Review of Road Passage Designs for Jaguars

A Final Submission to the U.S. Fish and Wildlife Service
in Partial Fulfillment of Contract F14PX00340

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28 August 2014
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Executive Summary

Human activities are increasingly fragmenting the natural landscape. Understanding and minimizing the effects of this fragmentation on biological communities is essential to their conservation. Roads are among the most widespread infrastructure that imposes some of the greatest fragmentation pressures on the natural landscape. Recognizing the negative consequences that roads have on ecological processes, the field of “road ecology” has emerged as an applied science that assesses impacts of roads and traffic, and tests approaches to avoid or minimize these impacts on ecological processes (Forman et al. 2003).

A growing body of literature and case studies has quantified an array of impacts of roads on wildlife. Roads and high traffic volumes can create moving barriers that interfere with animals’ ability to move across landscapes to meet biological needs such as finding food, water, cover, and dispersing to new habitats to secure access to mates to increase genetic diversity. Mortality of wildlife due to collisions with vehicles can have direct impacts at the population-level; for example, road mortality is among the major threats to the survival of 21 endangered or threatened species in the U.S. (Huijser et al. 2008). For many imperiled or sensitive species, the impacts of roads may be uncertain; for example, the U.S. Fish and Wildlife Service (2012) Recovery Outline for the Jaguar (Panthera onca) identified the need to assess the impact of roads on jaguars and measures to enable these rare carnivores to safely cross roads in order to help better manage the recovery of this species. This document addresses these measures by synthesizing information about techniques that have high potential to facilitate safe movements of jaguar across roads at the northern extent of their historic range in Mexico and in the southwest United States (i.e., the Northwestern Recovery Unit).

The impacts of roads and traffic on wildlife may be reduced via three primary approaches including manipulating driver behaviors, manipulating animal behaviors, or physically separating wildlife from traffic on roadways. The latter technique, applied by using wildlife crossing structures and fencing to guide animals to passages over or under roads, has proven to be most successful in reducing animal-vehicle collisions while allowing animals to move across the landscape when appropriately designed and placed.

This report summarizes the justification for incorporating wildlife crossing structures into transportation systems; types of wildlife crossing structures; and considerations for the placement, design, construction, maintenance, and monitoring of crossings to increase the likelihood of their effectiveness in moving wildlife across transportation corridors. Given these structures are largely absent or unstudied throughout the jaguar’s range, we highlight the findings of case studies on the most appropriate surrogate taxonomic group or species, in most cases large carnivores, generally, or pumas (Puma concolor L.), specifically.

Integrating wildlife crossing structures with guide fences into transportation systems is most effective through collaborative, interdisciplinary planning, design, placement, construction, and
monitoring the use of these structures in order to assess how well these investments achieve conservation goals. Wildlife crossing and infrastructure design requires the input of a unique suite of disciplines, including ecologists, landscape architects, land use planners, engineers, and transportation specialists. Road ecologists must work proactively with federal agencies and state departments of transportation that are responsible for infrastructure planning, design, and construction. These collaborations have the potential to transform the ways in which human infrastructure and animals coexist.
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Background

Habitat loss and degradation have been identified as the principle cause of the loss of biodiversity worldwide and the primary threat to the world’s mammals (Wilcove et al. 1998, Baillie et al. 2004, Crooks et al. 2011). Crooks et al. (2011) explain “As habitat is destroyed, concurrent fragmentation often partitions the remaining natural areas into progressively smaller, more isolated patches among a human-modified matrix. This isolation of habitat patches can restrict connectivity, which is the movement of organisms or ecological process across the landscape (Taylor et al. 1993).” Conserving landscape connectivity is essential for individual animal movement between habitat patches (Stephens and Krebs 1986); demographic and genetic exchange among populations through dispersal (Clobert et al. 2001); recolonization of ranges when subpopulations go extinct (Hanski 1999); and natural range shifts in response to long-term environmental transitions (Heller and Zavaleta 2009). Maintaining these ecological processes by conserving connectivity enhances population viability for many species (Gilpin and Soulé 1986, Meffe and Carroll 1997, Tewksbury et al. 2002, Damschen et al. 2006) and is a vital component of biodiversity conservation (Beier and Noss 1998, Bennet 1999, Crooks and Sanjayan 2006, Hilty et al. 2006).

Connectivity is essential to facilitate the movement of animals between habitat patches in the pursuit of food or other resources and mates, and for dispersal from their natal ranges, allowing for the exchange of genetic material among otherwise isolated populations (Stephens and Krebs 1986, Clobert et al. 2001). Reductions in genetic connectivity imposed by habitat fragmentation can in some instances lead to inbreeding within isolated populations. Inbreeding can lead to reduction in survival (Keller et al. 1994, Liberg et al. 2005, Hostetler et al. 2010), reproduction (Ortego et al. 2007, Charpentier et al. 2008), and, ultimately, fitness (Slate et al. 2000, Höglund et al. 2002). Deleterious inbreeding effects can be reduced or even eliminated by conserving connectivity through dispersal and other processes between populations (Hanski and Gaggiotti 2004, Hilty et al. 2006, Hostetler et al. 2013).

At broad spatial and temporal scales, connectivity between populations provides for natural range shifts in response to changing environmental conditions, including ecological adaptation to global climate change (Heller and Zavaleta 2009). As carbon dioxide and other atmospheric emissions increase into the future, climate change is expected to become the first or second greatest driver of global biodiversity loss alongside land-use change (Sala et al. 2000). Field research and modeling exercises have shown that well-connected populations are more resilient to environmental changes and natural disturbances, such as drought and fire (Tewksbury et al. 2002, Damschen et al. 2006).
Carnivores are particularly vulnerable to extinction in fragmented landscapes, owing to intrinsic biological traits, such as large body sizes, large area requirements, low densities, and slow population growth rates, as well as external anthropogenic threats, including hunting and other forms of direct mortality (Noss et al. 1996, Woodroffe and Ginsberg 1998, Crooks and Soule 1999, Crooks 2002, Cardillo et al. 2004, 2005). Many carnivores have experienced dramatic population-level extinctions and species-level range contractions on global, continental, and regional scales, mostly where there are high human population densities, or where other human impacts, such as intensive agriculture, grazing, and/or hunting, have been severe (Ceballos and Ehrlich 2002, Laliberte and Ripple 2004). Thus, carnivores have become the focus of pressing conservation concern (Ginsberg 2001, MacDonald 2001, Estes et al. 2011, Ripple et al. 2014).


Roads and associated traffic can detrimentally affect wildlife populations in four ways: 1) decrease habitat amount, availability, and quality; 2) increase mortality due to collisions with vehicles; 3) limit access to resources; and 4) fragment habitat and wildlife populations into smaller and more vulnerable subpopulations (Maehr 1997, Forman and Alexander 1998, Smith 1999, Forman et al. 2003, Mills and Conrey 2003, Jaeger et al. 2005, Riley et al. 2006, Strasburg 2006). Habitat loss can be direct, in the form of habitat removal when roads are built. Habitat loss can also be indirect, where habitat quality close to roads is diminished due to noise, light, pollutants, or other road-associated impacts. Increased mortality rates are due to collisions between vehicles and wildlife. Population persistence can be compromised if higher birth rates do not compensate for increased mortality (Fuller 1989, Ferreras et al. 1992, van der Zee et al. 1992). For some species, roads noise and visual movement of vehicles associated with traffic can restrict movement and access to resources, including food, mates, and breeding sites. These barriers and reduced access to resources can lead to lower reproductive and survival rates (Brody and Pelton 1989, Reijnen and Foppen 1994, Ortega and Capen 1999, Forman et al. 2003, Beckmann et al. 2010), higher population subdivision by restricting flow of individuals and genetic material between subpopulations, and, thus, threaten population persistence (Swihart and Slade 1984, Noss et al. 1996, Gerlach and Musolf 2000).
The jaguar is a large, wide-ranging felid, whose presence or absence provokes strong feelings and conservation concern throughout the Americas (Medellin et al. 2002). Jaguars are the largest felids extant in the New World, with adults typically with head and body length of 1-2 meters and body mass from 36 to 158 kg (Seymour 1989). They are robust and successful predators, able to hunt, kill, and consume over 85 different wildlife species (Seymour 1989), as well as domesticated animals like cows and sheep (e.g., Rosas-Rosas et al. 2010), competing successfully with pumas, and less so with human beings for prey (Rosas-Rosas et al. 2008). Jaguars occupy a wide range of habitats, from deserts to tropical rain forests (Seymour 1989, Sanderson et al. 2002b); they traverse beaches and mountains up to 2,000 m (Troeng 2001). It is not well understood what limits their range beyond the need for cover, food, and freedom from human persecution (Seymour 1989, Crawshaw and Quigley 1991, Hatten et al. 2005).

Thousands of years of jaguar range expansion have been reversed in the last few hundred years, particularly on the margins of their range. The details of that loss, however, are in debate, especially in areas of the U.S. and Mexico (Sanderson and Fisher 2011). Accounts of the range collapse are complicated by the paucity of records and the different standards for scientific observation over the last 200 years, leading to debate about how range maps should be constructed, what different range maps imply about conservation actions, and how those actions interact with the language of specific statutes like the Endangered Species Act (Sanderson et al. in prep).

The loss of jaguar range in the U.S. and northern Mexico mirrors losses of range at the southern end and in other places where human land use has driven out jaguar prey. Jaguars currently occupy 61% of their former pre-1900 range (Sanderson et al. 2002b, Zeller 2007), which was once continuous from the southern U.S. to central Argentina (Swank and Teer 1989). It is not clear what biogeographic or climatological factors limit the jaguar’s range (Sanderson and Fisher 2011). Jaguars can be extirpated from areas through hunting for the fur trade, persecution in response to livestock depredation, and habitat loss (Swank and Teer 1989, Sanderson et al. 2002b, Yackulic et al. 2011a, b). Although the fur trade stopped in the 1970s, direct killing has remained a significant source of mortality, and population declines occur, especially where poorly-controlled or poorly-practiced ranching overlaps areas where jaguars live, enabling them to learn to take livestock. Often in these situations, both controlled and indiscriminant killing of jaguars ensues.

