

# Maintaining and restoring connectivity in landscapes fragmented by roads

ANTHONY P. CLEVINGER AND JACK WIERZCHOWSKI

## INTRODUCTION

Transportation networks and systems are vital to today's economy and society (Button and Hensher 2001). Not only do roads provide for safe and efficient movement of goods and people across cities and continents, throughout the world they have become a permanent part of our physical, cultural, and social environment (Robinson 1971; Lay 1992). Roads and their networks are one of the most prominent human-made features on the landscape today (Sanderson *et al.* 2002). Compared to polygonal blocks of built areas, road systems are linear and etched into the landscape to form a woven network of arteries that maintain the pulse of societies. However, as road networks extend across the landscape and their weave intensifies, natural areas become increasingly fragmented and impoverished biologically (Forman *et al.* 2003).

Although less studied compared to other agents of fragmentation, roads cause changes to wildlife habitat that are more extreme and permanent than other anthropogenic sources of fragmentation (Forman and Alexander 1998; Spellerberg 2002). Road networks and systems not only cause conspicuous changes to physical landscapes, but also alter the patterns of wildlife and the general function of ecosystems within these landscapes (Swanson *et al.* 1988; Transportation Research Board 1997;

Olander *et al.* 1998). Busy roads can be barriers or filters to animal movement (Hels and Buchwald 2001; Rondinini and Doncaster 2002; Chruszcz *et al.* 2003) and in some cases the leading cause of animal mortality (Maehr *et al.* 1991; Jones 2000; Kaczensky *et al.* 2003). Sustainable transportation systems must provide effectively for natural processes and biodiversity, and safe and efficient human mobility.

Over the last decade, federal land management and transportation agencies have become increasingly aware of the effects of roads on wildlife. Significant advances in our understanding of these impacts have been made; however, the means to adequately mitigate these impacts have been slower in coming. Effective wildlife fencing and crossing structures can significantly reduce many harmful impacts of roads on wildlife populations (Kistler 1998; Clevenger *et al.* 2001a; Cain *et al.* 2003). Yet currently there is limited knowledge on the design of wildlife crossing systems that promote sustainable wildlife populations and functioning ecosystems (Transportation Research Board 2002a). Knowledge of the locations of primary wildlife crossings and/or problem areas is the first step in planning mitigation on highways; however, few methodological approaches to identify and prioritize these key areas have been explored. Departments of Transportation, resource agencies, universities, and non-governmental organizations have attempted to fill this gap by conducting workshops, often with Department of Transport sponsorship; biologists, researchers, and regulatory specialists come together in a workshop setting to make decisions on conservation and connectivity needs based on analysis of best available environmental data (see Beier *et al.* Chapter 22). Anticipated population growth and ongoing highway investments in most regions, coupled with the resounding concern for maintaining large-scale, landscape connectivity, have generated increasing interest in wildlife crossings or mitigation passages as conservation tools.

The impact of transportation systems on wildlife ecology and remedial actions to counter these effects is an emerging science. Research remains scarce on the influence of road systems on habitat fragmentation and the conservation value of crossings in restoring connectivity (Spellerberg 2002; Transportation Research Board 2002b; Forman *et al.* 2003). Moreover, research has primarily focused at the level of individuals and single species (Guyot and Clobert 1997; Ortega and Capen 1999; Gibbs and Shriver 2002). Key questions remain regarding population- and community/ecosystem-level impacts of roads and the benefits of wildlife crossings to reduce those impacts (Clevenger and Waltho 2000, 2005; Underhill and Angold 2000).

In this chapter, we discuss roads as agents of habitat fragmentation and means of restoring connectivity across roads with wildlife crossings. Developing strategies to mitigate road impacts begins with a step-wise approach that contemplates project goals and context, followed by decisions regarding specific placement and design of the measures implemented. We describe some general guidelines used in the planning process, information needs, and practical applications. As part of a project evaluating mitigation measures along the Trans-Canada Highway in Banff National Park, Alberta, Canada, we present several geographic information system (GIS)-based approaches to model animal movements for planning sustainable transportation projects.

## ROADS AS AGENTS OF HABITAT FRAGMENTATION

The impact of roads on wildlife has been the focus of many studies (Canters 1997; Evink *et al.* 1999; Forman *et al.* 2003). These studies show that roads affect wildlife in numerous ways (Reijnen and Foppen 1994; Vos and Chardon 1998; Sweanor *et al.* 2000). Apart from the most obvious direct impact of wildlife mortality, roads affect habitat by changing habitat condition and levels of connectivity.

### Habitat change

Road construction and improvements result in habitat loss for wildlife by transforming natural habitats to pavement and cleared roadsides or verges. Some species are more vulnerable to habitat loss than others. For example, species such as wide-ranging carnivores, with large area requirements, relatively low densities, and low reproductive rates, tend to be the most sensitive to road-induced habitat loss (Trombulak and Frissell 2000; Carroll *et al.* 2001; Carroll Chapter 15), although road networks also affect other taxa, such as herpetofauna (Vos and Chardon 1998; Gibbs and Shriver 2002). Road construction can increase the amount of edge habitat in a landscape due to the long thin shape of roads, resulting in a decrease in the amount of habitat for interior, edge-sensitive species. Metapopulation theory suggests that more mobile species are better able to tolerate habitat loss (Hanski 1999), yet mortality of individuals in the matrix habitat (e.g., road corridors) does not typically figure into metapopulation theory (Taylor *et al.* Chapter 2; Moilanen and Hanski Chapter 3). Studies have shown that when mortality is high in the matrix habitat, highly mobile species are actually more vulnerable to habitat loss (Carr and Fahrig 2001; Gibbs and Shriver 2002).

Roads and disturbance from traffic also can reduce the quality of nearby habitat. Disturbance from roads can affect wildlife behaviorally and numerically. Behavioral responses can be of two types: (1) an avoidance response (avoidance zone) associated with regular or constant disturbance from high-volume highways, and (2) avoidance due to irregular, individual disturbances generally found on roads with less traffic. Numerical responses from roads consist of a decrease in abundance or density of breeding individuals. There are many examples of numerical responses by wildlife, primarily birds, to an array of road types and traffic disturbance (Van der Zande *et al.* 1980; Reijnen and Foppen 1994).

Alternatively, wildlife can be attracted to road corridors or roads themselves for a variety of reasons, often as a result of conditions related to habitat (nesting, living space) or food resources. For example, higher use by raptors and ravens of roadsides compared to adjacent habitat was due to the greater availability of perch sites and wide verges (Knight and Kawashima 1993; Meunier *et al.* 2000). Road construction also can create high-quality habitat where food resources are more abundant compared to adjacent areas. Lush forage created by fencing along medians and verges attracts herbivores, from microtine rodents to large mammals such as deer and elk. Locally abundant small-mammal populations living in these fenced-off areas become targets for avian and terrestrial predators such as owls, hawks, coyotes, and foxes. With prey and their predators foraging close to traffic in the road corridor, collisions with vehicles are inevitable, thus resulting in roadside carrion and attracting aerial and terrestrial scavengers if not promptly removed.

### **Connectivity**

Landscape connectivity is the degree to which the landscape facilitates animal movement and other ecological flows (Forman 1995; Bennett 1999; Taylor *et al.* Chapter 2). High levels of landscape connectivity occur when the matrix areas of the landscape comprise relatively benign types of habitats without barriers, thus allowing organisms to move freely (Tischendorf and Fahrig 2000). Reduced landscape connectivity and impeded movements due to roads may result in higher mortality, lower reproduction, and ultimately smaller populations and lower population viability (Gerlach and Musolf 2000; Keller and Lagiardèr 2003). These deleterious effects have underscored the need to maintain and restore essential movements of wildlife across roads, particularly those with high traffic volumes.

Fragmentation effects caused by roads begin as individual animals become reluctant to move across roads to access mates or otherwise preferred habitats for food and cover. This aversion to roads is generally attributed to road features (traffic volume, road width) or habitat changes caused by the road. High-volume roads have the greatest impact in blocking animal movements (Brody and Pelton 1989; Rondinini and Doncaster 2002; Chruszcz *et al.* 2003). Yet secondary highways and unpaved roads can impede animal movements as well (DeMaynadier and Hunter 2000; Develey and Stouffer 2001; Laurance *et al.* 2004). Ultimately, the barrier effect of a road (i.e., the “hardness” of the edge) will impact populations differently depending on species behavior, dispersal ability, habitat needs, and population densities (Lima and Zollner 1996; Cassady St Clair 2003). For example, an open road corridor with grass-covered verges can be a formidable barrier to a forest-specialist small mammal regardless of mortality risks due to vehicles on the roadway. In the last decade, studies have begun assessing barrier permeability and dispersal success of animals in a patch-matrix landscape (Lima and Zollner 1996; Tewksbury *et al.* 2002).

Although roads can limit movement of some taxa, they can potentially facilitate dispersal and range extensions of others, including both native and non-native species, although such evidence is limited (Spellerberg and Gaywood 1993). Studies in Holland and Australia have reported increased movement along roads by small mammals and invertebrates, suggesting they are able to connect core habitats using road verge habitat (Vermeulen 1994; Straker 1998). The US Interstate Highway System, bordered by dense grass, has created an extensive array of potential avenues for dispersal by grassland fauna throughout the country (Huey 1941; Getz *et al.* 1978). Although large carnivores often occur at lower densities in highly roaded areas, predators can utilize roads for movement because they provide ease of travel and greater access to prey (Koehler and Britnell 1990; Thurber *et al.* 1994; James and Stuart-Smith 2000). The extent to which roads influence the distribution and abundance of non-native fauna is poorly known (May and Norton 1996; Forman *et al.* 2003). In Australia, non-native cane toads were more abundant on road surfaces, using them as dispersal corridors, than in many surrounding habitats (Seabrook and Dettman 1996). In general, despite roads being a dominant and permanent landscape feature, relatively few studies have investigated road systems and their role in habitat fragmentation (see Gibbs 1998).

