
Frog	344	-8.271 ($P < 0.001$)	-0.0003 ($P = 0.694$)	0.627 ($P = 0.001$)	0.058 ($P = 0.026$)	0.104 ($P < 0.001$)
Lizard	54	-7.416 ($P = 0.042$)	-0.0003 ($P = 0.813$)	0.002 ($P = 0.996$)	0.167 ($P = 0.023$)	0.082 ($P = 0.095$)
Mammal	80	-11.037 ($P = 0.001$)	0.001 ($P = 0.587$)	0.531 ($P = 0.257$)	-0.008 ($P = 0.849$)	0.231 ($P = 0.006$)
Snake	264	-2.758 ($P < 0.001$)	-0.001 ($P = 0.037$)	0.104 ($P = 0.2$)	0.001 ($P = 0.865$)	0.057 ($P < 0.001$)
Toad	394	-6.047 ($P < 0.001$)	-0.002 ($P = 0.005$)	0.319 ($P = 0.019$)	0.033 ($P = 0.027$)	0.097 ($P < 0.001$)
Turtle (hatchling)	34	-4.16 ($P = 0.161$)	-0.0001 ($P = 0.938$)	0.328 ($P = 0.251$)	0.06 ($P = 0.228$)	0.037 ($P = 0.501$)

[a] Total count of roadkill and null datapoints modeled.

[b] Sample sizes reflect the number of data records containing complete information for the best model predictors, and so are larger than the sample used in the backwards selection, which required complete data records for a more extensive set of potential covariates.

effects terms; Fig. 2) are consistent with a late-summer migration, which has been observed among roadkills of ranid frogs in New Brunswick, Canada (Mazerolle 2004), and of leopard frogs (*Lithobates pipiens*) at a large southern Ontario wetland (Long Point; Ashley and Robinson 1996). The sharp reduction in frog roadkill probability in June may reflect the peak period of (sedentary) breeding among members of this taxon, occurring between immigration and emigration events (e.g., Paton and Crouch 2002).

A fall peak in turtle hatchling roadkills almost undoubtedly resulted from a synchronized hatching event of snapping turtles (*Chelydra serpentina*), which were the most represented (59%) turtle species (Appendix 1, available online at www.onlinelibrary.wiley.com). In contrast, the June peak of skink and mammal mortalities was probably due to a period of (adult) mate-searching which occurs from late-May to early July for skinks (Committee on the Status of Endangered Wildlife in Canada, unpublished status report, available at http://www.sararegistry.gc.ca/document/dspText_e.cfm?ocid=5361), and in summer for the eastern chipmunk (*Tamias striatus*; the most-represented species among mammal roadkills, 45%; Appendix 1, available online at www.onlinelibrary.wiley.com; Loew 1999). An early-fall peak in snake roadkills consisted mainly of small, pale eastern foxsnakes (*Pantherophis gloydi*)—likely a mixture of hatchlings and juveniles—and may reflect a dispersal event for these age classes (Farmer and Brooks 2008).

Best Predictors

The high absolute *t*-statistic for road speed limit (Table 3) relative to other model parameters indicates that road speed limit is particularly good as a roadkill predictor. This finding is consistent with a prior analysis of our data which used hierarchical partitioning of generalized linear models built for each park × taxon combination to estimate the model-independent influence of a similar set of predictor variables (Chevan and Sutherland 1991, Farmer 2007). In this earlier analysis, posted road speed limit was consistently ranked as the most effective roadkill predictor across all models; in this study, $\beta_{\mathrm{RoadSpeed}}$ was also highly significant and positive. Similarly, in our cross-validation analyses, posted road speed limit was the most reliable predictor of roadkill probability