There are differences of opinion regarding the characteristics and significance of jaguars in the U.S. (U.S. Fish and Wildlife Service 2012). Rabinowitz (1999) reported that although the jaguar cannot simply be considered an accidental wanderer into the southwestern U.S., the region has never been, at least in recent times, more than marginal habitat at the extreme northern limit of the jaguar’s range. Rabinowitz (1999) concludes that there is no indication that habitat in the southwest U.S. is critical for the survival of the species.
In contrast, both McCain and Childs (2008) and Grigione et al. (2007) reported that the number of female jaguars with young historically recorded in Arizona suggests that there was once a breeding population in the state, and contemporary sightings represent small segments of a large, but widely-distributed, low-density population at the northern extreme of the species’ range. Additionally, Brown (1983) reported that when plotted at 10-year intervals, records of jaguars killed in Arizona and New Mexico between 1900 and 1980 show a decline characteristic of an over-exploited resident population. Brown (1983) concluded that if the jaguars killed during this period originated in Mexico, the numbers of killings should have always been irregular and erratic, without a declining pattern.

Maintaining connectivity for jaguars from southern Arizona and New Mexico south through the Sierra Madre Occidental, however, is of significant conservation concern (Zeller 2007, Rabinowitz and Zeller 2010, U.S. Fish and Wildlife Service 2012). Studies of genetic variation among jaguars have shown little evidence of significant geographical partitions and barriers to gene flow range-wide wide (Eizirik et al. 2001, Johnson et al. 2002, Ruiz-García et al. 2009). Given this, and the demographic benefits of connectivity, maintaining connectivity between jaguar breeding areas is a vital component in conservation planning for the species (Rabinowitz and Zeller 2010). Thus, the Jaguar Recovery Team and the U.S. Fish and Wildlife Service listed maintaining and improving, when necessary, connectivity for movement of jaguars throughout the landscape and between populations to increase the long-term survival of subpopulations among preliminary recovery actions for the species (U.S. Fish and Wildlife Service 2012). Specifically, the U.S. Fish and Wildlife Service (2012) recommended the development and maintenance of highway under or overpasses and other design measures to facilitate jaguar movement.

To that end, this report provides a broad review of enhancements, including efforts to modify driver and animal behavior and physical structures to channel wildlife movements safely under/over road corridors. To the extent that published literature provides insights in this regard, we will evaluate enhancements that have the potential to accommodate jaguar movements. Given the paucity of jaguar-specific examples from which we can infer, we draw heavily from literature that addresses similar large felids and other carnivores such as cougars (*Puma concolor*) with the assumption that these animals may respond to roads and wildlife crossings similarly. In our forthcoming second report, we will make recommendations for enhancements that may increase the likelihood of safe passage of jaguars across road corridors in a variety of different habitat types in the Northwestern Recovery Unit (Figure 1).

**Enhancements to Modify Driver Behavior**

For a full review of mitigation measures aimed at influencing driver behavior, see Huijser et al. (2008) and Huijser and McGowen (2010). Mitigation measures aimed at influencing driver behavior range from public information and education, to various types of permanent warning signs, seasonal warning signs, animal detection systems that warn drivers of wildlife on the
roadway in real-time, and measures that increase the visibility for drivers. There is a significant amount of information on each of these and our purpose here is not to review each of these except to make key points. First, permanently visible wildlife warning signs do not appear to be effective in reducing wildlife-vehicle collisions (Rogers 2004, Meyer 2006). Second, although enhanced wildlife warning signs (e.g., signs with flashing lights and additional flagging, dynamic message signs) can lower driver speeds (Hardy et al. 2006, Stanley et al. 2006), enhanced warning signs have not been shown to significantly reduce the number of wildlife-vehicle collisions (Pojar et al. 1975, Stanley et al. 2006). In contrast to wildlife warning signs, road-based animal detection systems use sensors to detect large animals that approach the road and correspondingly activate dynamic warning signs indicating drivers should watch for wildlife crossing at that time. The effectiveness of reliable animal detection systems in reducing collisions with large ungulates has been estimated at 82% (Mosler-Berger and Romer 2003) and 91% (Dodd and Gagnon 2008) in certain conditions and settings. However, depending on the type of detection technology used (e.g., microwave radar break-the-beam systems), detection probabilities are potentially higher for larger animals such as ungulates than smaller animals (Huijser et al. 2009c). The reliability of these types of systems for large carnivores is generally unknown, although success rates will likely be lower for carnivores in comparison to ungulates, an idea that warrants further investigation. Further, road-based animal detection systems are more effective in detecting the presence of animals in more open habitats, an issue to consider across the wide range of habitats occupied by jaguars, especially dense tropical vegetation in the neo-tropic regions of the western hemisphere.

Huijser and McGowen (2010) acknowledge there are several advantages to animal detection systems compared to wildlife crossing structures, including 1) detection systems have the potential to provide wildlife with safe crossing opportunities anywhere along roadways deemed appropriate for these systems; 2) they are less restrictive to wildlife movement than fencing or crossing structures; 3) they can be installed without major road construction or traffic control for long periods; and 4) they are likely to be less expensive than wildlife crossing structures. Disadvantages of animal detection systems are their unreliability and somewhat sporadic behavior at the present time (e.g., during storms or high wind events that give “false animal detection”), although these issues are improving with more research on and development of these systems (Huijser et al. 2009c).

**Enhancements to Modify Animal Behavior**

There are two basic approaches to modifying animal behavior to reduce traffic impacts on wildlife: 1) deter wildlife from approaching roads, or 2) direct wildlife movements to places to cross roads safely. Deterring wildlife from approaching roads has the potential to reduce wildlife-vehicle collisions, but has negative consequences associated with limiting wildlife movements across landscapes to meet biological needs; thus, we do not detail these approaches further. A comprehensive review of methods used to deter wildlife from approaching roads can be found in Huijser et al. (2008). Another approach that has been successful in reducing
collisions with ungulates in particular includes population reductions via hunting or culling local herds, relocating wildlife, anti-fertility treatments, and habitat alterations including intercept feeding away from the roadway (Huijser et al. 2008). Because these approaches are not appropriate for the conservation of threatened and endangered species, we do not review these techniques further. Measures that modify wildlife behavior to direct their movements to locations where they can cross the road safely are primarily based on physical barriers such as fencing that separate animals from traffic while providing opportunities for wildlife to cross via conduits under and over roadways.

Enhancements to Direct Wildlife Safely Under/Over Roads

Wildlife crossing structures are a relatively new category of transportation infrastructure that offer safe crossing opportunities for wildlife, thereby connecting habitats and wildlife populations, reducing wildlife mortality on roads, and increasing motorist safety. Wildlife crossing and infrastructure design involve questions on the optimal location of wildlife crossings, the size of the structure, and how species-specific behaviors should be incorporated into the structure design. Stakeholders involved in the crossing structure design process, including ecologists and transportation specialists, make use of the published and grey literature to apply best practices to current and future projects.

Wildlife use of crossing structures depends on several factors, including location on the landscape, distance between structures, habitat surrounding the structures, dimensions of the structure, presence or absence of cover, substrate type, light, moisture, temperature, approaches, directional fencing, human use and anthropogenic noise in the area, species-specific preferences, and time from installation since animals have a learning curve for finding structures (Foster and Humphrey 1995, Clevenger and Waltho 2000, Jackson and Griffin 2000, Clevenger et al. 2002a, Mata et al. 2005, Huijser et al. 2007). Each of these factors should be considered when crossing structures are being incorporated into roadway corridor planning and crossing structure design. Selecting appropriate locations (Clevenger and Waltho 2005) and proper design elements (Foster and Humphrey 1995, Land and Lotz 1996) contribute to meeting performance objectives for wildlife crossing structures. These concerns need to be addressed within the context of project logistics, which include costs of the structure, available material and expertise, and physical limitations of the site (e.g., soil, terrain, hydrology).

Selecting the type of wildlife crossing structure most suitable for a given location begins by identifying a structure that conforms to the wildlife habitat connectivity potential for the target species and topography of the site chosen (Clevenger and Huijser 2011). Clevenger and Huijser (2011:49-51) provide guides for selecting general wildlife crossing structure types based on the wildlife habitat quality (classified as high, medium, and low) and topographical constraints (classified as level or riparian, sloped or cut and fill, below grade, and raised). Wildlife crossing structures fall into two general categories: overpasses and underpasses that direct animals to cross over or under the roadway. Clevenger and Huijser (2011:Appendix C) further divide these
two general categories into eleven different designs and provide specific details on design intentions, dimension guidelines, species-specific guidelines, possible variations, maintenance, and photographs. A diversity of crossing structure designs may be necessary to satisfy species-specific needs within a project area (Barnum 2003, Iuell et al. 2003, Clevenger and Waltho 2005, Mata et al. 2005), as no one crossing structure design has been shown to be appropriate for all wildlife species. For example, Mata et al. (2005) monitored terrestrial vertebrate use of 82 crossing structures along the A-52 motorway in northwestern Spain using marble dust beds and electronic cameras. Crossing structures included circular culverts, adapted box culverts, open span bridges, wildlife underpasses, wildlife overpasses, and overpasses designed for human use. The authors concluded that different taxa prefer different crossing structure designs and adaptable species used more than one type of structure, while other species demonstrated a more limited tolerance.

While these structures can safely pass wildlife under or over roadways without the use of fencing to guide animals to the crossings, field studies have shown that fencing built to prevent wildlife access to the road and funnel animals to the crossings, when appropriately constructed and maintained, can reduce animal-vehicle collisions by 96% for ungulates and 84% for all wildlife species (Clevenger et al. 2001). Unless stated otherwise, the information reviewed here assumes over- and under-passes include this additional and important feature of fencing.

The size of a crossing structure is positively related to the size of taxa that use the structure (Iuell et al. 2003, Clevenger and Waltho 2005, Donaldson 2005, Mata et al. 2005, Hardy et al. 2007, Clevenger and Huijser 2011). The degree to which a passage is open often dictates wildlife use of a crossing structure (Gordon and Anderson 2003, Iuell et al. 2003, Ng et al. 2004, Clevenger and Waltho 2005). For example, deer (Odocoileus spp.) and other ungulates are more likely to use structures with wide, open passages at least 2.1 m high with natural bottoms and a clear view of the habitat on the opposite side (Foster and Humphrey 1995, Barnum 2003, Servheen and Lawrence 2003, Clevenger and Waltho 2005, Hardy et al. 2007). Research into the use of wildlife crossing structures by carnivores suggests structures built at-grade level and providing an unobstructed view of the habitat on the opposite side of the structure increase use (Beier 1995, Foster and Humphrey 1995, Forman et al. 2003, Ruediger 2007).