## MAINTAINING AND RESTORING CONNECTIVITY ACROSS ROADS

### Mitigation of road impacts on connectivity

One of the earliest recommendations to arise from studies of habitat fragmentation was that habitat patches linked by a corridor of similar habitat are likely to have greater conservation value than isolated fragments of similar size (Diamond 1975). This early recommendation was based entirely on theory of island biogeography (MacArthur and Wilson 1967). Since then, there has been widespread interest in corridors as conservation measures (Saunders and Hobbs 1991; Beier and Noss 1998; Bennett 1999; this volume).

Wildlife crossings are designed to link critical habitats and provide safe movement of animals across busy roads. Typically they are combined with high fencing and together are proven measures to reduce road-related mortality of wildlife and restore movements (Foster and Humphrey 1995; Clevenger *et al.* 2001a; Cain *et al.* 2003). In recent years there has been an increase in construction of crossings in North America and worldwide (McGuire and Morrall 2000; Goosem *et al.* 2001; Bank *et al.* 2002). The US Transportation Equity Acts of the last decade have enabled mitigation passages to be part of the early stages of highway project planning and thus more are being built today (US Department of Transportation 1999; Marshik *et al.* 2001). With the reauthorization of the Transportation Equity Act in August 2005, we will continue to see more wildlife crossings in future highway construction and improvement projects in the USA.

### Function and performance of wildlife crossings

The principles of corridor theory can be applied to wildlife crossings to help assess how well they function. Until now, the general idea of how well a crossing ultimately performs has not gone far beyond the simplest level of scrutiny – if animals use it, then it is working and must be functional. Answering this question is difficult, although it appears to be simple and straightforward. There are many interpretations of what functional and well-performing wildlife crossings should do. Beier and Noss (1998) reported that generalizations about the conservation value of habitat corridors remain elusive because of the species-specific nature of the problem. The same is true for wildlife crossings, as there is no common answer to the questions “Do wildlife crossings provide connectivity?” or “Are wildlife crossings performing?”

These questions only make sense when referring to a particular focal or target species (Crooks and Sanjayan Chapter 1; Taylor *et al.* Chapter 2; Noss and Daly Chapter 23). However, we know that species do not function in isolation but are components of ecological systems that inherently fall into the category of organized complexity (Allen and Starr 1982; O'Neill *et al.* 1986). Consequently, any single-species mitigation structure may have cascading effects (some positive, some negative) on other non-target species. If mitigation measures for habitat connectivity are to succeed, then it is paramount that a multi-taxonomic approach be adopted to evaluate the efficacy of such mitigation on non-target species as well. If the goal of wildlife crossings is to maintain biological diversity at multiple levels of organization (Noss 1990; Redford and Richter 1999), then means of evaluating measures of crossing structure efficacy can become quite complex.

#### **Measuring wildlife crossing performance and conservation value**

Most studies of wildlife crossings have simply described the number of species using crossings and their frequency of use (Foster and Humphrey 1995; Taylor and Goldingay 2003; Ng *et al.* 2004). Others have used passage data as a dependent variable to identify factors that facilitate passage by wildlife (Yanes *et al.* 1995; Rodríguez *et al.* 1996; Clevenger and Waltho 2000, 2005). Few studies have actually measured performance of mitigation in meeting design goals (Woods 1990; Clevenger *et al.* 2001a; Cain *et al.* 2003). Until now, virtually all studies have been focused at the level of individuals and suggested benefits at the population level. We are not aware of any studies that have empirically addressed whether wildlife crossings enhance or diminish the population viability of species impacted by roads.

After several decades of increased activity building wildlife crossings, engineers and land managers still lack guiding principles as a large void exists in devising functional designs based on criteria that are relevant to real conservation decisions. This is largely because few studies have rigorously evaluated the efficacy of wildlife crossings (Romin and Bissonette 1996; Forman *et al.* 2003). There are approximately 100 highway passages built specifically for wildlife in North America (Evink 2002). Yet seldom are monitoring programs part of mitigation projects. When monitoring is conducted, rarely is it designed to evaluate performance based on pre- and post-construction tests (Hardy *et al.* 2003). Thus, results from most studies are based on anecdotal information. Furthermore, monitoring is generally for short periods and fails to address the need for wildlife

to respond to such large-scale landscape change. Such adaptation periods can take several years depending on the species as they experience, learn, and adjust their own behaviors to the wildlife crossings (Opdam 1997; Clevenger *et al.* 2002a). Small sampling windows, typical of 1- or 2-year monitoring programs, are too brief, can provide spurious results, and do not adequately sample the range of demographic and behavioral variability in most wildlife populations.

Wildlife crossings are in essence site-specific movement corridors strategically placed over a deadly matrix habitat of pavement and high-speed vehicles. Consequently, crossings that function as habitat or landscape connectors should allow for the following: (1) movement within populations and genetic interchange; (2) biological requirements of finding food, cover, and mates; (3) dispersal from maternal ranges and recolonization after long absences; (4) redistribution of populations in response to environmental changes and natural disasters; and (5) long-term maintenance of metapopulations, community stability, and ecosystem processes. These functions encompass the three levels of biological organization, *i.e.*, genes, species–population, community–ecosystem (see Noss 1990).

Measuring the conservation value of wildlife crossings is a complex and time-consuming task. Nonetheless, it is important to have clear goals and objectives for proper assessment. Up until now, few monitoring efforts were designed to test specific hypotheses (Forman *et al.* 2003). Hypothesis testing will aid in better understanding whether crossings enhance the population viability of species. Some questions may be broad or general and require answers from several scales and perspectives. General principles have to be well founded, and they are often based on intensive studies of the life histories of animals in local environments. The hierarchy concept also recognizes that effects of environmental stresses from roads and traffic can reverberate through other levels, often in unpredictable ways, as secondary and cumulative effects.

We provide an example of how a monitoring and assessment project might be implemented using the following eight steps. These guidelines provide a framework that can be used to design monitoring schemes to evaluate the conservation value of wildlife crossings:

1. *Establish goals and objectives.* What are the mitigation goals? In many cases, the goals are to reduce wildlife–vehicle collisions and/or reduce barrier effects to movement and maintain genetic interchange.
2. *Establish baseline conditions.* To develop a mitigation scheme it will be important to determine the extent, distribution, and intensity of road

impacts to wildlife in the area of concern. The impacts may consist of mortality, habitat loss, habitat fragmentation (reduced movements), or some combination thereof. In most cases, the conditions occurring pre-construction/mitigation will comprise the baseline.

3. *Identify specific questions to be answered by monitoring.* These questions will be formulated from the goals and objectives identified in Step 1 and conditions identified in Step 2. Some questions might include: Is road-related mortality increasing or decreasing? Is animal movement across the road increasing or decreasing? Are animals able to disperse and populations carry out migratory movements? Are populations residing in the transportation corridor stable and reproducing? Before implementing a monitoring program it will help if transportation and land managers can agree on specific benchmarks and thresholds at which management actions may or may not intervene. For example,  $\geq 50\%$  reduction in road-kill would be acceptable, but  $< 50\%$  reduction would initiate management actions to improve mitigation performance, including highway-related mitigation (e.g., reinforcing fencing) or driver-related actions (e.g., reducing traffic speed, animal detection systems, motorist awareness).
4. *Select indicators.* Identify indicators at multiple levels of biological organization that correspond to goals and objectives identified in Step 1 and questions in Step 3. For example: *genetic*, gene flow and genetic structure; *population–species*, demographic processes such as dispersal, survivorship, mortality; *community–ecosystem*, herbivory and predation rates.
5. *Identify control and treatment areas.* If pre-construction/mitigation data are not available, then control areas (unmitigated road sections) may be used to compare indicators with treatments (mitigated roads).
6. *Design and implement a monitoring plan.* Applying principles of experimental design, select sites for monitoring the identified goals and objectives from Step 1 and questions in Step 3. Although treatments and controls should be replicated, that may not always be possible.
7. *Validate relationships between indicators and benchmarks.* Detailed research carried out over the long-term will be needed to determine how well the selected indicators correspond to the mitigation goals and objectives.
8. *Analyze trends and patterns, and recommend management actions.* One analysis strategy is to construct a time series, a sequence of measurements typically taken at successive points in time. Time series