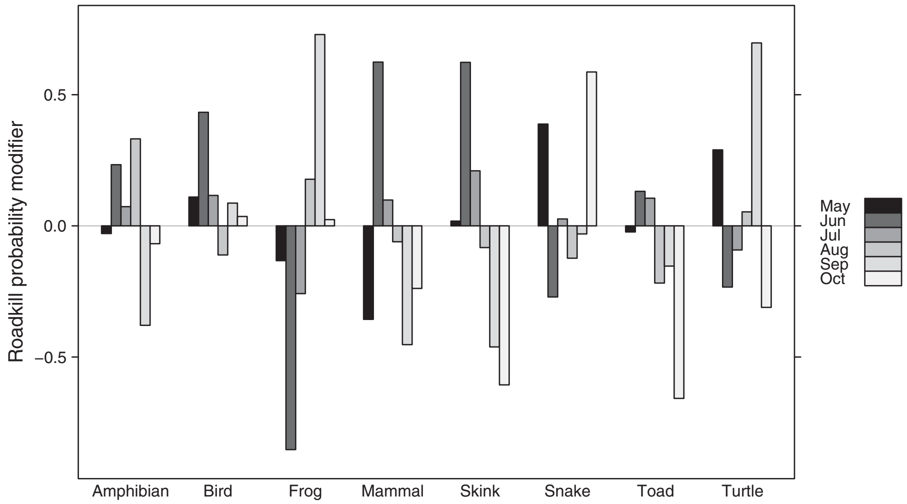

Figure 2. Random effects (intercept modifiers) for months-within-taxa from the best multi-taxon roadkill model (data collected from Point Pelee and Rondeau Parks, Ontario, Canada, 2005). Values are the adjustment for a particular group mean compared to the pooled mean from among all groups, and thus represent independent deviations from overall (i.e., all-taxon) trends.

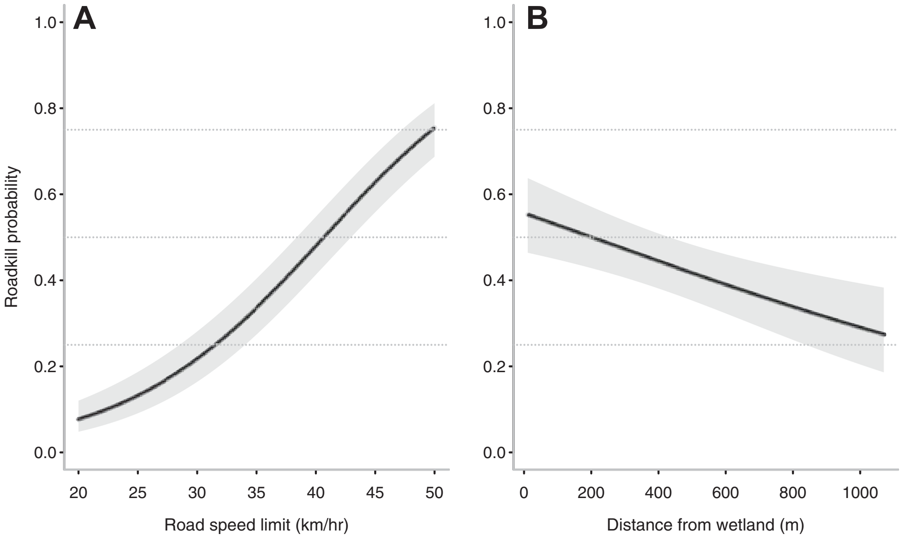

Figure 3. Predicted effect of posted road speed limit (A) and distance from wetland edges (B) on the season's roadkill probability at a given location for all modeled taxa combined, all other model factors being equal (data collected from Point Pelee and Rondeau Parks, Ontario, Canada, 2005). Shaded areas are 95% confidence intervals.

in GLMMs calculated for separate taxa (Table 4), again showing a consistently significant and strongly positive relationship with roadkill probability.

Observations from other studies suggest that road speed limits can be related to traffic volume (Clevenger et al. 2003, Seiler 2005). Consequently, it is probably inappropriate to presume that driver reaction distance, along with other factors that are also directly related to greater vehicle speeds, are the primary mechanisms behind the observed road speed limit–roadkill relationship. Traffic volume, and thus automobile presence, may also be an effective predictor. We note that past research has occasionally shown inconsistent patterns (Inbar and Mayer 1999, Mazerolle 2004, Coelho et al. 2008) or no pattern (Shepard et al. 2008*b*) between roadkill frequency and traffic volume; this may in some cases relate to road avoidance behaviors by animals that can occur above certain traffic volume thresholds (Clarke et al. 1998, Seiler 2005, Bouchard et al. 2009, Brockie et al. 2009, Eigenbrod et al. 2009, but see Ford and Fahrig 2008). In our case, none of the surveyed roads featured traffic volumes exceeding 3,000 vehicles per day (an estimated threshold value for road avoidance; Seiler 2005, Brockie et al. 2009); thus, we do not expect a local traffic volume effect to be nonlinear. From a management perspective, posted road speed limits are more easily changed than traffic volumes, and traffic volume changes may occur in concert with any such speed limit modification; hence, we believe that the roadkill–speed limit relationship observed here still has clear practical relevance, even if it is influenced by a combination of driver awareness and traffic volume effects.