The spacing of wildlife crossings on a given section of roadway will depend largely on the target species and the terrain and habitats that intersect the roadway (Clevenger and Huijser 2011). Although there is no simple formula to determine the recommended distance between wildlife crossings, Clevenger and Ford (2010), in a review of eight projects in the U.S. and Canada, estimated that the spacing interval for crossing structures for large mammals varied from one wildlife crossing per 1.5 km to one crossing per 6.0 km. Clevenger and Ford’s (2010) review demonstrated that wildlife crossings are variably spaced, but average about 1.9 km apart when multiple crossing structures have been used on various projects for large mammals.
Mitigation structures such as overpasses require a significant fiscal investment, but these costs often represent a small fraction of an overall road construction or redevelopment project budget. Additionally, the expenses are mostly up-front, although routine maintenance expenses require an additional commitment of resources over the 70-80 year life expectancy of a structure (Clevenger and Huijser 2011). Several studies have demonstrated that the savings in reduced costs from fewer wildlife-vehicle collisions ends up saving states, agencies, and the public money over time (see Hardy et al. 2007, Huijser et al. 2009b, Beckmann et al. 2010). For example, Hardy et al. (2007) calculated an economic measure of effectiveness of the construction of wildlife crossing structures along U.S. Highway 93. The authors estimated the total value of an average deer-vehicle collision was $7,890 and the total construction costs of deer crossing structures were approximately $6.1 million dollars. Given an average of 90 deer-vehicle collisions per year, the authors estimated savings would exceed construction costs 15 years post construction with a 60% reduction in collisions and 10 years post construction with a 90% reduction in collisions. Thus, a properly sighted, designed, and constructed overpass with associated fencing to guide animals to the overpass can be highly successful in reducing wildlife-vehicle collisions and increasing connectivity over a relatively large distance roadway (Clevenger et al. 2002a), justifying the return-on-investment in terms of a years of annual net savings yielded as a result of collisions avoided based on the given percent reduction in collisions over time.

Several comprehensive guidelines for designing and monitoring wildlife crossing structures are now available (Iuell et al. 2003, Hardy et al. 2007, Huijser et al. 2007, Bissonette and Cramer 2008). Clevenger and Huijser (2011) offer perhaps the most detailed synthesis of literature complimented with decades of collective expertise on design, placement and monitoring considerations for wildlife crossing structures. This handbook includes “hot sheets” that provide design details for eleven types of crossings with fencing and gate designs, along with each crossing structures’ suitability for six species guilds and twenty species of North American wildlife. The following is a general review of crossing structures describing the intended uses, functions, and parameters for selecting locations for of some of the most common crossing structure types currently in use. Photographs and schematics illustrating an array of crossing structure designs, placement considerations, and other technical requirements are available in Clevenger and Huijser (2011) found at:


**Overpasses**

**Wildlife overpasses** include all passages that cross roadways above the level of the traffic and are often human-made, landscaped bridges or road tunnels dug into the terrain (Forman et al. 2003, Iuell et al. 2003, Huijser et al. 2007, Clevenger and Ford 2010, Clevenger and Huijser 2011). Bridges designed as wildlife crossing structures are typically shorter in span and wider than conventional vehicular bridges designed to accommodate two or four lanes of traffic. Ideally,
well-designed wildlife overpasses are engineered to support a thick layer of soil and vegetation, referred to as a landscaped surface that emulates surrounding habitat conditions. Overpasses are intended to provide for the movement of a broad spectrum of taxa, from large mammals to invertebrates, provided suitable design features and habitat elements afford appropriate substrate and cover along the span. The most effective wildlife overpasses are closed to human activities, and other roads should not be on or near wildlife overpasses, as these activities can hinder wildlife use of the structure (Clevenger and Ford 2010). Overpasses can be a costly but effective means of minimizing, at least locally, the fragmentation effects of transportation infrastructure for terrestrial taxa (Iuell et al. 2003) when placed, designed, and managed appropriately in combination with fencing that guides wildlife to the crossings while restricting wildlife access to roadway surface crossings.

Wildlife overpasses are generally 50 to 70 m wide, although some are as narrow as 20 to 50 m and others as wide as 100 m or more (Iuell et al. 2003, Clevenger and Ford 2010). Most European overpass designs are 90 m wide at the ends, narrowing to 70 m at the middle of the span (Jackson and Griffin 2000, Clevenger et al. 2002a). Width, design, and vegetation depend largely on the target species; however, the wider an overpass, the more taxa and ecological functions an overpass will encompass (Iuell et al. 2003, Clevenger and Huijser 2011). Overpass width should also increase with the length of the structure. Iuell et al. (2003) suggest a minimum width to length ratio greater than 0.8.

Vegetation along the span of a wildlife overpass is intended to guide and provide cover for taxa across the overpass and ideally mimics the surrounding local vegetation in order to provide a suitable habitat corridor (Iuell et al. 2003). Maintenance, engineering limitations (e.g., cumulative weight loads), and traffic safety (e.g., preventing trees from falling off an overpass onto passing traffic) are important considerations in selecting suitable plant species native to the local area. Iuell et al. (2003) suggest soil depths of 0.3 m for grasses and herbs, 0.6 m for bushes and shrubs, and 1.5 m for trees.

Generally, overpasses can be quieter than underpasses, provide habitat more similar to the surrounding landscape, and accommodate more species than underpasses (Jackson and Griffin 2000, Iuell et al. 2003). They are probably less effective, however, for semi-aquatic species, such as muskrats (Ondatra zibethica), beavers (Caster canadensis), and alligators (Alligator mississippiensis) (Jackson and Griffin 2000) unless water features are included in the engineering and design of the structure.

Multiuse overpasses are designed for use by both wildlife and humans. These overpasses tend to be bridges with local roads or pedestrian pathways with the simple addition of an earth-covered strip to promote habitat features that can accommodate wildlife use. They are often narrower than wildlife overpasses and accommodate a smaller subset of taxa (often human-tolerant species) because of frequent human use and activity. Thus, they are not an alternative for
wildlife-specific overpasses, but are an additional measure with potential to improve general permeability of transportation-related barriers for both people and wildlife (Iuell et al. 2003).

**Underpasses**

**Wildlife underpasses** include passages built as a connection under the level of the traffic, ranging from open-span bridges to small-diameter culverts (Iuell et al. 2003, Huijser et al. 2007, Clevenger and Ford 2010, Clevenger and Huijser 2011). While typically designed for vehicle passage over wetlands or deep canyons (i.e., not built specifically for wildlife movement), span bridges and viaducts, and causeways across these natural features can provide ideal passageways for a wide range of species. In situations where a roadway crosses a valley or other area that lies lower than the target level of the infrastructure, a **low viaduct** is an ecologically-preferred alternative to adding fill with culverts to accommodate water passage under an embankment where a road passes over the topographic chasm (Iuell et al. 2003). Viaducts and similar structures provide better habitat linkages and are suitable for a wider range of species than other types of underpasses (Iuell et al. 2003).

In situations where the roadway is built on hilly terrain or an embankment where fill is used to maintain roadway elevation over undulating topography, underpasses are often constructed for wildlife passage. Although underpasses are cited as less suitable for connecting habitats, because of the lack of light and water that allows only limited growth of vegetation (Iuell et al. 2003), well-designed underpasses do provide safe passage opportunities for wildlife.

The **dimensions of wildlife underpasses** are measured by their height, width, and length. The length of an underpass generally corresponds to the width of the roadway plus the additional distance that the base of the fill under the roadway requires (depending on the topography and engineering design approach); however, the width and, to a lesser degree, the height can be designed according to species-specific requirements (Iuell et al. 2003). Ideally, wildlife crossings are not be greater than 70 to 80 m in length except in special situations, such as spanning greater than six-lane highways or spanning highways in addition to other types of infrastructure (for example, frontage roads and railway line) (Clevenger and Huijser 2011). The dimensions of an underpass are often indexed or standardized as relative openness (also called its “openness ratio”) and measured as the product of the opening width and opening height divided by the length of the crossing (width x height / length) (Reed and Ward 1985, Gordon and Anderson 2003, Iuell et al. 2003, Servheen and Lawrence 2003). For example, an underpass with a width of 12 m, a height of 4 m, and a length of 25 m would have a relative openness index of 1.9.

Relative openness, however, should not be used as a sole measurement, and minimum values for height and width, particularly for large species, should be considered. In fact, Clevenger and Huijser (2011) do not recommend the use of the openness index in planning and designing wildlife crossing structures because the relationship between openness and underpass use may be species-specific and time dependent, variations in how openness is measured can occur (e.g., as
an index, a ratio, or simply a state or concept), and designing for the “minimum” is not recommended or appropriate in most cases. Clevenger and Huijser (2011) do recommend the use of underpass measures (length, width, height) in conjunction with other structural (e.g., divided vs. undivided highway configurations) and environmental (e.g., habitat quality, target species) factors when designing wildlife crossing structures. General recommendations for minimum wildlife underpass dimensions vary from 3 m in width and 3.7 m in height (Donaldson 2005, primarily white-tailed deer) to 15 m in width, 3 to 4 m in height, and a minimum openness index of 1.5 (Iuell et al. 2003, Clevenger and Huijser 2011, multiple species including large carnivores).

Fencing

Fencing alone is an effective means of reducing wildlife-vehicle collisions; however, without crossing structures to accommodate wildlife movements under or over roadways, this approach increases habitat fragmentation and decreases landscape permeability. Thus, fences are considered a mitigation measure for fragmentation and habitat connectivity only in combination with wildlife crossing structures that effectively compensate for the negative barrier effects of fences by accommodating wildlife movements (Iuell et al. 2003, Jaeger and Fahrig 2004, Clevenger and Huijser 2011). The efficacy of overpasses and underpasses reducing wildlife-vehicle collisions and enhancing connectivity is highly dependent on associated wildlife fencing that keeps animals off roadways and funnels them towards crossing structures (Clevenger et al. 2002a, Iuell et al. 2003). Wildlife crossing structures with continuous exclusion fencing between them have been shown to reduce ungulate-vehicle collisions by 96% on controlled access highways (Clevenger et al. 2001), and for all wildlife species combined, Clevenger et al. (2001) found appropriate fencing reduced wildlife-vehicle collisions by 84%. Without fencing, wildlife use of large underpasses along State Route 260 in Arizona was limited as most animals continued to cross at-grade, and wildlife-vehicle collisions increased significantly (Dodd et al. 2007a, b). After fencing was installed, passage through underpasses increased nearly five-fold, with elk (*Cervus canadensis*) use of the crossing structures increasing 60%, and elk-vehicle collisions declining 85% (Gagnon et al. 2010).