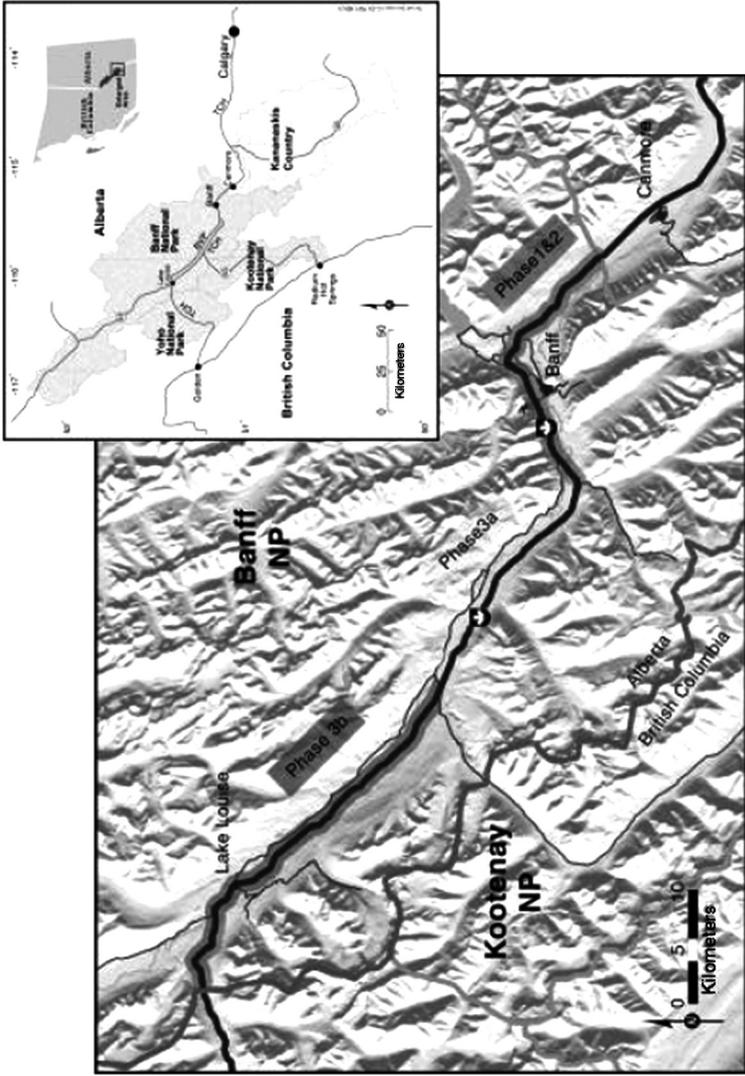
analysis includes a broad spectrum of exploratory and hypothesis testing methods that have two main goals: to identify the nature of the phenomenon represented by the sequence of observations (e.g., mortalities, successful crossings), and forecasting future trends and patterns. Analyses of this type will provide a more accurate assessment of the biological value of the measures over the long term and whether changes in mitigation are warranted.

## WILDLIFE CROSSING PLACEMENT

The previous section has shown that decision-making in the design of effective wildlife crossings has been hampered by lack of study. Determining placement of wildlife crossings is even more of a challenge given the few methodological approaches. Transportation planning has generally considered a one-dimensional linear zone along the highway. Thus the engineering and design dimensions have been the main concern for planners. However, we know the ecological effects of roads are far greater than the road itself and can be immense and pervasive (Forman and Alexander 1998; Trombulak and Frissell 2000). Due to the broad landscape context of road systems, it is essential to incorporate landscape patterns and processes in the planning and construction process (Forman 1987). When used in a GIS environment, regional or landscape level connectivity models can facilitate the identification and delineation of barriers and corridors for animal movement (van Bohemen *et al.* 1994; Bekker *et al.* 1995). This provides for the development of a more integrated land-management strategy.

In this section, we look at questions regarding spatially explicit mitigation planning and their methodologies, focusing primarily on an unmitigated section of the Trans-Canada Highway in Banff National Park, Alberta (phase 3B) (Fig. 20.1). Our case study area represents an exceptionally problematic area of the Greater Rocky Mountain ecological network (Noss *et al.* 1996; Page *et al.* 1996). This work was part of a larger research project aimed at evaluating highway mitigation measures and road impacts to wildlife where a major transportation corridor bisects a critically important protected area. We developed several GIS-based approaches to model animal movements across the Trans-Canada Highway. The modeling exercise varied depending on model objectives and research questions.

Situated approximately 120 km west of Calgary, Banff is the most heavily visited national park in North America with over 5 million visitors



**Fig. 20.1.** The Trans-Canada Highway (thick line) in the Bow Valley of Banff National Park, Alberta, Canada. The phases represent the sequence of highway mitigation; phase 1, 2, and 3a is 45 km of fenced highway with wildlife crossings; phase 3b is 30 km of unfenced highway without mitigation at present. Inset map shows Banff National Park and the Trans-Canada Highway with respect to other mountain national parks, provincial parks (Kananaskis Country), and roads in the Central Canadian Rocky Mountains.

per year (Parks Canada, unpublished data). The Trans-Canada Highway is a major transportation corridor that bisects Banff and neighboring Yoho National Park (Fig. 20.1). Annual average daily traffic volume at the park east entrance was over 16 000 vehicles per day in 2003 and volumes have increased 40% in the last 10 years (Parks Canada, unpublished data). Since the 1980s, fencing and wildlife crossings (overpasses and underpasses) have been installed along 45 of the 70 km of the Trans-Canada Highway in Banff (Woods 1990; McGuire and Morrall 2000). These mitigated sections of highway are referred to as phase 1, 2, and 3A (see Fig. 20.1).

In 2005, expansion to four lanes with construction of fencing and wildlife crossings began on the remaining 30 km section between Castle Mountain junction and the border with British Columbia (phase 3B). Our modeling efforts focused on this unmitigated section of highway, specifically to identify and prioritize locations for mitigating highway impacts on wildlife habitat connectivity and road-related mortality.

The first modeling approach, although not specifically applied to guide mitigation on the Trans-Canada Highway, explores a real-life transportation dilemma, where wildlife crossings need to be built on a stretch of highway, but baseline information is lacking and time constraints do not allow for pre-construction data collection. To do this, we developed two expert-based models to identify cross-highway habitat linkages and potential locations for mitigation measures, and compared these predictions to an empirically based habitat model.

The second and third approaches are real Banff applications. They are based on the use of empirical data and reflect a situation where pre-construction data were available to develop linkage models from species' habitat use patterns and spatial analysis using a GIS. We created models at two different spatial scales that simulate animal movements across the Trans-Canada Highway. In the first, we created regional-scale, spatially explicit species movement models for identifying potential highway mitigation areas along the unmitigated section of the Highway, and to help assess whether placement of the existing wildlife crossings on the mitigated stretch of the Highway was appropriate (see Fig. 20.1). These models were generalized, and predicted crossing locations accordingly had a relatively wide margin of error (= 1000 m).

In the third and last approach, movement modeling was taken one step further. We modeled movements at the local level, which is the appropriate scale and resolution for accurately predicting the locations

of key highway crossing areas and future mitigation placement. Recommendations for identifying and prioritizing future placement of wildlife crossings on the unmitigated Trans-Canada Highway were based on this work (Clevenger *et al.* 2002a).

### **Expert-based linkage models**

Planning the most suitable location for wildlife crossings is typically derived from road-kill information (Evink 1996); however, where animals unsuccessfully cross roads are not necessarily the same locations where they are able to successfully cross (Clevenger *et al.* 2002a). Other means of locating crossings might use data obtained from monitoring animal movements along roads (Evink 1996; Kobler and Adamic 1999; Thompson 2003). Rarely are good pre-construction data available before construction or sufficient time given to acquire these data.

Expert information can be used to develop simple, predictive, habitat linkage models in a relatively short period of time (Marcot 1986; Clevenger *et al.* 2002b; Yamada *et al.* 2003). The objective of this exercise was to determine the accuracy of expert-based models and whether they might be a useful tool for mitigation planning under data and time constraints. For a single species, black bears, we developed three different but spatially explicit habitat models to identify linkage areas across the Trans-Canada Highway. One model was based on empirical data, while the other two were based on expert opinion and expert literature. We used the empirical model as a yardstick to measure the accuracy of the two expert-based models (Clevenger *et al.* 2002b). We selected black bears to model habitat use and identify linkage areas because we had sufficient empirical data to build a habitat model and enough data from crossings and mortality locations to validate it.

### **Methods**

*Empirical model* We developed the empirical habitat model by first determining the habitat requirements of black bears in the study area using radiolocation data and a suite of biophysical variables, such as elevation, aspect, and slope. A habitat suitability model was then developed using a resource selection function and probability of occurrence (PO) classes. We defined four PO categories: low (<25%), moderate (25–50%), high (50–75%), and very high (>75%) probabilities that bears would occupy an area. We generated a stratified random sample of points ( $n = 580$ ) to compare with the biophysical variables within each of the PO categories (see Clevenger *et al.* 2002b for details).

*Expert models* Expert habitat models were developed as weighted linear combinations of each model's layers (biophysical variables) obtained by (a) expert opinion or (b) review of the literature on black bear habitat requirements. We used the pair-wise comparison method developed by Saaty (1977) in the context of a decision-making process known as the analytical hierarchy process (Rao *et al.* 1991; Eastman *et al.* 1995). The procedures for carrying out the expert modeling process are described in detail in Clevenger *et al.* (2002b). Seasons were defined based on the biological needs of bears: pre-berry (den exit to July 15) and berry (July 16 to den entry). Five habitat variables were selected by experts to be used in the analysis: elevation, slope, aspect, greenness, and distance to nearest drainage.

*Linkage zone identification and data analysis* We identified highway crossing/habitat linkage zones for the empirical and expert models based on the assumption that: (1) the probability of a bear crossing a highway increases in areas where the highway bisects high-quality bear habitat; and (2) the highest probability of crossings occur in areas where topographic and landscape features are conducive to lateral, cross-valley movements. For each model we generated four classes of linkage zones based on juxtaposition of habitat and human development adjacent to the highway (see Clevenger *et al.* 2002b). We then tested our linkage zone predictions for each of the three models using an independent data set of 37 black bear crossing and mortality locations. These were acquired by intensive radiotracking of movements and by mortality locations obtained by a spatially accurate (<3 m error), global positioning system (GPS) unit. We generated random points of highway crossings, equal in sample size to the actual crossing data, and calculated the distances from both sets of points to the linkage zones predicted for each model.