The utility of maximum daily temperature as a roadkill predictor is consistent with the life histories and roadkill incidence of the ectothermic taxa studied here (e.g., frogs, skinks, snakes, toads; Ciesiolkiewicz et al. 2006, Shepard et al. 2008*a*). Furthermore, warmer temperatures may correlate with the activity levels of the remaining warm-blooded taxa (birds, mammals) and elevate their risk of becoming roadkill as well, although this effect could also be relatively weak (e.g., Table 4). However, in spite of the fairly broad taxonomic applicability of the temperature relationship, management strategies based on temperature information must necessarily be more adaptive and more rapidly implemented (e.g., temporary signage reducing speed limits or urging driver caution) than those based on permanent road speed limits, owing to the short-term variability and unpredictable nature of some weather systems. Future work should consider if the relationship between roadkill incidence and temperature might have a quadratic shape.

In addition to temperature, the best model also indicated that habitat is a good predictor of roadkill, where areas of higher habitat diversity and areas closer to wetlands tend to be at greater risk. Considering the predictors of high-risk habitats in detail, the positive relationship between habitat diversity and roadkill probability is consistent with evidence from large mammals (Malo et al. 2004). Given that roads themselves are an ecological edge, we speculate that roadside habitats featuring a variety of natural edges may support large and rich communities of animals attracted to edges, which translates to greater overall roadkill counts. An exception to this pattern is the significant risk factor for roads next to (homogeneous) wetland habitat, which is well-supported by past research (Ashley and Robinson 1996, Langen et al. 2009). Because many at-risk species from wetland ecosystems are semiaquatic, often with an attraction to roads during certain life history phases (e.g., nesting turtles; Gibbs and Steen 2005), roadkill management action affecting areas near wetlands should have disproportionate benefits in terms of population-level effects. In general, aggressively managing modifiable risk factors (e.g., posted road speed limits) along roads traveling through high-risk habitats can reduce vertebrate roadkill.

We caution that the observed relationships between the predictor variables and roadkill incidence may reflect cumulative effects over many years. Areas with few current kills may have had high historic roadkill frequencies that depleted local vertebrate populations over time (Fahrig et al. 1995, Findlay and Bourdages 2000), or else favored road avoidance behaviors (Sullivan 2000, Shepard et al. 2008b), creating the illusion of little roadkill risk at present. This study thus reflects the association of certain factors with roadkill under current circumstances, with the riskier areas potentially corresponding to areas with the most numerous vertebrate populations. Management decisions should consider the distribution of nearby wildlife populations as part of developing a comprehensive road-wildlife management strategy.

We emphasize that the patterns observed here apply to our particular study population, including its relative species composition (Appendix 1, available online at www.onlinelibrary.wiley.com) and study location (southern Ontario; Fig. 1). Whereas the predictor variables that we have identified may be applicable to many novel species and locations, managers should use caution when implementing our recommendations, ideally taking an adaptive management approach which monitors the ongoing local effectiveness of related mitigation strategies and makes changes if warranted.

MANAGEMENT IMPLICATIONS

Managers are encouraged to reduce posted road speed limits in areas close to wetlands and through diverse habitats to reduce the incidence of vertebrate roadkill. Such speed reductions may require aggressive enforcement in combination with signage changes (Pojar et al. 1975, Jones 2000). Placing speed-reduction infrastructure such as speed bumps may be the most reliable approach (Dalrymple and Reichenbach 1984, Jones 2000). Where speed reduction is not a practical alternative or where multiple alternatives are appropriate, managers with sufficient resources should consider constructing crossing structures (e.g., Clevenger and Waltho 2000, Jones 2000, Aresco 2003, Taylor and Goldingay 2003, McCollister and van Manen 2010) and (or) barriers (Aresco 2003) for high-priority taxa. In situations involving brief, massive movements of species (e.g., dispersal events; Bonnet et al. 1999, Clevenger et al. 2001), managers might also consider implementing temporary speed reductions or road closures.