Exclusion fencing needs to be designed to funnel animals toward crossing structures while preventing them from jumping or climbing over, crawling or burrowing under, or pushing through to the roadway. Clevenger and Huijser (2011) suggest fencing configuration used to mitigate road impacts depends on several variables associated with the specific location, primary adjacent land use, and traffic volumes. Both sides of the road must be fenced (not only one side) and fence ends across the road need to be symmetric and not offset or staggered. Continuous fencing is most often associated with large tracts of public land with little or no interspersed private property or in-holdings. Long stretches of continuous fence with fewer gaps reduces problems of managing wildlife movement around multiple fence ends and accessing the roadway. Partial or discontinuous fencing is more common with highway mitigation for wildlife in mixed (public and private) land use areas. This fencing strategy generally receives wider
acceptance by public stakeholders, but requires additional measures such as modified cattle
guard designs at fence openings (e.g., where driveways or other roads access the stretch of road
that is fenced to prevent wildlife access) to be installed and monitored to discourage wildlife
movement through fence gaps and onto the roadway (see Clevenger and Huijser 2011:170-173).

Fence material often consists of woven-wire (page-wire) or galvanized chain-link fencing.
Clevenger and Huijser (2011:173-174) present a suite of fencing and fence post design
specifications. Fence material must be attached to the back-side (non-highway side) of the posts,
so impacts will only take down the fence material and not the fence posts. Fences 2.2 to 2.4 m
tall prevent deer from jumping over (Ward 1982, Iuell et al. 2003, D’Angelo et al. 2005,
Clevenger and Huijser 2011). Smaller fence mesh; metal, as opposed to wooden, posts; and
outrigger (90 degree lips installed at the top of fencing) prevent bears (Ursus spp.) and pumas
from climbing over fences (Clevenger et al. 2001, Hardy et al. 2007, Clevenger and Huijser
2011). Burying the bottom of the fence or a section of chin-link fence spliced to the bottom of
the fence approximately 1 m, often referred to as a buried apron, can limit animals from crawling
or burrowing under fencing (Woods 1990, Clevenger et al. 2001, Clevenger and Huijser 2011).

Despite the best fencing designs, wildlife will occasionally continue to gain access and become
trapped inside fenced roadways creating a hazardous situation for drivers and wildlife alike
(D’Angelo et al. 2005). Animals able to climb fencing (e.g., bears and pumas) will likely exit
fenced roadways the same way (Hardy et al. 2007). Ungulates, however, require features
designed to allow for safe exit from the roadway. One-way gates allow animals to exit; however,
the reluctance of some species to use gates, some species learning to use gates to access the
roadway, and lack of proper maintenance or people available to respond and open these gates
when ungulates are trapped inside the fences limit their effectiveness (Woods 1990, Hardy et al.
2007). Alternatively, jump-out ramps are earthen, sloped surfaces that lead from the roadway to
the top of the fence, allowing animals caught inside the roadway to escape and preventing
animals from using jump-outs to “jump in” to access the roadway. The most effective ramps are
placed at V-shaped funnels in the fencing and vegetated similarly to the natural surrounds
(Waters 1988, Bissonette and Hammer 2000). Small sections of perpendicular fencing on the
jump-outs can also intercept and guide animals to jump out as they move along the inside of the
fence.

Wildlife often access fenced roadways with greatest frequency at the ends of fencing (Ward
and Huijser (2011) suggest fence ends should terminate at a wildlife crossing structure. If a
wildlife crossing cannot be installed at the fence ends, then fences should terminate in the least
suitable location or habitat for wildlife movement—i.e., places wildlife are least likely to cross
roads (Clevenger and Huijser 2011). Additionally, fences should end in areas with high motorist
visibility, reduced vehicle speeds, and proper signage of potential wildlife activity. Measures
designed to limit roadway access at fence ends include wing fencing, cattle or wildlife guards,

Clevenger and Huijser (2011) caution that fences are not permanent structures and are subject to damage from and being compromised by vehicular accidents, falling trees, soil erosion, excavation by animals, flooding, and vandalism. They suggest checking fences every six months by walking the entire fence line in order to identify and repair gaps, breaks, and other defects that compromise the utility of the fence in preventing wildlife access to the roadway.

Enhancements and Large Mammals

Species-specific preferences are important factors in designing effective wildlife crossing structures (Clevenger et al. 2002a, Iuell et al. 2003, Hardy et al. 2007). Efforts to locate, design, construct, and monitor crossing structures should incorporate findings from other projects. Data and specifications on suitable size, design, planning, sighting, construction, and use of crossing structures for ungulates are well documented (e.g., Dodd et al. 2007a, Dodd and Gagnon 2010). However, data on the efficacy of various crossing structures are limited for carnivores, and thus using data on ungulates or similar sized carnivores as guides may be useful in planning, designing, sighting, and constructing crossing structures for jaguars as well.

Clevenger and Huijser (2011:62) synthesized the last 10 years of monitoring and research of crossing structures in North America and categorized the suitability of alternate crossing structures for 26 wildlife species or taxa. For pumas, they recommended large over and underpasses and underpasses with water flow as optimal solutions. They did not recommend multi-use structures for pumas.

Generally speaking and lacking empirical support, Ruediger (2007) suggested a 7 m wide by 4 m high underpass structure would likely be acceptable for black bears (*U. americanus*), pumas, and most other common carnivores. However, he suggested open-span wildlife crossings would be more effective for grizzly bears (*U. arctos horribilis*) and gray wolves (*Canis lupus*). For species with little or no empirical data available to determine wildlife crossing structure size, Ruediger (2007) recommended designing structures for the largest target species. Puma use of crossing structures and data on the size of structures that facilitated puma use would serve as an appropriate surrogate for jaguar.

Pumas in Banff National Park selected underpasses far from human activity with sufficient cover leading to the passage (Gloyne and Clevenger 2001, Clevenger et al. 2002a). Artificial light might also discourage pumas from using wildlife crossings (Beier 1995, Jackson 1999, Cramer and Bissonnette 2005). Beier (1995) observed dispersing pumas in coastal southern California readily approached highways, but usually stopped 50-100 m from a newly encountered roadway until daylight, then crossing or retracing its route the next evening. He observed dispersers regularly crossed under highway bridges built to accommodate watercourses; however, dispersers and adults usually avoided large and small culverts under freeways or two-lane rural
highways. One male puma, however, made frequent use of 1.8 m box culverts to cross under an eight-lane freeway.

Additionally, wolves in Banff National Park used 15.2 m wide by 4.0 m high open-span underpasses (Forman et al. 2003) and 52 m wide overpasses (Clevenger et al. 2002a). Grizzly bears used open-span underpasses and overpasses more than expected (Clevenger et al. 2002a, Forman et al. 2003). Black bears and pumas used a variety of crossing structures, including overpasses, open-span underpasses, 7 m wide by 4 m high culverts, and 2.5 m wide by 3 m high box culverts.

In coastal southern California, Ng et al. (2004) monitored 15 underpasses and drainage culverts beneath highways representing a range of design specifications using remotely triggered cameras and gypsum track stations. They found the presence of suitable habitat on both sides of the crossing structure and passage dimensions were particularly important factors predicting use. Only a single record of a puma using a structure was collected, precluding statistical evaluations. Bobcats (Lynx rufus) and coyotes (Canis latrans), however, frequently used structures far from developed habitat and human activity.

Along the same stretches of highway in coastal southern California as Ng et al. (2004), Riley et al. (2006) studied coyote and bobcat populations separated by the Ventura Freeway (U.S. 101), a congested 10-12 lane roadway 40 km from downtown Los Angeles. Riley et al. (2006) combined radio-telemetry data and genetically based assignments to reveal 5-32% of sampled carnivores crossed the freeway over a 7-year period. However, despite moderate levels of migration, populations on either side of the freeway were genetically differentiated, implying individuals that crossed the freeway rarely reproduced. Riley et al. (2006) demonstrate freeways are filters favoring dispersing individuals that add to migration rates but little to gene flow. They conclude that roadways can restrict gene flow even in wide-ranging species and suggest migration rates need to be an order of magnitude larger than commonly assumed.

In many landscapes, longer distance movements by carnivores are often associated with water or riparian habitats (Noss 1991, Hilty et al. 2006). Thus, for jaguars in many parts of their range, higher probability crossing locations are likely to be associated with water (see Selection of Wildlife Crossing Locations below) and therefore may already have bridges spanning and near the riparian areas. Additionally, because of the associated water at these potential high probability crossing locations, any underpass constructed or modified for wildlife would likely also serve the dual-purpose of maintaining water flow.

**Dual-purpose underpass** structures are designed to accommodate dual needs of moving water and wildlife (Clevenger and Ford 2010:40, Clevenger and Huijser 2011:139). They are generally located in multi-species wildlife movement corridors given their association with riparian habitats. These underpass structures are frequently used by several large mammal species, and use will depend on how the structure may be adapted for each species’ specific crossing
requirements. According to Clevenger and Ford (2010), for these types of underpass structures, it is important to include travel paths adjacent to the water that are generally at least 3 m wide and have a vertical clearance of 4 m. Placement of these travel paths will be important such that they are available even during periods of high-water flows. However, some smaller structures may have travel paths at least 2 m wide with 3 m vertical clearance (see Clevenger and Ford 2010).

Overpasses can be highly effective structures at reducing vehicle collisions with large mammals if designed and placed correctly on the landscape with associated fencing to guide animals to the overpass and jump-outs that provide opportunities to move outside of the fenced section of roadway if animals do access the road surface (Clevenger and Ford 2010). As an example, in places such as Banff National Park in Canada, overpass structures and associated fencing have reduced vehicle collisions with all ungulates by > 90% and with all large mammals by 86% (Woods 1990, Clevenger et al. 2002; see Case Studies: Trans-Canada Highway – Banff National Park below).