### Results and discussion

Our tests showed that the empirical habitat model was statistically sound. The overall cross-validated classification accuracy was 87% and the model correctly classified 79% of the radiolocations into prime black bear habitat. Through the statistical analysis of crossing data and random points we found that the Class III linkages (sections of the Highway that crossed prime bear habitat and were  $\geq 250$  m away from any permanent human development) were most accurate for mapping cross-highway movement for all three models; crossing and mortality locations were

significantly closer to Class III linkages predicted by the models than random points.

Our findings confirmed that the expert-literature-based model was consistently more similar and conformed to the empirical model better than the pre-berry and berry expert-opinion-based models. These results were based on the test of distribution of the actual crossing and mortality locations in relation to the modeled linkages, the descriptive characteristics of the Class III linkages, the measure of agreement between models, and the measure of agreement between model linkage zones (see Clevenger *et al.* 2002b).

We believe the poor predictive power of the expert-opinion-based model can be attributed to an overestimation of the importance of riparian habitat, as compared to the opinions expressed in the literature. Another possible explanation is that the expert-literature model is based on an analytical process (data collected, statistically analyzed, and summarized), whereas the expert-opinion model is based on information taken from how experts perceive attributes from memory and experience.

#### **Regional-scale movement models**

Broad-scale GIS-based linkage models have been developed to evaluate habitat fragmentation resulting from human activities and to identify predominant landscape permeability patterns for wildlife (Servheen and Sandstrom 1993; Carroll Chapter 15). GIS weighted-distance and least-cost corridor analysis also has been used to evaluate landscape permeability, primarily for large carnivores (Walker and Craighead 1997; Kobler and Adamic 1999; Singleton *et al.* 2002; Theobald Chapter 17). The spatial resolution of nearly all of the above models was relatively large ( $\geq 1000$  m) as some linkage and corridor maps covered large regions, entire states, or several contiguous states (e.g., northern US Rocky Mountains).

Simple individual-based movement models have been used successfully to simulate responses of animals to their habitat and terrain features (Boone and Hunter 1996; Turchin 1998; Tracey Chapter 14). We modeled movement patterns of large mammals at a regional scale in the Central Canadian Rocky Mountains using rules for simulated movements based on habitat quality and permeability of landscape elements. We were interested in using a GIS to determine whether easily available spatial data can successfully describe key linkages and crossing areas for large mammals across busy transportation corridors.

Specifically the aims of this work were: (1) to develop regional habitat suitability models for four wide-ranging large mammal species (black

bear, grizzly bear, moose, and elk); and (2) create regional-scale movement models for the four species, indicating the location of potential mitigation based on the intersection of predicted pathways with transportation corridors (Clevenger *et al.* 2002b). We also identified potential locations for future mitigation on phase 3B of the Highway, and compared the placement of existing wildlife crossing structures on phases 1, 2, and 3A to the predicted regional movement pathways. The results are being used to provide land managers with an empirical assessment of the impediments transportation corridors pose to the regional movement patterns of wildlife in an exceptionally problematic area of the Rocky Mountain cordillera.

### Methods

*Habitat model* We modeled regional scale movements of black bear, grizzly bear, moose, and elk and identified their potential linkage areas across the Trans-Canada Highway. These species were selected because: (1) they exhibit long-ranging movement patterns and potential for interactions with transportation corridors in the study area (Noss *et al.* 1996; Carroll *et al.* 2001), (2) sufficient empirical location data were available to construct predictive spatial models of habitat suitability, and (3) empirical crossing and mortality data were available to independently test the models. Habitat suitability models were developed using a resource selection function, as described for the expert models earlier. We stratified the radiolocation data for bears into pre-berry and berry seasons, and for ungulates into summer (moose: May–October; elk: April–October) and winter (moose: November–April; elk: November–March) seasons.

*Movement model* We based the movement component of the model on the least-cost movement principle (Theobald Chapter 17) and quantified the effects of slope angle and orientation (with respect to movement direction) on movement pathway. We used the habitat probability surfaces for the habitat component of the movement model. We simulated the movement pathways for each species by identifying 11 potential entry and exit points located outside the Bow Valley and the Trans-Canada Highway transportation corridor. Entry and exit points were situated in high-quality, valley bottom habitat, the most likely population source areas from which animals would be expected to disperse. For any given pair of entry–exit points there were three iterations resulting in three different pathways. The first iteration simulated the least-cost movement pathway with no

obstructions imposed. In the second iteration, the first pathway was blocked, forcing the creation of a new pathway distinct from the original. In the third iteration, the first two pathways were blocked and an alternative route taken. These three distinct model runs produced primary, secondary, and tertiary movement pathways.

*Highway crossing zone analysis* We mapped the potential wildlife crossing zones along the Trans-Canada Highway by calculating the number of simulated pathway intersections along the highway. Our method often identified long sections of highway, which may be too generalized when recommending the placement of wildlife crossings. We addressed this problem by modifying the model to analyze 1-km-long segments of highway. Given the 120-m pixel size of habitat and topography layers and the obtained fit of the habitat models, we considered 1 km to be the minimum segment length we could safely use.

*Model testing* We tested the accuracy of highway crossing zones predicted by black bear and elk movement models with an independent set of empirical crossing and mortality points. Data on grizzly bear and moose crossing and mortality were insufficient to test their models. Empirical crossing and mortality locations were defined as described earlier for expert models, but included snowtracking data for elk and moose. The method of testing also was the same as the previous model, i.e., whether empirical crossing points were randomly distributed with respect to the distance to the predicted crossing zones created by the models.

Within the fenced part of the Trans-Canada Highway (phases 1, 2, 3a: Fig. 20.1), we evaluated correlations of the predicted regional movement patterns with frequency of use of the existing wildlife crossings by the four target species (Clevenger *et al.* 2002a). We also identified the potential locations for highway mitigation on the unfenced phase 3B section of the Highway by plotting the pathway crossing frequencies by 1-km segments. We defined high crossing frequency segments as those that registered the number of intersections greater than the given distribution's mean value.

### Results and discussion

The overall cross-validated classification accuracies and habitat model validation tests suggested that all of the models showed a reasonably good fit with the empirical data. In the black bear model there was strong

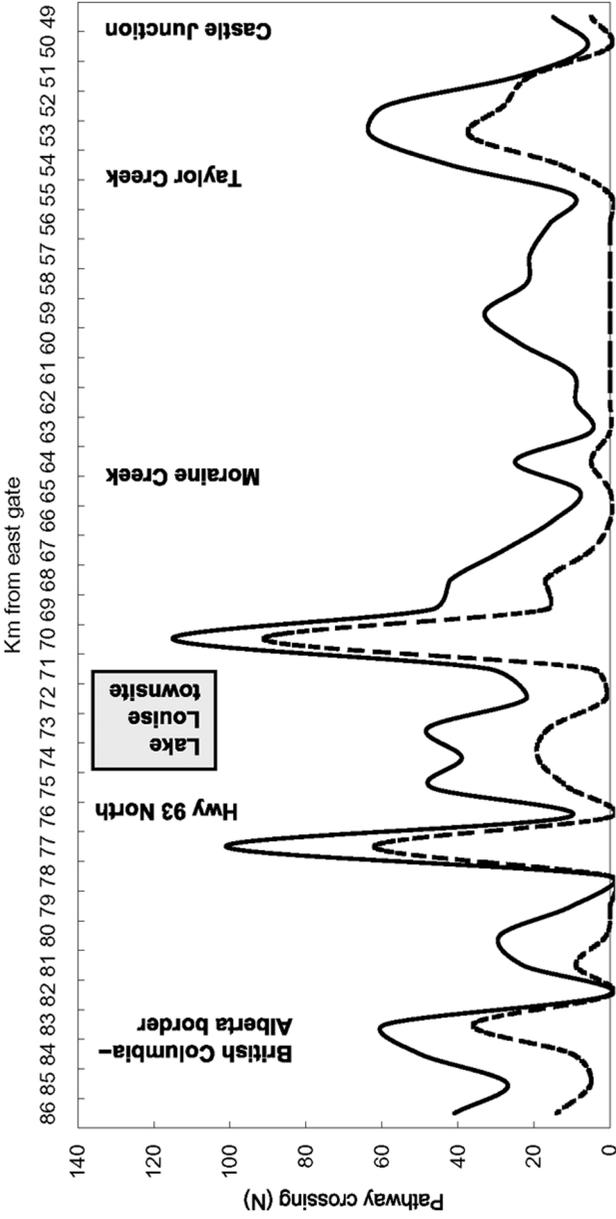
statistical evidence that the empirical bear crossing and mortality locations were closer to predicted high- and moderate–high-frequency crossing zones than expected by chance. Similarly, empirical elk winter crossing and mortality locations were closer to the predicted high-frequency crossing zones than random points, but there was no difference between empirical points and the moderate–high-frequency crossing zone locations. We concluded that the model and empirical data correlated well (Clevenger *et al.* 2002a).

We plotted the number of cumulative primary pathways and total pathways (primary, secondary, and tertiary) in relation to the existing wildlife crossings along the mitigated, fenced part of the Trans-Canada Highway. The predicted primary pathway crossing frequencies on km 0–24 of the Highway showed a close association with the empirical data for wildlife crossing use by the four large mammal species. We found a close association between total pathway crossing frequencies and observed wildlife crossing use on the same section of highway; however, this pattern was not as strong as the primary pathway crossings.

Primary pathway crossing frequencies between km 25 and 50 also showed a strong association with the empirical data for wildlife use of crossing structures. There were no highway segments with greater predicted than empirical crossings, nor were there any high predicted crossings in areas without crossing structures. Total pathway crossing frequencies compared to crossing structure use were nearly identical to the primary pathway crossing frequencies.