Compared to posted speed limits, the 3 other significant roadkill predictors identified by our best model (maximum temperature, habitat diversity, distance from wetlands) are not practically modifiable by managers. These non-modifiable predictors are nonetheless useful for identifying high-risk locations and time periods for roadkill, where targeted modifications, such as localized or temporary speed reductions, can take place. Our data indicate that more ecologically diverse roadside habitats and areas near wetlands should be given management priority over less-diverse and drier locations, with particular enforcement attention given to hotter days if temporary measures (e.g., temporary signage) are to be used.

ACKNOWLEDGMENTS

We thank S. Anderson, K. Crosby, S. Gautreau, J. Mersey, T. Nudds, J. Porter, D. Rivard, and V. Thomas for their comments on early versions of this manuscript. We also thank the staff at Ontario Parks and Parks Canada for assisting with the field study, including H. Brown, J. Brownlie, S. Dobbyn, R. Donley, G. Harvey, R. Hornsby, J. Keitel, T. Marchand, V. McKay, D. Reive, and J. Wade. Funding support was provided by a Natural Sciences and Engineering Research Council of Canada grant to RJB, and the contents of this research paper formed the main chapter of a Master's thesis by RGF.

LITERATURE CITED

Andrews, K. M., and J. W. Gibbons. 2005. How do highways influence snake movement? Behavioral responses to roads and vehicles. Copeia 4:772–782.

Aresco, M. 2003. Highway mortality of turtles and other herpetofauna at Lake Jackson, Florida, USA, and the efficacy of a temporary fence/culvert system to reduce roadkills. Pages 433–449 *in* Proceedings of the International Conference on Ecology and Transportation, C. Leroy Irwin, Paul Garrett, and K. P. McDermott, editors. Center for Transportation and the Environment, North Carolina State University, 24 August–29 August 2003, Lake Placid, New York, USA.

Ashley, E. P., and J. T. Robinson. 1996. Road mortality of amphibians, reptiles and other wildlife on the Long Point causeway, Lake Erie, Ontario. Canadian Field-Naturalist 110:403–412.

Bonnet, X., N. Guy, and R. Shine. 1999. The dangers of leaving home: dispersal and mortality in snakes. Biological Conservation 89:39–50.

Bouchard, J., A. T. Ford, F. E. Eigenbrod, and L. Fahrig. 2009. Behavioral responses of northern leopard frogs (*Rana pipiens*) to roads and traffic: implications for population persistence. Ecology and Society 14:23.

Brockie, R. E., R. Sadleir, and W. L. Linklater. 2009. Long-term wildlife road-kill counts in New Zealand. New Zealand Journal of Zoology 36:123–134.

Chevan, A., and M. Sutherland. 1991. Hierarchical partitioning. American Statistician 45:90–96.

Ciesiolkiewicz, J., G. Orlowski, and A. Elanowski. 2006. High juvenile mortality of grass snakes *Natrix natrix* (L.) on a suburban road. Polish Journal of Ecology 54:465–472.

Clarke, G. P., P. C. L. White, and S. Harris. 1998. Effects of roads on badger *Meles meles* populations in south-west England. Biological Conservation 86:117–124.

Clevenger, A. P., and N. Waltho. 2000. Factors influencing the effectiveness of wildlife underpasses in Banff National Park, Alberta, Canada. Conservation Biology 14:47–56.

Clevenger, A. P., M. McIvor, D. McIvor, B. Chruszcz, and K. Gunson. 2001. Tiger salamander, *Ambystoma tigrinum*, movements and mortality on the Trans-Canada Highway in southwestern Alberta. Canadian Field-Naturalist 115:199–204.

Clevenger, A. P., B. Chruszcz, and K. E. Gunson. 2003. Spatial patterns and factors influencing small vertebrate fauna road-kill aggregations. Biological Conservation 109:15–26.

Coelho, I. P., A. Kindel, and A. V. P. Coelho. 2008. Roadkills of vertebrate species on two highways through the Atlantic Forest Biosphere Reserve, southern Brazil. European Journal of Wildlife Research 54:689–699.

Dalrymple, G. H., and N. G. Reichenbach. 1984. Management of an endangered species of snake in Ohio, USA. Biological Conservation 30:195–200.