The siting of wildlife crossing structures is equally as important as their design (Clevenger and Huijser 2011). There are a number of methods used to determine key locations where important wildlife habitat and transportation infrastructure intersect. These methods enable ecologists, engineers, and transportation specialists to construct appropriate wildlife crossing structures at optimal locations along transportation corridors.

Selection of Wildlife Crossing Locations

The non-random movement of wildlife within and between suitable habitats often involves crossing transportation infrastructure on daily, seasonal, and annual forays as they reproduce, seek shelter, forage, migrate, and disperse (Clevenger et al. 2002a, Barnum 2003, Hardy et al. 2007). Habitat connectivity and wildlife movement patterns are significant factors in determining where to place wildlife crossing structures (Anderson and Gutzwiller 1996, Cramer and Bissonette 2005). Installing structures at locations wildlife choose to cross roadways will increase the likelihood of use (Foster and Humphrey 1995). Generalized landscape features found to be consistently important to the use of passages are the presence of suitable habitat on both sides of the road (Veenbaas and Brandjes 1999, Gloyne and Clevenger 2001, Barnum 2003), the placement of crossing structures at naturally-occurring travel routes and trails (Foster and Humphrey 1995, Land and Lotz 1996, Grist et al. 1999), and low levels of human activity (Rodriguez et al. 1997, Clevenger and Waltho 2000, luell et al. 2003).

Applying these generalities to determine optimal locations for wildlife crossing structures are often undertaken using a project- or systems-level approach (Clevenger and Ford 2010, Clevenger and Huijser 2011). These approaches are two different scales of habitat connectivity planning and means of incorporating measures to reduce the effects of roads on wildlife populations (Clevenger and Huijser 2011). A project-level approach focuses on the site scale and is most common with North American transportation agencies. Project-level mitigation of roads
for wildlife conservation often originates from specific transportation projects intended to address multiple transportation management concerns, one of which may be reducing wildlife-vehicle collisions. Project-level approaches, however, may not consider the context of a crossing enhancement within animal movement patterns, corridor networks, and other landscape-scale ecological processes. Failing to consider a landscape context, wildlife crossing structures could lead to ecological “dead-ends” or “cul-de-sacs,” where structures fail to link wildlife to a larger functional landscape that provides access to food, shelter, and mates; landscape-scale movements; and dispersal corridors (Clevenger and Ford 2010).

**System-level approaches** that take a broader spatial-scale view (which considers landscape-scale processes) have become more common in recent years (Smith 1999, Singleton et al. 2002, Kintsch 2006, Clevenger and Ford 2010). With landscape-scale ecological data, systems-level approaches identify key habitat linkages or zones of wildlife connectivity that are bisected by transportation corridors. Linkages and potential wildlife crossing locations can be prioritized based on future transportation investments, scheduling, and ecological criteria. This approach helps to strategically plan mitigation investments at a regional or ecosystem scale (White 2007, Clevenger and Ford 2010).

A systems-level assessment of wildlife habitat linkages and movement corridors can help identify and prioritize segments of transportation networks with high levels of wildlife-road conflict over a large area (Beier et al. 2008). These assessments serve as a foundation for initiating discussions with transportation and regulatory agencies on mitigation plans in the short and long term. Specific placement of wildlife crossings is generally determined at the project level or after a thorough field survey as part of a larger system-level assessment. Additional decisions involved in specific placement of wildlife crossing mitigation are species or taxa specific and make use of the following methods. Ideally, a combination of these approaches would be used in order to “cross check” their outcomes (Clevenger et al. 2002).

**Landscape-Scale Techniques to Select General Wildlife Crossing Locations**

Landscape-scale Geographic Information System (GIS)-based models allow for the assessment of spatially-related attributes to identify key habitat linkages, evaluate fragmentation resulting from human activities, and identify general locations for potential highway mitigation sites for wildlife (Kautz et al. 1999, Singleton and Lehmkuhl 1999, Crooks and Sanjayan 2006, Hardy et al. 2007, Clevenger and Ford 2010). Clevenger and Huijser (2011) suggest the basic GIS layers useful for identifying habitat linkages and siting wildlife crossings include digital elevation models, water and hydrology, vegetation or ecological land classifications, wildlife habitat suitability, areas of human development and activity, and roads networks. Models that simulate wildlife movements often use resource selection functions that map habitat quality (Manly 1974, Manly et al. 1993, Nathan et al. 2008, Schick et al. 2008, Chetkiewicz and Boyce 2009). The data used to develop simulated wildlife movements are based on animal distribution data, generally obtained by radio telemetry locations, sooted track plates, tracking beds, remotely
triggered cameras, DNA sampling, or scat-detection dogs. The following sections outline many of the GIS-based techniques of habitat linkage modeling and identifying general locations for wildlife crossing structures.

Geographic Information System Models

Least-Cost Path

Least-cost path (or permeability) models have been the most commonly used method of predicting wildlife movement and identifying corridors in the past, although recent advances in other spatial techniques (see discussions below) have led to a decline in the use of these models (Walker and Craighead 1997, Hoctor et al. 2000, Singleton et al. 2002, Carroll and Miquelle 2006, Larue and Nielsen 2008). This approach compromises between minimum travel distance among habitat patches and minimum exposure to unsuitable habitat (Walker and Craighead 1997, Adriaensen et al. 2003, Epps et al. 2007). Models are based on raster maps that divide landscapes into cells with unique values depicting different habitat or vegetation types, elevation, slope, or other landscape features. Cells are given weights or “resistance values” reflecting the presumed influence of each variable on movement of the focal species. Least-cost path routines then are used to: 1) calculate the relative cost of all possible routes among populations or islands of core habitat; 2) determine the least costly route for animal movement between pairs of populations or core areas of habitat; and 3) plot these most probable routes on maps for use in conservation planning. See Majka, D., J. Jenness, and P. Beier. 2007. CorridorDesigner: ArcGIS tools for designing and evaluating corridors, available at http://corridordesign.org.

Least-cost methods, however, have been criticized for the assignment of resistance values often only being based on expert opinion, inference of resistance values from presence/absence or abundance data reflecting habitat use rather than movement cost, use of single points as starting and ending points as opposed to larger polygons that more accurately represent the true habitat mosaic, and the assumptions that animals require a global knowledge of landscape structure and must be totally rational in their decision making (Epps et al. 2007, Clevenger and Ford 2010). Singleton et al. (2002) used least-cost corridor analysis to conduct a regional-scale evaluation of landscape permeability for large carnivores between five concentrations of large carnivore habitat in Washington and adjacent portions of British Columbia and Idaho. They developed GIS-based landscape permeability models for wolves, wolverines (Gulo gulo), lynx (Lynx canadensis), and grizzly bear and a general large carnivore model for the four focal species. Their models evaluated land cover type, road density, human population density, elevation, and slope to provide an estimate of landscape permeability. The authors identified the portions of the Washington state highway system that passes through habitat linkages between the habitat concentration areas and areas accessible to the focal species. Their assessment was intended to provide information for developing conservation strategies, to contribute to future field survey efforts, and to help identify management priorities. The authors caution their analyses were
conducted by using regional-scale spatial data sets that are effective for evaluating broad-scale patterns and should not be expected to provide precise information for specific locations on the ground. Additionally, their analysis provides measures for comparing estimated landscape permeability between different areas; however, the actual functionality of the linkages identified required evaluation through field surveys and additional research.

**Resource-Selection Functions**

Resource-selection functions model the probability of an animal using different resources based on measured characteristics of those resources (Manly et al. 2002). These models can be used to predict relative probability of use across a landscape based on mapped distributions of resources or to evaluate the relative influence of different habitat characteristics. As such, they can be used to assess habitat suitability at broad and fine scales and to predict the proximity of suitable habitat to roads (Clevenger and Ford 2010, Colchero et al. 2011).

Colchero et al. (2011) developed a Bayesian movement model based on resource selection functions and state-space modeling applied to radio-telemetry and global positioning system data to infer the movement behavior of jaguars in the Mayan Forests of Mexico and Guatemala. They evaluated jaguar response to vegetation, roads, and human population density. They used the results of the model to simulate jaguar movements along a road that bisects the major reserve system in their study area. The aim of their simulations was to identify suitable locations for wildlife crossing structures.

Colchero et al. (2011) found that jaguars moved preferentially to undisturbed forests and that females avoided moving close to roads and to areas with even low levels of human occupation. Males also avoid roads, but to a lesser degree, and appeared undisturbed by human population density across the levels in the Calakmul region in the Yucatan Peninsula of Mexico. Simulations reflected these differences: potential crossing sites for females were limited to a strip of a few kilometers, whereas males were able to cross at many different sites. Still, the authors identified a 1 km strip along the road where the likelihood of crossing for both sexes was highest, ideal for the construction of a wildlife pass.

**Circuit Theory**

Circuit theory is a class of ecological connectivity models based on the analogy between the movement of wildlife through a landscape and movement of a charge through an electrical circuit (McRae 2006, McRae et al. 2008). The greater the redundancy in travel routes between nodes (connection points which represent habitat patches, populations, or cells in a raster landscape) enhances flow between them. Cells in a landscape are treated as nodes connected to neighboring cells by resistors. Resistance values are determined in a manner similar to least-cost path analyses resistance (“cost”) surfaces by the landscape resistance values of cells. Paths between patches are created by linking consecutive resistors in series. The total resistance of a route is equivalent to its cost-weighted distance (McRae et al. 2008). Resulting models include
directionality; degree of connectivity between nodes, accounting for the positive effects of path redundancy; and an ability to evaluate contributions of multiple movement pathways. Circuit theory may also help identify suitable paths that are too long to be considered important routes in least-cost path analysis because current is not weighted by distance.

Dickson et al. (2013) evaluated the impacts of landscape change on the quality and connectivity of habitats for pumas across the states of Arizona and New Mexico. They used an expert-based approach to conclude the presence of woodland and forest cover types, rugged terrain, and canyon bottom and ridgeline topography influence the quality, location, and permeability of habitat for pumas. Road density, distance to water, and human population density were negatively correlated with the quality and permeability of habitats. Using these results, the authors identified 67 high quality patches across the study area and applied circuit theory to estimate regional patterns of connectivity among patches. A resulting map of maximum current flow between patches highlighted possible pinch points for connectivity along Interstates 40 and 25 for pumas moving directly between patch pairs. Cumulative current flow was highest in Arizona north of the Colorado River, around Grand Canyon National Park, and in the Sky Islands region owing to the many small habitat patches present.