The models identified several areas along the 0–50 km mitigated section of highway that were noteworthy in terms of their importance for wildlife movement. These predicted crossing locations were in agreement with the rank-ordered importance of wildlife crossings as indicated by usage by all wildlife species (Clevenger *et al.* 2002a).

At the species level, the pattern of movement across the entire length of the Trans-Canada Highway (km 0–86) as predicted by the species' movement models was consistent, varied slightly, and overall was similar to that described above at the group level. To roughly assess potential locations for wildlife crossings along the unmitigated section of the Highway (km 50–86), we weighted the four species equally, utilized the cumulative movement patterns generated by the models, and examined the intersection of primary and total pathways with the highway. Eight locations were indicated by high frequencies of predicted primary crossings across the highway (Fig. 20.2).



**Fig. 20.2.** Predicted distribution and frequency of cumulative movement pathways by four large mammal species along the unmitigated section (km 50–86) of the Trans-Canada Highway as indicated by primary (intermittent line) and total pathways (solid line). Geographic landmarks on the Highway are shown on top.

### Planning of wildlife crossing placement

There are few methodological approaches to identify the placement of wildlife crossings along road corridors and even fewer ways to determine how to space them. The placement of crossings has generally been related to location, i.e., riparian corridors, road-kill hotspots, or wildlife travel or migration routes (Bekker *et al.* 1995; Evink 1996; Iuell 2003). Generally, wildlife crossings are spaced at 1.5 to 2.0 km intervals (Evink 1996; Marshik *et al.* 2001; Cleverger *et al.* 2002a).

We suggest a mitigation planning scheme that consists of (1) locating crossing structures in the area of key crossing zones as predicted by the models, and (2) locating additional crossings so that there is at least 1.5 km between all crossings. The proposed spacing interval is not empirically based, but knowledge of species' movement patterns, variability in movement patterns over time, and predictability of the impacts of landscape change will help guide planning.

Our results also suggest that by providing additional crossing opportunities in areas not identified by the model, the structures will be used if positioned and designed properly. To maximize connectivity across roads for multiple large mammal species, road construction schemes should include a diversity of crossing structures of mixed size classes. This strategy will likely provide greater permeability of roads by accommodating a variety of species and behavioral profiles (Cleverger and Waltho 2005). Lastly, to improve the permeability of roads for small- and medium-sized mammals, we recommend that small culverts (smaller than wildlife crossing structures) be placed at intervals of 150–300 m to provide sufficient opportunities for smaller animals to avoid crossing busy roads. We also recommend a mixed size class of culverts to accommodate the greatest variety of species possible (Cleverger *et al.* 2001b).

### Local-scale movement models

Broad-scale linkage models have been important tools to identify critical habitats for conservation and to integrate land use planning with large-scale conservation priorities. These mapping efforts have evaluated how road networks may undermine the integrity of large ecological networks, like the Yellowstone-to-Yukon ecoregion (L. Craighead, unpublished data). However, a key improvement to the linkage model concept for highway mitigation planning would require fine-scale resolution models that incorporate local habitat and highway-specific parameters necessary for placement of mitigation passages.

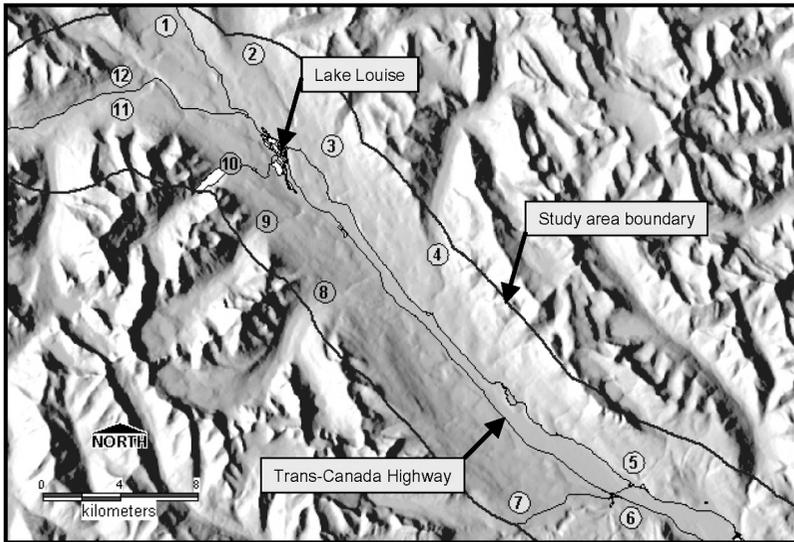
After creating regional-scale models to predict animal movements in our larger study area, we then focused specifically on the section of highway soon to be upgraded with crossings and fencing. Animal movement at the local level is likely to be influenced by the location and intensity of sound sources and viewshed variables such as vegetation density and distribution and hiding cover (Servheen and Sandstrom 1993; Reijnen and Foppen 1994; Mace *et al.* 1996). Spatial models of sound propagation and terrain visibility that take into account local topography, vegetation type, and vegetation density would improve accuracy. In the final exercise, we modeled animal movements across our focal, unfenced section of the Trans-Canada Highway. These models differed from the regional models by inclusion of high-resolution, digital data layers for the upper Bow River Valley transportation corridor and the incorporation of sound and viewshed components.

#### Methods

*Habitat model development* We developed habitat probability surfaces for five large mammal species (elk, moose, black bear, grizzly bear, and wolf) in the unmitigated phase of the Trans-Canada Highway, phase 3B (Fig. 20.1). Seasons were defined as in the regional model; for wolves they were the same as for elk.

The habitat selection analysis was carried out as described for the previous models. Most of our databases were at 1:50 000 scale or less. To facilitate local-level habitat and movement analyses, we created data sets comparable in resolution to the empirical data used to test the models, i.e., GPS-derived crossing and mortality data. All data sets were created at 10-m pixel resolution for the entire study area. We developed 21 biophysical variables in a GIS format grouped into six categories (Clevenger *et al.* 2002a).

*Movement model development* As in the regional model earlier, we used individual-based models with rules for simulated movements based on habitat quality and permeability of landscape elements. We simulated movement patterns using 12 entry and exit points located on the periphery of the area (Fig. 20.3). Nine entry–exit points coincided with the movement corridors identified in the previous regional models; three secondary points were located at the entry to three prominent side valleys within the Bow Valley. Movements were simulated from all possible combinations of entry and exit points, as in the regional models.



**Fig. 20.3.** Location of 12 entry–exit points used for local-scale modeling of large mammal movements in the upper Bow Valley transportation corridor, Banff National Park, Alberta, Canada. The study area is bordered by thick black line.

*Highway crossing zone analysis* We mapped the potential wildlife crossing zones on the Trans-Canada Highway by calculating the number of simulated pathway intersections with segments of highway 200 m in length. We believed the 200-m segment to be small enough to match the resolution of the model and long enough to provide the flexibility in selecting locations for wildlife crossings. We ran the model for each species and season separately, as well as for the cumulative, all-species, all-season model. We considered the all-species iteration to be the most useful for planning highway mitigation measures, such as wildlife crossings, as they should reflect the multi-species, year-round habitat, and movement conditions in the valley.

*Model testing* We tested the accuracy of highway crossing zones predicted by black bear, elk, and combined-species models as in the previous models, using empirical data and comparing their distributions with random points. We defined high-frequency crossing segments as in the regional model.

### Results and discussion

We generated nine habitat suitability models from the five species data sets. The overall cross-validated classification accuracies and validation tests suggested that all models showed a reasonably good fit with the empirical data. We found that the empirical black bear crossing/mortality locations were significantly closer to the modeled high-frequency crossing zones than expected by chance. There was no significant difference between the distances of the random and empirical elk winter crossing locations to the modeled high-frequency crossing zone; however, crossing locations on average were closer to the modeled high-frequency crossing zones than the random points. The empirical locations were significantly closer to the modeled high-frequency crossing zones for the cumulative model pathway intersections than expected by chance.

The increased resolution of spatial databases and the introduction of sound and viewshed models led to a marked improvement in the spatial resolution and reliability of the Trans-Canada Highway linkage model. It is worth stressing the wide applicability of the local-scale models to other planning issues in mountainous environments. The models could be applied to other human infrastructure, such as railways, trails, or other road systems. It is our long-term goal to adapt the models to allow the incorporation of spatial databases (e.g., forest cover data), thus extending its applicability to provincial lands in British Columbia and Alberta.

### Management implications

#### Expert-based models

There are several advantages to the expert-based techniques presented from our work. There are an assortment of GIS tools designed for model building purposes that are readily available today. GIS applications such as Idrisi (Clark University, Worcester, MA, USA), and ArcView (Environmental Systems Research Institute, Redlands, CA, USA) are relatively inexpensive and easy to use. Idrisi has decision support procedures as a program module built into the geographic analysis system. Remotely sensed data, digital landcover data, and habitat suitability maps are readily accessible, frequently updated, and refined for individual users or government agencies (Smith 1999; Serrano *et al.* 2002). Further, empirical data from field studies of many wildlife species, particularly game species, are obtainable in most countries where road mitigation practices are implemented. The use of the Saaty's pair-wise comparison matrix requires little training and ensures consistency in developing relative

weights in the development of the expert-based models (Saaty 1977). This procedure is available in the Idrisi software package.

Both expert model types we presented can provide a useful tool for resource and transportation planners charged with determining the location of mitigation passages for wildlife when baseline information is lacking and when time constraints do not allow for pre-construction data collection. Regarding the latter, we spent approximately 2 months developing the empirical and expert models. More than half of that time was dedicated to developing the more complex, data-intensive, empirical black bear habitat model. We do not advocate modeling linkage zones using exclusively expert information if empirical data are available. However, we do encourage others with empirical data for model building and testing to develop expert models concurrently so that their findings may be contrasted with ours.