Eigenbrod, F., S. J. Hecnar, and L. Fahrig. 2009. Quantifying the road-effect zone: threshold effects of a motorway on anuran populations in Ontario, Canada. Ecology and Society 14(1), 24.

Eng, J. 2005. Receiver operating characteristic analysis: a primer. Academic Radiology 12:909–916.

Fahrig, L., and T. Rytwinski. 2009. Effects of roads on animal abundance: an empirical review and synthesis. Ecology and Society 14(1), 21.

Fahrig, L., J. H. Pedlar, S. E. Pope, P. D. Taylor, and J. F. Wegner. 1995. Effect of road traffic on amphibian density. Biological Conservation 73:177–182.

Farmer, R. G. 2007. Factors associated with vertebrate roadkill in southern Ontario parks. MSc. Thesis, University of Guelph, Guelph, Ontario, Canada.

Farmer, R. G., and R. J. Brooks. 2008. *Pantherophis gloydi* behavior. Herpetological Review 39:356–357.

Findlay, C. S., and J. Bourdages. 2000. Response time of wetland biodiversity to road construction on adjacent lands. Conservation Biology 14:86–94.

Ford, A. T., and L. Fahrig. 2008. Movement patterns of eastern chipmunks (*Tamias striatus*) near roads. Journal of Mammalogy 89:895–903.

Fortin, M.-J., and M. R. T. Dale. 2005. Spatial analysis: a guide for ecologists. Cambridge University Press, New York, New York, USA.

Fox, J., and G. Monette. 1992. Generalized collinearity diagnostics. Journal of the American Statistical Association 87:178–183.

Gelman, A., and J. Hill. 2007. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, Cambridge, United Kingdom.

Gibbs, J. P., and W. G. Shriver. 2002. Estimating the effects of road mortality on turtle populations. Conservation Biology 16:1647–1652.

Gibbs, J. P., and D. A. Steen. 2005. Trends in sex ratios of turtles in the United States: implications of road mortality. Conservation Biology 19:552–556.

Grumbine, R. E. 1994. What is ecosystem management? Conservation Biology 8:27–38.

Inbar, M., and R. T. Mayer. 1999. Spatio-temporal trends in armadillo diurnal activity and road-kills in central Florida. Wildlife Society Bulletin 27:865–872.

Jaeger, J. A. G., J. Bowman, J. Brennan, L. Fahrig, D. Bert, J. Bouchard, N. Charbonneau, K. Frank, B. Gruber, and K. T. von Toschanowitz. 2005. Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. Ecological Modelling 185:329–348.

Jones, M. E. 2000. Road upgrade, road mortality and remedial measures: impacts on a population of eastern quolls and Tasmanian devils. Wildlife Research 27:289–296.

Kerr, J. T., and J. Cihlar. 2004. Patterns and causes of species endangerment in Canada. Ecological Applications 14:743–753.

Kerr, J. T., and I. Deguise. 2004. Habitat loss and the limits to endangered species recovery. Ecology Letters 7:1163–1169.

Klocker, U., D. B. Croft, and D. Ramp. 2006. Frequency and causes of kangaroo-vehicle collisions on an Australian outback highway. Wildlife Research 33:5–15.

Knutson, M. G., J. R. Sauer, D. A. Olsen, M. J. Mossman, L. M. Hemesath, and M. J. Lannoo. 1999. Effects of landscape composition and wetland fragmentation on frog and toad abundance and species richness in Iowa and Wisconsin, USA. Conservation Biology 13:1437–1446.

Langen, T. A., A. Machniak, E. K. Crowe, C. Mangan, D. F. Marker, N. Liddle, and B. Roden. 2007. Methodologies for surveying herpetofauna mortality on rural highways. Journal of Wildlife Management 71:1361–1368.

Langen, T. A., K. M. Ogden, and L. L. Schwarting. 2009. Predicting hot spots of herpetofauna road mortality along highway networks. Journal of Wildlife Management 73:104–114.

Loew, S. S. 1999. Sex-biased dispersal in eastern chipmunks, *Tamias striatus*. Evolutionary Ecology 13:557–577.

Malo, J. E., F. Suarez, and A. Diez. 2004. Can we mitigate animal-vehicle accidents using predictive models? Journal of Applied Ecology 41:701–710.