**Graph Theory**

Graph theory, similar to circuit theory, represents the landscape network as a graph (mathematical structure used to model pairwise relations between a set of objects) composed of nodes (representing patches) functionally connected to some degree by links (representing paths among patches) that join pairs of nodes to assess connectivity (Harary 1969). Graph theory metrics quantify, for example, the total length and configuration of links required to connect all nodes in a graph or the number of links passing through a given node (an indication of the node’s importance to maintaining connectivity of the graph) (Bunn et al. 2000, Urban and Keitt 2001, Minor and Urban 2008). Graph-based metrics measure functional connectivity (the probability of species movement among nodes) by accounting for species-specific habitat preferences and movement behaviors. Links are calculated as a function of effective distance between nodes, defined as the accumulated cost of movement through the least-cost path between nodes, taking into account the movement of preference of the species through different land cover types as given by the resistance map (Adriaensen et al. 2003) and the dispersal distance of the focal species (Bunn et al. 2000). See the FUNCONN GIS tool box, available at [http://wiki.landscapetoolbox.org/doku.php/tools:funconn](http://wiki.landscapetoolbox.org/doku.php/tools:funconn).

Gurrutxaga and Saura (2014) used graph theory to prioritize highway locations where wildlife crossing structures would be most effective at restoring landscape connectivity in the Basque country of northern Spain. The authors demonstrated how habitat network analysis can identify and rank potential crossing structure locations that would most contribute to improving connectivity at a landscape scale, with the aim of prioritizing these locations where barrier mitigation and permeability restoration measures could be most effective. The contribution to
connectivity of each location depended on 1) its topological position in the landscape, 2) the relative decrease in the effective distance among habitat areas that results from the permeability restoration at that location, 3) the distance from the defragmentation location to other alternative wildlife crossing structures already existing in the landscape, 4) the amount of habitat in the areas connected by the linkages that run through the defragmentation location, and 5) the dispersal abilities of the focal species.

Brownian Bridges

Brownian bridges model the continuous trajectory or path of an animal’s movement using animal locations collected at discrete intervals along their trajectory, often via global positioning system (GPS) telemetry (Bullard 1999, Calenge 2006, Horne et al. 2007). A Brownian bridge is a continuous-time stochastic model of movement in which the probability of being in an area is conditioned on starting and ending locations, the elapsed time between locations, and the mobility or speed of movement. Brownian bridge models take into consideration: 1) time lapse between points, 2) distance between successive locations, 3) positional error associated with locations, and 4) animal movement characteristics associated with the Brownian motion variance term (Horne et al. 2007, Sawyer et al. 2009). The term describing the Brownian motion variance contains information on how straight a movement path is as well as variation in speed and distance (Horne et al. 2007, Kranstauber et al. 2012). However, because the Brownian motion variance is calculated using a leave-one-out approach (i.e., if three location points are collected only two are used in the analysis), a minimum of three locations is necessary for estimation.

Horne et al. (2007) extended the use of Brownian bridges for the general purpose of estimating the movement path of individual animals. To demonstrate an application, Horne et al. (2007) used a Brownian bridge model to identify places along Highway 95 in northern Idaho where female black bears frequently cross by estimating the probability of occurrence along the roadway. Their results suggested that certain sections of the highway were substantially more likely to be used for crossing than others and the probability of crossing the highway was negatively correlated with the amount of developed area and positively correlated with distance to water and mean canopy cover.

Combination of analytic tools: Brownian Bridges and Resource-selection functions

Most recently, combinations of the above techniques have found favor with ecologists investigating road ecology. For example, Lewis et al. (2011) and Andreasen et al. (2014) used a two-step process to identify habitat and highway characteristics potentially important to predict where black bears, and moose (Alces alces) and elk, respectively, cross roadways. The authors modeled the movement of animals between successive GPS locations on either side of the road to estimate a probability distribution where the animal crossed the road using Brownian bridge movement models (BBMM; Horne et al. 2007). Then they modeled resource selection of animals at the highway crossing locations identified by the BBMM using resource selection functions
(RSFs; Manly et al. 2002). Using multi-model inference (Burnham and Anderson 2002) to select the best model, Lewis et al. (2011) and Andreasen et al. (2014) then mapped the models to illustrate the relative probability of highway crossings along the entire roadway by study animals. Ultimately these GPS collar data-based approaches and resulting models can inform decisions aimed at reducing wildlife-vehicle collisions, improve driver safety in a given study area, and inform decisions and situations involving target species crossing other highways in similar systems.

No Data

In many cases, transportation and natural resource agencies lack empirical data for planning the location of wildlife crossing structures using GIS or similar modeling tools. Often the planning schedules of road projects may preclude conducting preconstruction studies. A variety of approaches have been used to model wildlife connectivity and select general locations for wildlife crossing structures.

Expert-Based Habitat Model

Simple, predictive, habitat linkage models can be developed using expert knowledge of the wildlife populations, landscape attributes, and synthesizing relevant literature in a relatively short period of time (Store and Kangas 2001, Yamada et al. 2003). The analytical hierarchy process (Saaty 1990) is often used by environmental biologists (Dodson Coulter et al. 2006) among the variety of techniques used to quantitatively analyze expert opinion. Clevenger and Ford (2010) cite the following advantages: “1) it is quick and easy to carry out; 2) legitimacy can be quite high if a consensus model is employed by participants; 3) the method can be statically sound and biologically robust for identifying and prioritizing critical habitat linkages; and 4) GIS software to assist linkage identification is readily accessible.” Drawbacks to the approach include an often narrow taxonomic focus and reliable results require validation with field data.

Clevenger et al. (2002b) evaluated GIS-generated, expert-based models for identifying wildlife habitat linkages and locations for wildlife crossing structures. The authors developed three black bear habitat models to identify linkage areas across the Trans-Canada highway (TCH) transportation corridor between Castle Mountain junction and the provincial border between Alberta and British Columbia. Two expert habitat models were developed using landscape and biophysical variables, one via expert opinion and the other via a review of literature on black bear habitat requirements. The third model was based on empirical habitat data obtained by monitoring the movements of nine radio-collared black bears. Model performance was validated with an independent data set. The authors found the model based on expert literature most closely approximated the empirical model. They conclude that their expert models represent useful tools for planners in locating wildlife crossing structures when empirical data are lacking and schedules preclude a preconstruction study.
Rapid Assessment

A rapid assessment process involves experts on the project area coming to consensus on where key wildlife corridors are located on a given section of highway (Ruediger and Lloyd 2003, Clevenger and Ford 2010). This process differs from an expert-based habitat model because there is no quantitative analysis in a rapid assessment process. The advantages of a rapid assessment are similar to an expert-based habitat model. Unlike expert-based habitat models, however, rapid assessments can have a broad taxonomic focus. Clevenger and Ford (2010) cite two drawbacks to the approach: “1) criteria are rarely used for the selection of potential linkage areas; and 2) a lack of decision rules or weighting makes it difficult to identify and prioritize the most critical linkages in a statistically and biologically meaningful way.” Thus, large sections of a highway may be identified as limiting connectivity when finer-scale linkages are not readily identified. Applications of a rapid assessment process should be validated with empirical field data.

Local Knowledge

Local knowledge often plays a pivotal role in conducting wildlife research, managing habitat, and understanding how wildlife move across a landscape, including where and how wildlife navigate transportation corridors. Conventional, long-term wildlife research and monitoring programs directed by agency or academic biologists can be expensive and time consuming. Local residents can cost-effectively help guide the planning of wildlife crossing structures, thereby providing invested and participatory stakeholders in project planning.

For example, the Miistakis Institute established a citizen science framework for wildlife and transportation issues in the Crowsnest Pass in southwestern Alberta, Canada (Lee et al. 2010). The east-west Crowsnest transportation corridor through the Canadian Rocky Mountains consists of a two-lane highway (Highway 93), a railway line, and five principle settlements. The provincial transportation authority proposed widening Highway 3 to four-lanes due to expected increases in traffic volume. There was concern over high rates of wildlife-vehicle collisions and barrier effects limiting movement opportunities, especially for wide-ranging carnivores such as grizzly bears, pumas, and wolves (Carroll et al. 2001, Proctor et al. 2005, Apps et al. 2007). The Road Watch in the Pass program successfully engaged citizens in data collection, generated a large dataset of wildlife observations, and informed conservation planning processes in the region. The program also addressed challenges of data accuracy, the opportunistic nature of data collection, and sustaining volunteer participation.

Project-Scale Techniques to Select Precise Wildlife Crossing Locations

Following the selection of a general area for a wildlife crossing structure via a method or combination of methods described above, natural resource and transportation agency personnel often use more intensive, fine-scale analyses to determine precise locations for construction (Kautz et al. 1999, Klein 1999, Clevenger et al. 2002). Fine-scale analyses include ground...
truthing course-scale spatial data and site- and, often, species-specific field studies using one or some combination of the following methods.

**Field Data**

*Wildlife-Vehicle Collision and Road-Kill Carcass Data*

Wildlife-vehicle collision and road-kill data are useful in selecting locations for wildlife crossing structures if data collection methodology is consistent and data are spatially accurate (Grist et al. 1999, Hardy et al. 2007). Reporting standards (Knapp et al. 2004), spatial precision (Barnum 2003), accurate representations of actual numbers of collisions (Slater 2002, Sullivan and Messmer 2003, Sielecki 2004), and systematic monitoring are often lacking, reducing the usefulness of these data. Recent advances in personal data assistants and smart phone technology and applications are beginning to address these challenges (e.g., Olson et al. 2014). To be most effective, however, these approaches still require agency adoption and leveraging use by the general public through citizen science programs. Thus, collision and road-kill data have utility in determining the general area for wildlife crossing structures, but research suggests these data may have little in common with where wildlife safely cross roads, requiring further analysis to determine specific crossing and mitigation locations (Clevenger et al. 2002a, Barnum 2003). Given the discrepancy that often exists between collision data and data where animals successfully cross roads, it is important that the process to site/place any road mitigation structure should consider both these types of data.

*Radio and Satellite Telemetry*

Very-high frequency (VHF) and global positioning system (GPS) telemetry enable biologists to intensively monitor wildlife movements that can be used to identify and describe successful road crossing locations (van Manen et al. 2001, Clevenger et al. 2002b, Waller and Servheen 2005).