#### Multi-scale, regional, and local models

Simulation studies have greatest value when computer models can be coupled with field studies, both to calibrate model parameters and to test or confirm model predictions (Bennett 1999; Tracey Chapter 14). Statistical tests of our models showed that animal movement simulations consistently conformed to the empirical data on failed and successful highway crossings. Results from a mortality model we developed suggested an association between road crossing/mortality locations and areas of high-quality habitat (Clevenger *et al.* 2002a). This corroborates the primary assumption of the movement model, i.e., that movement follows a least-cost path defined by the juxtaposition of high-quality habitat patches. The above results validate the use of the GIS-based linkage model in mapping wildlife crossing zones on a major highway.

We recognize there are shortcomings of the work presented. Due to the large spatial scale (pixel size = 120 m) our regional models were generalized, and predicted crossing locations accordingly have a wide margin of error. Nevertheless, we feel they can be valuable tools for identifying locations of important bottlenecks or fracture zones at a regional scale. As suggested above, once these are identified, smaller, local-scale features of the landscape, including possible wildlife concerns and engineering constraints, can be evaluated to select the most appropriate site for wildlife crossings (Iuell 2003). Modeling of local-scale movements using high-resolution data that include fine-scale elements of landscape conditions will provide greater precision and weight in planning mitigation in transportation projects.

In these two exercises, we have equally weighted all four species. However, some management strategies may give higher precedence to key species of conservation concern (Mills *et al.* 1993; Lambeck 1997). Adjustments can be made to the models by weighting individual species according to management priorities. There are an assortment of techniques for the development of weights; however, one of the most promising appears to be that of pair-wise comparisons developed by Saaty (1977) as used in the expert-based model. It is particularly appealing because it serves as an excellent vehicle for discussion of the criteria and objectives involved and their relative strengths (Starfield and Herr 1991; Lewellyn *et al.* 1996).

## CONCLUSION

During the past 30 years, the environmental impacts of transportation have been addressed through policy initiatives, planning and analysis, new programs, and new technologies (Transportation Research Board 1997; Button and Hensher 2001). Wildlife conservation and habitat connectivity concerns have received little attention by transportation agencies until now, because the primary concern of most transportation agencies is regulatory compliance of federal and state laws, e.g., the US National Environmental Policy Act and Endangered Species Act (Evink 2002). Traffic and roads are strongly implicated in many of the major environmental problems we face today: air and water pollution, fragmented natural habitats, wildlife and biodiversity losses, and urban sprawl. During the next 25 years, significant growth and changes in North America's population and economy are expected to occur. The impacts of roads on natural environments and the means of mitigating such damage are undoubtedly one of the most important land and wildlife conservation challenges of this new century.

Landscape-level thinking and ecosystem-level initiatives are becoming more common at federal, state, and provincial departments of transportation (US Department of Transportation 2006). These concerns have also percolated up to the US Congress. For the first time, the new transportation bill requires all state transportation departments to consult with resource agencies at the beginning of the planning process, if roads are built with federal money. Also, for the first time, the bill considers wildlife–vehicle collisions to be a major safety issue and allocates federal money for fencing, wildlife crossings, and other measures to reduce wildlife-related accidents.

Healthy and well-functioning ecosystems are vital to the protection of our diverse biological resources and to sustaining the economies and communities that rely on their products and benefits (Luck *et al.* 2003). Federal and state transportation agencies have recognized that early stakeholder involvement and identification of issues and areas of concern is essential if their projects are to be environmentally sustainable. Recent developments in state-wide, GIS-based information for transportation planning and mapping priority habitat conservation needs provides an unprecedented opportunity to coordinate ecological and transportation networks at a state-wide scale.

State transportation plans such as Statewide Transportation Improvement Program (STIP) identify critical areas for infrastructure investments in the short and long term. Similarly, state natural resource agencies are developing comprehensive wildlife conservation strategies that address wildlife and habitat conservation issues (Anonymous 2004; The Biodiversity Partnership 2006). The marrying of transportation and ecological networks would significantly advance environmental streamlining. Integrating these plans would help ensure that habitat conservation and connectivity concerns appear at the beginning of the planning process and guide transportation and land management actions. Looking at the broader picture instead of reacting to a specific project is certainly a novel approach for transportation practitioners. Mapping ecological and transportation corridors will help better understand stakeholder concerns, prioritize agency objectives, and incorporate landscape patterns and processes in the planning and construction process (Forman 1987). An effort of this type would greatly enhance interagency collaboration while working toward a common goal – sustainable surface transportation.

We have described several modeling approaches in this chapter that can be used to identify fracture or conflict zones between transportation and habitat corridors. GIS-based connectivity models are becoming more popular with transportation and natural resource agencies charged with identifying and delineating barriers and corridors for animal movement (Singleton *et al.* 2002). Nonetheless, surprisingly few states have actually integrated transportation and ecological networks using the wealth of data available in a GIS format (Smith 1999). These models can be particularly valuable tools for transportation planners and land managers as they are proactive, provide for the development of a more integrated land-use strategy by taking into account different land management practices, and help prioritize habitat conservation concerns.

It is our hope that the site-specific, one-dimension (linear), sectional road planning approach traditionally used by transportation practitioners quickly succumbs to more integrated, larger-scale methodological schemes that contemplate landscape patterns and ecological connectivity (Bennett 1999; Iuell 2003). However, this cannot be realized without political and agency support. The emerging principles of road ecology are providing useful guidelines and best practices for mitigating road impacts on ecological connectivity, but they ultimately need to become embedded in federal and state administrative policies and legal frameworks. High-quality targeted research precedes effective applications. The need for more science-based knowledge for decision-making is urgent and unprecedented, as an aggressive transportation program is being carried out across the land. This will provide a sound scientific basis for effective planning, policy, and implementation. Perhaps more important, it will inspire confidence in individuals, agencies, and society as a whole that transportation impacts on wildlife, connectivity, and biodiversity loss is worthy of substantial and continuing investment.

#### ACKNOWLEDGEMENTS

The research was funded by research contracts with Parks Canada, Public Works and Government Services Canada, and grants from the Wilburforce Foundation's Yellowstone-to-Yukon Science program. We thank Bryan Chruszcz and Kari Gunson for their assistance. We sincerely thank Kevin Crooks for his many helpful comments on the chapter. Jeff Tracey and Jerald Powell helped streamline the chapter. The Woodcock Foundation, Wilburforce Foundation, and US Humane Society provided support for the lead author during the preparation of this chapter.

#### REFERENCES

- Allen, T. F. H., and T. B. Starr (eds.) 1982. *Hierarchy: Perspectives for Ecological Complexity*. Chicago, IL: University of Chicago Press.
- Anonymous. 2004. *Comprehensive Wildlife Conservation Strategies State Progress Report* Washington, DC: No. 2, March 2004. International Association of Fish and Wildlife Agencies. Available online at <http://www.teamingwithwildlife.org/>
- Bank, F. G., C. L. Irwin, G. L. Evink, et al. 2002. *Wildlife Habitat Connectivity across European Highways*, Office of International Programs, Publication No. FHWA-PL-02-011. Washington, DC: Federal Highway Administration.

- Beier, P., and R. Noss. 1998. Do habitat corridors provide connectivity? *Conservation Biology* 12:1241–1252.
- Bekker, H., V. D. B. Hengel, and H. van der Sluijs. 1995. *Natuur over Wegen* [Nature over motorways]. Delft, The Netherlands: Ministry of Transport, Public Works and Water Management.
- Bennett, A. F. 1999. *Linkages in the Landscape: The Role of Corridors and Connectivity in Wildlife Conservation*. Gland, Switzerland: International Union for the Conservation of Nature.
- Boone, R. B., and M. L. Hunter. 1996. Using diffusion models to simulate the effects of land use on grizzly bear dispersal in the Rocky Mountains. *Landscape Ecology* 11:51–64.
- Brody, A. J., and M. R. Pelton. 1989. Effects of roads on black bear movements in western North Carolina. *Wildlife Society Bulletin* 17:5–10.
- Button, K., and D. A. Hensher. 2001. *Handbook of Transportation Systems*. New York: Pergamon Press.
- Cain, A. T., V. R. Tuovila, D. G. Hewitt, and M. E. Tewes. 2003. Effects of a highway and mitigation projects on bobcats in Southern Texas. *Biological Conservation* 114:189–197.
- CanTERS, K. (ed.) 1997. *Habitat Fragmentation, and Infrastructure*. Delft, The Netherlands: Ministry of Transport, Public Works and Water Management.
- Carr, L. W., and L. Fahrig. 2001. Effect of road traffic on two amphibian species of differing vagility. *Conservation Biology* 15:1071–1078.
- Carroll, C., R. F. Noss, and P. Paquet. 2001. Carnivores as focal species for conservation planning in the Rocky Mountain region. *Ecological Applications* 11:961–980.
- Cassady St. Clair, C. 2003. Comparative permeability of roads, rivers, and meadows to songbirds in Banff National Park. *Conservation Biology* 17:1151–1160.
- Chruszcz, B., A. P. Clevenger, K. Gunson, and M. Gibeau. 2003. Relationships among grizzly bears, highways, and habitat in the Banff–Bow Valley, Alberta, Canada. *Canadian Journal of Zoology* 81:1378–1391.
- 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., and N. Waltho. 2005. Performance indices to identify attributes of highway crossing structures facilitating movement of large mammals. *Biological Conservation* 121:453–464.
- Clevenger, A. P., B. Chruszcz, and K. Gunson. 2001a. Highway mitigation fencing reduces wildlife–vehicle collisions. *Wildlife Society Bulletin* 29:646–653.
- Clevenger, A. P., B. Chruszcz, and K. Gunson. 2001b. Drainage culverts as habitat linkages and factors affecting passage by mammals. *Journal of Applied Ecology* 38:1340–1349.
- Clevenger, A. P., B. Chruszcz, K. Gunson, and J. Wierzchowski. 2002a. *Roads and Wildlife in the Canadian Rocky Mountain Parks: Movements, Mortality and Mitigation*, Final Report. Banff, Alberta, Canada: Parks Canada.
- Clevenger, A. P., J. Wierzchowski, B. Chruszcz, and K. Gunson. 2002b. GIS-generated expert based models for identifying wildlife habitat linkages and mitigation passage planning. *Conservation Biology* 16:503–514.