Marchand, M. N., and J. A. Litvaitis. 2004. Effects of habitat features and landscape composition on the population structure of a common aquatic turtle in a region undergoing rapid development. Conservation Biology 18:758–767.

Mazerolle, M. J. 2004. Amphibian road mortality in response to nightly variations in traffic intensity. Herpetologica 60:45–53.

McCollister, M. F., and F. T. van Manen. 2010. Effectiveness of wildlife underpasses and fencing to reduce wildlife-vehicle collisions. Journal of Wildlife Management 74:1722–1731.

Murtaugh, P. A. 2009. Performance of several variable-selection methods applied to real ecological data. Ecology Letters 12:1061–1068.

Nielsen, C. K., R. G. Anderson, and M. D. Grund. 2003. Landscape influences on deer-vehicle accident areas in an urban environment. Journal of Wildlife Management 67:46–51.

Orlowski, G., J. Ciesiolkiewicz, M. Kaczor, J. Radwanska, and A. Zywicka. 2008. Species composition and habitat correlates of amphibian roadkills in different landscapes of south-western Poland. Polish Journal of Ecology 56:659–671.

Paton, P. W. C., and W. B. Crouch. 2002. Using the phenology of pond-breeding amphibians to develop conservation strategies. Conservation Biology 16:194–204.

Philcox, C. K., A. L. Grogan, and D. W. Macdonald. 1999. Patterns of otter *Lutra lutra* road mortality in Britain. Journal of Applied Ecology 36:748–762.

Pinheiro, J. C., and D. M. Bates. 2004. Mixed-effects models in S and S-PLUS. Springer, New York, New York, USA.

Pojar, T. M., R. A. Prosence, D. F. Reed, and T. N. Woodard. 1975. Effectiveness of a lighted, animated deer crossing sign. Journal of Wildlife Management 39:87–91.

Ramp, D., V. K. Wilson, and D. B. Croft. 2006. Assessing the impacts of roads in peri-urban reserves: road-based fatalities and road usage by wildlife in the Royal National Park, New South Wales, Australia. Biological Conservation 129:348–359.

Row, J. R., G. Blouin-Demers, and P. J. Weatherhead. 2007. Demographic effects of road mortality in black ratsnakes (*Elaphe obsoleta*). Biological Conservation 137:117–124.

Seiler, A. 2005. Predicting locations of moose-vehicle collisions in Sweden. Journal of Applied Ecology 42:371–382.

Shepard, D. B., M. J. Dreslik, B. C. Jellen, and C. A. Phillips. 2008*a*. Reptile road mortality around an oasis in the Illinois Corn Desert with emphasis on the endangered Eastern Massasauga. Copeia 2:350–359.

Shepard, D. B., A. R. Kuhns, M. J. Dreslik, and C. A. Phillips. 2008*b*. Roads as barriers to animal movement in fragmented landscapes. Animal Conservation 11:288–296.

Steen, D. A., M. J. Aresco, S. G. Beilke, B. W. Compton, E. P. Condon, C. K. Dodd, H. Forrester, J. W. Gibbons, J. L. Greene, G. Johnson, T. A. Langen, M. J. Oldham, D. N. Oxier, R. A. Saumure, F. W. Schueler, J. M. Sleeman, L. L. Smith, J. K. Tucker, and J. P. Gibbs. 2006. Relative vulnerability of female turtles to road mortality. Animal Conservation 9:269–273.

Steyerberg, E. W., F. E. Harrell, G. Borsboom, M. J. C. Eijkemans, Y. Vergouwe, and J. D. F. Habbema. 2001. Internal validation of predictive models: efficiency of some procedures for logistic regression analysis. Journal of Clinical Epidemiology 54:774–781.

Sullivan, B. K. 2000. Long-term shifts in snake populations. Biological Conservation 94:321–325.

Taylor, B. D., and R. L. Goldingay. 2003. Cutting the carnage: wildlife usage of road culverts in north-eastern New South Wales. Wildlife Research 30:529–537.

Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S. Springer-Verlag, New York, New York, USA.

Zorn, P., W. Stephenson, and P. Grigoriev. 2001. An ecosystem management program and assessment process for Ontario national parks. Conservation Biology 15:353–362.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, New York, USA.

Associate Editor: Gary Roloff.