*Capture-Mark-Recapture*

Live trapping and marking animals allows biologists to monitor individual movements across roads, map population distributions, and estimate population densities. In recent years these methods are being eclipsed by more noninvasive survey methods, such as track surveys, remote cameras, and genetic sampling, described below (MacKenzie 2005, Schwartz et al. 2006, Long et al. 2008).

*Track Surveys*

In areas with consistent snow cover, locations where animals cross roadways can be identified via ground-based transects adjacent and parallel to roads or by driving slowly along the road and searching for tracks (Clevenger et al. 2002a, Barnum 2003). Standard design and data collection protocols for snow tracking efforts are available for a suite of carnivore species (British Columbia Ministry of Environment, Lands 1998, 1999, Bayne et al. 2005). Tracks recorded in
substrates other than snow (e.g., dust, mud) have limited use because of inconsistency in the availability of track-recording substrates across the survey area (Heinemeyer et al. 2008). Track beds, beds of sand, or other tracking media laid out parallel to sections of roadway have been used to detect animals crossing the roadway (Hardy et al. 2007).

Remote Cameras

Remote cameras along roadways have not proven reliable for obtaining information on where animals actually cross roads, a problem associated with their limited range of detection (Huijser et al. 2008). Remote cameras, however, can be deployed in a high-density grid pattern to estimate wildlife distributions and relative abundance within a study area along a road corridor (Long et al. 2008).

Genetic Sampling

Similar to camera traps, noninvasive genetic sampling (i.e., through scat or hair collection) can provide estimates of wildlife distributions, relative abundance, and general locations for potential wildlife crossing structures, as well as minimum estimates of local population size, individual identification, sex, and genetic relatedness (Schwartz et al. 2006). In landscape-scale analyses, these data can demonstrate where connectivity might be reduced or lacking and the associated impacts of roads.

Case Studies: Wildlife Crossings and Large Mammals

In this section of the review we provide a series of case studies of currently constructed wildlife crossings and their use by large mammals summarized largely from Beckmann et al. (2010). Given these structures are largely absent or unstudied throughout the jaguar’s range, we highlight the findings of these case studies on the most appropriate surrogate taxonomic group or species, in most cases carnivores generally or pumas specifically.

Trans-Canada Highway – Banff National Park

The Trans-Canada Highway (TCH) is a major commercial thoroughfare, connecting goods and people between the Canadian Atlantic and Pacific coasts. Since the 1970s, the TCH was recognized as an important source of large ungulate mortality and as a potential barrier for large mammal movement in the Canadian mountain parks and the substantially larger Central Rocky Mountain ecosystem (Flygare 1978, Holroyd 1979, Damas and Smith 1982, Banff-Bow Valley Study 1996, Ford et al. 2010). Segments of the TCH traversing the Bow Valley of Banff National Park were of particular concern and have since become one of the most intensely mitigated and studied stretches of highway in the world (Ford et al. 2010).

The TCH in Banff was reducing wildlife population viability through increasing mortality and disrupting animal movement across the highway. For example, the 1990 elk population in Banff was estimated at 800 individuals and was predicted to fall to fewer than 175 individuals by 2010,
largely due to wildlife-vehicle collisions along the TCH (Woods 1990). Further, genetic connectivity across the TCH in Banff was being mediated by male grizzly bears, but demographic connectivity was being disrupted because female movement across the TCH was limited (Gibeau 2000, Proctor 2003). In 1978, the federal government proposed expanding the width of the TCH in Banff from two to four lanes (McGuire and Morrall 2000). The TCH expansion and wildlife mitigation efforts proceeded in a series of phases, beginning with Phase I in 1979 and continuing through the current Phase IIIB (Ford et al. 2010, McGuire 2012).

Phase I included the first 13 km of the TCH east of Canmore, Alberta. Mitigation focused on altering ungulate movement patterns to minimize the probability of wildlife-vehicle collisions involving elk and moose. Collisions involving carnivore species and small mammals were raised during the planning process but as “lesser concerns” (Federal Environmental Assessment Review Office 1979). A wildlife exclusion fence (2.4 m high page-wire fence) was installed along both sides of the highway to reduce animal access to the highway right-of-way and six exclusive 16.5 m wide by 4 m high wildlife underpasses were installed to allow animals to cross beneath the road (Ford et al. 2010, McGuire 2012). Phase II ran between kilometers 13 (the end of Phase I) to 27 of the TCH east of Canmore. Planning and mitigation measures mirrored those of Phase I. Unburied fencing and four additional wildlife underpasses were constructed following the design of the Phase I crossing structures.

The cost of these environmental mitigations amounted to approximately 13% of total construction costs. The success of these mitigations was immediately evident, with the number of ungulate mortalities as a result of wildlife-vehicle collisions reduced by 95%. A one-year monitoring effort indicated that the crossing structures were being used by elk and other ungulates; however, no further monitoring took place (McGuire 2012).

Phase IIIA included kilometers 27 (the end of Phase II) to 48 of the TCH east of Canmore and was the start of a new era in highway mitigation. The successfulness of crossing structures in earlier phases and lack of post-construction monitoring were questioned and challenged (McGuire 2012). Public concern centered on the lack of evidence that the previously constructed 16.5 m crossing structures and fencing actually provided for carnivore movement across the THC (McGuire 2012). Thus, the environmental assessment for Phase IIIA was conducted independent of Parks Canada (Parks Canada 1995, Ford et al. 2010). The assessment concluded that impacts could be mitigated through fencing and underpass structures and that large carnivore conservation should be a priority in implementing mitigation measures (Parks Canada 1995, Ford et al. 2010, McGuire 2012).

Initially two 30 m wide underpasses and seven smaller crossings, one installed every two km (similar to those installed on Phase I and II), were planned for Phase IIIA. Recognition, however, of the need to provide movement across the TCH for large carnivores, including grizzly bears, wolves, and pumas, resulted in the construction of two 50 m wide overpasses and ten wildlife underpasses. Additionally, the fencing in Phase IIIA was buried with a 1 m deep section of
chain-link fence material, referred to as a buried apron, to deter carnivores from digging under the unburied fence seen on Phase I and II (Bunyan 1990).

The cost of these mitigations amounted to approximately 25% of total construction costs. Parks Canada embarked on a 12-year monitoring program to evaluate reductions in wildlife-vehicle collisions and gauge the use of crossing structures by various species and genders. Fencing reduced wildlife-vehicle collisions by over 90% for ungulates and 86% for all large mammals (Woods 1990, Clevenger et al. 2002a). Fence intrusions were 83% lower on highway fence sections with buried fence aprons compared to those with unburied fence sections (Clevenger et al. 2002a). Clevenger et al. (2009) recorded over 190,000 crossing events by 11 species of large mammals, including moose, bighorn sheep, deer, lynx, puma, coyotes, wolves, grizzly and black bears, and wolverines since 1996. Clevenger and Waltho (2000) found that human activity at or adjacent to the crossing structures was the most important factor negatively affecting wildlife, particularly carnivore, use. Clevenger and Waltho (2005) furthered their analysis by selecting crossing structures remote from areas of human activity, and compared use of crossing structures by species with crossing structure variables encompassing structural, landscape, and human activity. Distance to cover was the most important crossing structure landscape attribute for pumas (negative correlation). Pumas also favored more constricted crossing structures (i.e., long in length, low, narrow, and low openness ratios). The 12-year monitoring program also suggested that time was required for animals to adapt to the new structures, with ungulates using structures sooner than carnivores (Ford et al. 2010, McGuire 2012).

Evaluations of the effectiveness of crossing structures have recently been extended beyond the documentation of crossing structure use and reductions in wildlife-vehicle collisions to include demographic (Sawaya et al. 2013) and genetic connectivity (Sawaya et al. 2014). Sawaya et al. (2013) used multiple noninvasive methods to collect grizzly and black bear hair samples around the Bow Valley. Fifteen grizzly (seven female and eight male) and 17 black bears (eight female and nine male) used wildlife crossing structures. Grizzly bears used open crossing structures (e.g., overpasses) more often than the constricted crossings (e.g., culverts) used more often by black bears. Peak use of crossing structures for both species occurred in July, when high rates of foraging activity coincide with mating season. They compared the number of bears that used crossing structures with estimates of population abundance from a related study and determined substantial percentages of grizzly and black bear populations used crossing structures, concluding that wildlife crossing structures provide demographic connectivity for bear populations in Banff National Park. Sawaya et al. (2014) extended their analyses to evaluate how the TCH and associated crossing structures affect gene flow in grizzly and black bears. Parentage tests showed that 47% of black bears and 27% of grizzly bears that used crossing structures successfully bred, including multiple males and females of both species. In documenting gene flow by showing migration, reproduction, and genetic admixture, they concluded that wildlife crossings allow sufficient gene flow to prevent genetic isolation.
The final phase of the TCH expansion and mitigations, Phase IIIB, ran through the remainder of Banff National Park for a distance of 35 km. The locations of wildlife crossing structures were based on modeling empirical movement data, simulating movements of five large mammal species (wolves, grizzly and black bears, elk, and moose) and validated by independent data in the study area (Clevenger and Wierzchowski 2006, Clevenger and Ford 2010, Ford et al. 2010). Crossing structure locations were prioritized based on key habitat linkages identified (Clevenger et al. 2002b). The conclusions of Clevenger and Waltho (2000, 2005) were used to direct design specifications of the crossing structures to facilitate passage of large mammals. Parks Canada proposed fencing similar to Phase IIIA; increasing the frequency of crossing opportunities to one every 1.5 km; increasing width of overpass structures from 50 to 60 m; extending bridge structures past riparian zones to avoid fishery impacts and permit wildlife movement; and installing 0.4 m to 0.75 m diameter culverts every 400 m to accommodate small mammal and amphibian movements across the highway (McGuire 2012). Monitoring of wildlife use of Phase IIIB crossing structures is currently underway (Clevenger et al. 2013). Among carnivores, grizzly bears used the structures 62 times, wolves 50 times, black bears 34 times, coyotes 30 times, and pumas have not been recorded as of May 2013 (Clevenger et al. 2013). The cost of these mitigations amounted to approximately 36% of the total project construction costs of Canadian $315 million (McGuire 2012).