- DeMaynadier, P. G., and M. L. Hunter. 2000. Road effects of amphibian movements in a forested landscape. *Natural Areas Journal* 20:56–65.
- Develey, P. F., and P. C. Stouffer. 2001. Effects of roads on movements by understory birds in mixed-species flocks in central Amazonian Brazil. *Conservation Biology* 15:1416–1422.
- Diamond, J. M. 1975. The island dilemma: lessons on modern biogeographic studies for the design of natural reserves. *Biological Conservation* 7:129–146.
- Eastman, J. R., W. Jin, P. A. K. Kyeem, and J. Toledano. 1995. Raster procedures for multi-criteria/multi-objective decisions. *Photogrammetric Engineering and Remote Sensing* 61:539–547.
- Evinck, G. L., 1996. Florida Department of Transportation initiatives related to wildlife mortality. Pp. 278–286 in G. L. Evinck, D. Zeigler, P. Garrett, and J. Berry (eds.) *Highways and Movement of Wildlife: Improving Habitat Connections and Wildlife Passageways across Highway Corridors*. Tallahassee, FL: Florida Department of Transportation.
- Evinck, G. 2002. *Interaction between Roadways and Wildlife Ecology: a Synthesis of Highway Practice*, National Cooperative Highway Research Program Synthesis No. 305. Washington, DC: Transportation Research Board.
- Evinck, G., P. Garrett, and D. Zeigler (eds.) 1999. *Proceedings of the 3rd International Conference on Wildlife Ecology, and Transportation*. Tallahassee, FL: Florida Department of Transportation.
- Forman, R. T. T. 1987. The ethics of isolation, the spread of disturbance, and landscape ecology. Pp. 213–229 in M. G. Turner (ed.) *Landscape Heterogeneity, and Disturbance*. New York: Springer-Verlag.
- Forman, R. T. T. 1995. *Land Mosaics: The Ecology of Landscapes and Regions*. Cambridge, UK: Cambridge University Press.
- Forman, R. T. T., and L. E. Alexander. 1998. Roads and their major ecological effects. *Annual Reviews of Ecology and Systematics* 29:207–231.
- Forman, R. T. T., D. Sperling, J. Bissonette, et al. 2003. *Road Ecology: Science and Solutions*. Washington, DC: Island Press.
- Foster, M. L., and S. R. Humphrey. 1995. Use of highway underpasses by Florida panthers and other wildlife. *Wildlife Society Bulletin* 23:95–100.
- Gerlach, G., and K. Musolf. 2000. Fragmentation of landscape as a cause for genetic subdivision in bank voles. *Conservation Biology* 14:1066–1074.
- Getz, L. L., F. R. Cole, and D. L. Gates. 1978. Interstate roadsides as dispersal routes for *Microtus pennsylvanicus*. *Journal of Mammalogy* 59:208–213.
- Gibbs, J. P. 1998. Amphibian movements in response to forest edges, roads, and streambeds in southern New England. *Journal of Wildlife Management* 62:584–589.
- Gibbs, J. P., and G. Shriver. 2002. Estimating the effects of road mortality on turtle populations. *Conservation Biology* 16:1647–1652.
- Goosem, M., Y. Izumi, and S. Turton. 2001. Efforts to restore habitat connectivity for an upland tropical rainforest fauna: a trial of underpasses below roads. *Ecological Management and Restoration* 2:196–202.
- Guyot, G., and J. Clobert. 1997. Conservation measures for a population of Hermann's tortoise, *Testudo hermanni*, in southern France bisected by a major highway. *Biological Conservation* 79:251–256.
- Hanski, I. 1999. *Metapopulation Ecology*. Oxford, UK: Oxford University Press.

- Hardy, A., A. P. Clevenger, M. Huijser, and G. Neale., 2003. An overview of methods and approaches for evaluating the effectiveness of wildlife crossing structures: emphasizing the science in applied science. Pp. 319–330 in C. L. Irwin, P. Garrett, and K. McDermott (eds.) *Proceedings of the International Conference on Ecology and Transportation*. Raleigh, NC: Center for Transportation and the Environment, North Carolina State University.
- Hels, T., and E. Buchwald. 2001. The effect of road kills on amphibian populations. *Biological Conservation* 99:331–340.
- Huey, L. M. 1941. Mammalian invasion via the highway. *Journal of Mammalogy* 22:383–385.
- Iuell, B. (ed.) 2003. *Wildlife, and Traffic: A European Handbook for Identifying Conflicts and Designing Solutions*. Utrecht, The Netherlands: KNNV Publishers.
- James, A. R. C., and A. K. Stuart-Smith. 2000. Distribution of caribou and wolves in relation to linear corridors. *Journal of Wildlife Management* 64:154–159.
- 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.
- Kaczynsky, P., F. Knauer, B. Krze, et al. 2003. The impact of high speed, high volume traffic axes on brown bears in Slovenia. *Biological Conservation* 111:191–204.
- Keller, I., and C. R. Lagiardèr. 2003. Recent habitat fragmentation caused by major roads leads to reduction of gene flow and loss of genetic variability in ground beetles. *Proceedings of the Royal Society of London B* 270:417–423.
- Kistler, R. 1998. Wissenschaftliche Begleitung der Wildwarnanlagen Calstrom WWA-12-S July 1995–November 1997: Schlussbericht. Zurich, Switzerland: Infodienst Wildbiologie und Ökologie.
- Knight, R. L., and J. Y. Kawashima. 1993. Responses of raven and red-tailed hawk populations to linear right-of-ways. *Journal of Wildlife Management* 57:266–271.
- Kobler, A., and M. Adamic., 1999. Brown bears in Slovenia: identifying locations for construction of wildlife bridges across highways. Pp. 29–38 in G. L. Evink, P. Garrett, and D. Zeigler (eds.) *Proceedings of the 3rd International Conference on Wildlife Ecology and Transportation*. Tallahassee, FL: Florida Department of Transportation.
- Koehler, G. M., and J. D. Brittell. 1990. Managing spruce-fir habitat for lynx and snowshoe hares. *Journal of Forestry* 88:10–14.
- Lambeck, R. J. 1997. Focal species: a multi-species umbrella for nature conservation. *Conservation Biology* 11:849–856.
- Laurance, S. G. W., P. C. Stouffer, and W. F. Laurance. 2004. Effects of road clearings on movement patterns of understory rainforest birds in Central Amazonia. *Conservation Biology* 18:1099–1109.
- Lay, M. G. 1992. *Ways of the World*. New Brunswick, NJ: Rutgers University Press.
- Llewellyn, D. W., G. P. Shaffer, N. J. Craig, et al. 1996. A decision-support system for prioritizing restoration sites on the Mississippi River alluvial plain. *Conservation Biology* 10:1446–1455.
- Lima, S. L., and P. A. Zollner. 1996. Towards a behavioural ecology of ecological landscapes. *Trends in Ecology and Evolution* 11:131–135.
- Luck, G. W., G. C. Daily, and P. R. Erlich. 2003. Population diversity and ecosystem services. *Trends in Ecology and Evolution* 18:331–336.

- MacArthur, R. H., and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.
- Mace, R. D., J. S. Waller, T. L. Manley, L. J. Lyon, and H. Zuuring. 1996. Relationships among grizzly bears, roads and habitat in the Swan Mountains, Montana. *Journal of Applied Ecology* 33:1395–1404.
- Maehr, D. S., E. D. Land, and M. E. Roelke. 1991. Mortality patterns of panthers in southwest Florida. *Proceedings of the Annual Conference of Southeast Game and Fish and Wildlife Agencies* 45:201–207.
- Marcot, B. G. 1986. Use of expert systems in wildlife-habitat modeling. Pp. 145–150 in J. Verner, M. L. Morrison, and C. J. Ralph. (eds.) *Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates*. Madison, WI: University of Wisconsin Press.
- Marshik, J., L. Renz, J. L. Sipes, D. Becker, and D. Paulson. 2001. Preserving spirit of place: U.S. Highway 93 on the Flathead Indian Reservation. *Proceedings of the International Conference on Ecology and Transportation* 2001:244–256.
- May, S. A., and T. W. Norton. 1996. Influence of fragmentation and disturbance on the potential impact of feral predators on native fauna in Australian forest ecosystems. *Wildlife Research* 23:387–400.
- McGuire, T. M., and J. F. Morrall. 2000. Strategic highway improvements to minimize environmental impacts within the Canadian Rocky Mountain national parks. *Canadian Journal of Civil Engineering* 27:523–532.
- Meunier, F. D., C. Verheyden, and P. Jouventin. 2000. Use of roadsides by diurnal raptors in agricultural landscapes. *Biological Conservation* 92:291–298.
- Mills, L. S., M. E. Soulé, and D. F. Doak. 1993. The keystone-species concept in ecology and conservation. *BioScience* 43:219–224.
- Ng, S. J., J. W. Dole, R. M. Sauvajot, S. P. Riley, and T. J. Valone. 2004. Use of highway undercrossings by wildlife in southern California. *Biological Conservation* 115:499–507.
- Noss, R. F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* 4:355–364.
- Noss, R. F., H. B. Quigley, M. G. Hornocker, T. Merrill, and P. Paquet. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. *Conservation Biology* 10:949–963.
- Olander, L. P., F. N. Scatena, and W. L. Silver. 1998. Impacts of disturbance initiated by road construction in a subtropical cloud forest in the Luquillo Experimental Forest, Puerto Rico. *Forest Ecology and Management* 109:33–49.
- O'Neill, V., D. L. DeAngelis, J. B. Waide, and T. F. H. Allen. (eds.) 1986. *A Hierarchical Concept of Ecosystems*. Princeton, NJ: Princeton University Press.
- Opdam, P. F. M. 1997. How to choose the right solution for the right fragmentation problem? Pp. 55–60 in K. Canters (ed.) *Habitat Fragmentation, and Infrastructure*. Delft, The Netherlands: Ministry of Transportation, Public Works and Water Management.
- Ortega, Y. K., and D. E. Capen. 1999. Effects of forest roads on habitat quality for ovenbirds in a forested landscape. *Auk* 116:937–946.
- Page, R., S. Bayley, J. D. Cook, et al. 1996. *Banff–Bow Valley: At the Crossroads. Summary Report for the Banff–Bow Valley Task Force*. Ottawa, Ontario, Canada: Canadian Heritage.

- Rao, M., S. V. C. Sastry, P. D. Yadar, *et al.* 1991. *A Weighted Index Model for Urban Suitability Assessment – GIS Approach*. Mumbai, India: Bombay Metropolitan Regional Development Authority.
- Redford, K. H., and B. D. Richter. 1999. Conservation of biodiversity in a world of use. *Conservation Biology* 13:1246–1256.
- Reijnen, R., and R. Foppen. 1994. The effects of car traffic on breeding bird populations in woodland. I. Evidence of reduced habitat quality for willow warblers (*Phylloscopus trochilus*) breeding close to a highway. *Journal of Applied Ecology* 31:85–94.
- Robinson, J. 1971. *Highways and our Environment*. San Francisco, CA: McGraw-Hill.
- Rodríguez, A., G. Crema, and M. Delibes. 1996. Use of non-wildlife passages across a high-speed railway by terrestrial vertebrates. *Journal of Applied Ecology* 33:1527–1540.
- Romin, L. A., and J. A. Bissonette. 1996. Deer–vehicle collisions: status of state monitoring activities and mitigation efforts. *Wildlife Society Bulletin* 24:276–283.
- Rondinini, C., and C. P. Doncaster. 2002. Roads as barriers to movement for hedgehogs. *Functional Ecology* 16:504–509.
- Saaty, T. L. 1977. A scaling method for priorities in hierarchical structures. *Journal of Mathematical Psychology* 15:234–281.
- Sanderson, E. W., M. Jaiteh, M. A. Levy, *et al.* 2002. The human footprint and the last of the wild. *BioScience* 52:891–904.
- Saunders, D. A., and R. J. Hobbs. 1991. *Nature Conservation*, vol. 2, *The Role of Corridors*. Chipping Norton, NSW, Australia: Surrey Beatty and Sons.
- Seabrook, W. A., and E. B. Dettman. 1996. Roads as activity corridors for cane toads in Australia. *Journal of Wildlife Management* 60:363–368.
- Serrano, M., L. Sanz, J. Puig, and J. Pons, 2002. Landscape fragmentation caused by the transportation network in Navarra (Spain): two-scale analysis and landscape integration assessment. *Landscape and Urban Planning* 58:113–123.
- Servheen, C., and P. Sandstrom. 1993. Ecosystem management and linkage zones for grizzly bears and other large carnivores in the northern Rocky Mountains in Montana and Idaho. *Endangered Species Bulletin* 18:1–23.
- Singleton, P. H., W. L. Gaines, and J. F. Lehmkuhl. 2002. *Landscape Permeability for Large Carnivores in Washington: A Geographic Information System Weighted-Distance and Least-Cost Corridor Assessment*. Research Paper PNW-RP-549. Portland, OR: US Department of Agriculture Forest Service.
- Smith, D. 1999. Identification and prioritization of ecological interface zones on state highways in Florida. Pp 209–230 in G. L. Evinck, P. Garrett, and D. Zeigler (eds.) *Proceedings of the 3rd International Conference on Wildlife Ecology and Transportation*. Tallahassee, FL: Florida Department of Transportation.
- Spellerberg, I. F. 2002. *Ecological Effects of Roads*. Plymouth, UK: Science Publisher Inc.
- Spellerberg, I. F., and M. J. Gaywood. 1993. *Linear Features: Linear Habitats and Wildlife Corridors*, English Nature Research Report No. 63. Peterborough, UK: English Nature.
- Starfield, A. M., and A. M. Herr. 1991. A response to Maguire. *Conservation Biology* 5:435.

- Straker, A. 1998. Management of roads as biolinks and habitat zones in Australia. Pp. 181–188 in G. Evink, D. Zeigler, and J. Berry (eds.) *Proceeding of the International Conference on Wildlife Ecology and Transportation*. Tallahassee, FL: Florida Department of Transportation.
- Swanson, F. J., T. K. Kratz, N. Caine, and R. G. Woodmansee. 1988. Landform effects on ecosystem patterns and processes. *BioScience* 38:92–98.
- Sweaner, L. L., K. A. Logan, and M. G. Hornocker. 2000. Cougar dispersal patterns, metapopulation dynamics, and conservation. *Conservation Biology* 14:798–808.
- 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.
- Tewksbury, J. J., D. J. Levey, N. M. Haddad, *et al.* 2002. Corridors affect plants, animals, and their interactions in fragmented landscapes. *Proceedings of the National Academy of Sciences of the USA* 99:12923–12926.
- The Biodiversity Partnership. 2006. *Home page*. Available online at <http://www.biodiversitypartners.org/bioplanning/elements.shtml>
- Thompson, L. M. 2003. Abundance and genetic structure of two black bear populations prior to highway construction in eastern North Carolina. M.Sc. thesis, Knoxville, TN: University of Tennessee.
- Thurber, J. M., R. O. Peterson, T. D. Drummer, and S. A. Thomasma. 1994. Gray wolf response to refuge boundaries and roads in Alaska. *Wildlife Society Bulletin* 22:61–68.
- Tischendorf, L., and L. Fahrig. 2000. On the usage and measurement of landscape connectivity. *Oikos* 90:7–19.
- Transportation Research Board. 1997. *Toward a Sustainable Future: Addressing the Long-Term Effects of Motor Vehicle Transportation on Climate and Ecology*. Washington, DC: National Academy Press.
- Transportation Research Board. 2002a. *Environmental Research Needs in Transportation*. Conference Proceedings No. 28. Washington, DC: National Academy Press.
- Transportation Research Board. 2002b. *Surface Transportation Environmental Research: A Long-Term Strategy*. Special Report No. 268. Washington DC: National Academy Press.
- Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14:18–30.
- Turchin, P., 1998. *Quantitative Analysis of Movement*. Sunderland, MA: Sinauer Associates.
- Underhill, J. E., and P. G. Angold. 2000. Effects of roads on wildlife in an intensively modified landscape. *Environmental Review* 8:21–39.
- US Department of Transportation. 1999. *Transportation Equity Act for the 21st Century*. Washington, DC: Federal Highway Administration.
- US Department of Transportation. 2006. *Federal Highway Administration Report*. Available online at <http://www.fhwa.dot.gov/environment/ecosystems/ecoinitc.htm>
- Van Bohemen, H., C. Padmos, and H. de Vries. 1994. Versnippering-ontsnippering: Beleid en onderzoek bij verkeer en waterstaat. *Landschap* 1994:15–25.

- Van der Zande, A. N., W. J. Ter Keurs, and W. J. van der Weijden. 1980. The impact of roads on the densities of four birds species in an open field habitat: evidence of a long-distance effect. *Biological Conservation* 18:299–321.
- Vermeulen, H. J. W. 1994. Corridor function of a road verge for dispersal of stenotopic heathland ground beetles (Carabidae). *Biological Conservation* 69:339–349.
- Vos, C. C., and J. P. Chardon. 1998. Effects of habitat fragmentation and road density on the distribution pattern of the moor frog *Rana arvalis*. *Journal of Applied Ecology* 35:44–56.
- Walker, R., and F. L. Craighead. 1997. Analyzing wildlife movement corridors in Montana using GIS. *Proceedings of the 1997 ESRI User Conference*. Redlands, CA: Environmental Sciences Research Institute. Available online at <http://www.esri.com/library/userconf/proc97/proc97/to150/pap116/p116.htm>
- Woods, J. G. 1990. *Effectiveness of Fences and Underpasses on the Trans-Canada Highway and Their Impact on Ungulate Populations*. Banff, Alberta, Canada: Banff National Park Warden Service.
- Yamada, K., J. Elith, M. McCarthy, and A. Zenger. 2003. Eliciting and integrating expert knowledge for wildlife habitat modelling. *Ecological Modelling* 165:251–264.
- Yanes, M., J. M. Velasco, and F. Suárez. 1995. Permeability of roads and railways to vertebrates: the importance of culverts. *Biological Conservation* 71:217–222.