Interstate 75 and State Route 29 – Alligator Alley

The Everglades Parkway, also called State Road 84 and more commonly Alligator Alley, was completed in 1967 and was the first major highway to cross south Florida (Jansen et al. 2010). Concern over increasing human population growth and the already apparent negative hydrologic effects of Alligator Alley prompted the proposed construction of I-75 in 1968. Sixty-four km of the proposed 122 km I-75 paralleled the two-lane Alligator Alley. The Alley had come to be known as “Slaughter Alley,” as wildlife-vehicle collisions were common. The passage of wildlife, however, was not taken into consideration for another 10 years as I-75 project planning continued. The Florida panther (Puma concolor coryi), emerged as a concern in I-75 planning after the confirmation of panthers in Glades County and the Fakahatchee Strand Preserve State Park in 1972, dispelling the generally held belief they were extinct in the wild (Nowak 1973). The rediscovery and subsequent research lead the Florida Game and Fresh Water Fish Commission (now the Florida Fish and Wildlife Conservation Commission, FFWCC) to state in a 1982 letter to the Governor’s Office of Planning and Budgeting, “Because of the very small number of Florida panthers believed to be remaining, the loss of a single animal should be considered significant, and any redesign of roads in known panther habitat should fully accommodate this concern.” Thus, the I-75 project became one of the first implementations of wildlife crossings in roadway design in the U.S. (Jansen et al. 2010).

Improvements for terrestrial wildlife in the form of underpasses with associated crossings and continuous fencing were built along a 64 km stretch of Alligator Alley. Underpass sites were selected based on known panther and bear travel routes and the presence of vegetative features
that provided cover (Logan and Evink 1985). Thirty-five underpasses were installed, 23 designed for wildlife use only and 12 for both water and wildlife passage. The underpass design consisted of two 13.1 m long open-span bridges accommodating two lanes of traffic in each direction separated by a 22.3 m wide median that was open overhead. The “wildlife-only” underpasses averaged 22 m wide, whereas those with water averaged 40 m wide with a wildlife pathway averaging 9 m on one side. Each structure was $175,000 for a two-lane span (Lotz et al. 1996). All underpasses averaged 73 m in length from fencing to fencing, of which 51 m was the distance between the two spans and the open median. The height of the “wildlife-only” underpasses averaged 2.3 m, whereas the water and wildlife passages averaged 1.6 m high. The average distance between the underpasses was 1.67 km (range 0.43 to 5.13 km).

Two sections of 3.7 m high fencing topped by four to six strands of barbed wire were installed in the median to prevent wildlife access to the roadway. A continuous 3.4 m high galvanized-steel chain-link fence topped with a 1 m outrigger with three strands of barbed wire was planned for both sides of the 64 km I-75 project to keep wildlife off the roadway and funnel them to crossings. An interchange at State Route 29 was considered as part of the I-75 project in 1972, but was removed over concern that increased traffic volume on SR 29 would intensify panther mortality. Construction on the I-75 project began in 1986 and was phased in ten segments, emphasizing areas where panthers had been killed. The project was completed in 1993.

Concern for panthers along the two-lane SR 29 persisted where the controversial interchange to I-75 was built. Agency and environmental organizations agreed to the interchange, provided wildlife underpasses were constructed if panther deaths increased with subsequent traffic volume. In 1991, the FFWCC and the U.S. Fish and Wildlife Service recommended that six underpasses be built at locations on SR 29 where the highest mortality was occurring. Although the initial underpass design was to be similar to underpasses on I-75, SR 29 underpasses were of varying widths to evaluate wildlife usage. All six underpasses were 2.4 m high and 14.6 m long. The first two underpasses installed in 1995 were prefabricated box culverts and were 7.3 wide. Each structure cost $110,000 (Lotz et al. 1996). The next four underpasses were open-span bridges. The two completed in 1997 and 1998 were 22 and 35 m wide and cost $200,000 per structure. The two completed in 2007 were 15 m wide with a total project cost of $3.8 million for each (Jansen et al. 2010). Jansen et al. (2010) note that the cost of construction and materials more than doubled between 1995 and 2007. For instance, the cost of fencing increased from $12 to $26 per linear foot.

Continuous fencing was not installed on SR 29 because of the distance between underpasses, private property concerns, and agency concern over public access (Jansen et al. 2010). The first two underpasses were 3 km apart with 5.2 km of fencing on each side. The average length of fencing on the other four underpasses was just over 0.5 km north and south of each crossing. Fencing between the last two underpasses was only installed on one side of the road for a length of 2.3 km.
Prior to completion of the I-75 project, five panthers were killed by vehicles on Alligator Alley (Jansen et al. 2010). Since completion, two have been killed within the 64 km project area, one on an unfenced arterial on-ramp and another near a human-made breach in the fencing. Comparatively, six panthers have been killed in the unfenced 14 km of I-75 west of the project area and one was killed at the eastern end of the project fencing (Jansen et al. 2010).

Foster and Humphrey (1995) monitored radio-collared bobcat use, as surrogates for the less common panther, of four I-75 underpasses for an average of 10 months (range 2 to 16 months) during the construction phase from 1989 to 1991. They found that female bobcats rarely crossed roads, whereas males crossed frequently and were more susceptible to interstate-related mortality. Additionally, remote cameras recorded ten crossings by two male panthers. They concluded that the underpasses would compensate for the obstruction of the fenced interstate by providing panthers a safe means of travel across the interstate corridor. They recommended interstate fencing be inspected frequently and promptly repaired and the development of a contingency plan to rescue any panther caught on the interstate.

Lotz et al. (1996) found panther use of the I-75 underpasses increased since Foster and Humphrey (1995) and predicted that more panther use will likely occur as individuals learn the underpass locations. Jansen et al. (2010) examined home range data from 91 panthers (61 males and 30 females) whose home ranges fell within 1.6 km of I-75. Only five (17%) of the females had crossed I-75 and had done so an average of two times (range 1 to 3). In contrast, 32 (52%) of the males crossed the interstate. Four dispersing males crossed only once and the remaining 28 males crossed an average of 55 times (range 2 to 243).

The I-75 project has been deemed successful in preventing panther deaths along the 64 km project area. The interstate however, is considered a filter barrier, especially to female panthers, based on the findings of Jansen et al. (2010) that 48% of the male and 83% of female radio-collared panthers monitored with 1.6 km of I-75 have not crossed the interstate. Interestingly, some females that did not cross the four-lane interstate did cross a two-lane highway (SR 29) that runs perpendicular to the interstate. Jansen et al. (2010) suggest possible factors causing the reluctance to cross include the 51 m crossing distance, the increased traffic volume and associated noise levels, the periodic water inundation of underpasses, the lack of visibility due to dense vegetation, and the presence of human activity.

Panther mortality continues on SR 29 where fencing and underpasses do not exist. The lack of continuous fencing was attributed to the death of two panthers trapped and killed on the highway between the fencing. Although the smaller and more cost efficient underpass designs built on SR 29 are used by panthers, Jansen et al. (2010) conclude that the six underpasses and 12 km of fencing in 38 km of SR 29 do not provide the same level of protection to panthers as found in the I-75 project.
U.S. Highway 93 – Flathead Reservation, Montana

The Montana Department of Transportation and the Federal Highway Administration proposed reconstruction of a 97 km portion of U.S. Highway 93 in the early 1990s (Federal Highway Administration and Montana Department of Transportation 1995, Becker 1996, Becker and Basting 2010). High rates of population growth and increased tourism throughout western Montana intensified concern over various geometric highway engineering features that did not meet standards for safety and design. U.S. 93 is a major north-south transportation route in western Montana that traverses the Flathead Indian Reservation between the communities of Evaro and Polson. The Flathead Indian Reservation is home to the Confederated Salish and Kootenai Tribes (CSKT). The proposed reconstruction resulted in consideration of a wide variety of issues and concerns important to Tribal people and their culture, including wildlife and wildlife habitat. Growing traffic volumes on U.S. 93 raised concerns over the fragmentation of wildlife habitat and the loss of population linkage on the reservation for grizzly bears, black bears, deer, elk, gray wolves, Canada lynx, and other species (Becker 1996, Ruediger et al. 1999).

The selection of crossing structure locations was informed by observations of vehicle-caused wildlife mortality and wildlife crossing areas; habitat analyses identifying vegetative and concealment cover indicating where animals might be expected to cross the highway; and survey data of wildlife trails near the highway provided by remote cameras (Becker and Basting 2010).

Reconstruction plans included provisions for 42 metal pipe culverts or concrete box culverts designed to facilitate wildlife crossing the highway (Hardy et al. 2007, Becker and Basting 2010). Two small box culverts, 1.3 m high by 2 m wide, replaced standard corrugated steel culverts for drainage purposes to allow for more room for rodent and amphibian movement. Twenty-one large-arch culverts, ranging in sizes from 3.7 m high by 6.5 m wide to 5.0 m high to 7.4 m wide, made of corrugated steel or concrete were installed for passage of deer, elk, and bears. Seven open-span bridges, ranging from 12 m to 110 m in length and with a minimum 3.7 m of vertical clearance to facilitate wildlife passage (e.g., deer, elk, moose, and bear) and re-vegetation were constructed across larger rivers and streams that bisected the highway.

A single wildlife overpass, a 46 m wide bridge of landscaped wildlife habitat, was placed in the Evaro area for the following reasons: 1) the Evaro Hill area was modeled as an important habitat to link the Northern Continental Divide Grizzly Bear Recovery Area with the Selway-Bitterroot Grizzly Bear Recovery Area (Mietz 1994); 2) this was one of the few areas of the project that had forested habitat on both sides of the road and was likely to provide cover for many species of wildlife moving through the area, including “more elusive” species, such as grizzly bears, wolves, lynx, wolverines, and fishers (Pekania pennanti), that might move from one mountain range to another; and 3) the CSKT owned much of the land in the area where the over-crossing was built and the tribes committed to not developing or selling this land but to conserving the
land as a wildlife corridor (Hardy et al. 2007). Bridge design was patterned after one at Banff National Park.

In conjunction with the wildlife crossing structures, 26.7 km of 2.4 m-high page-wire, wildlife exclusion fencing was installed in the project area (Becker and Basting 2010). The final design included five sections of greater than 0.8 km of fencing designed to direct wildlife to most of the crossing structures (Hardy et al. 2007). Continuous fencing throughout the entire project area was not planned due to excessive costs, numerous access points to the highway, and the fact that most collisions with larger wildlife species generally occurred at select locations. This design characteristic differs from the Banff Trans-Canada Highway fencing, which has continuous fencing with passages along the controlled-access highway. In areas where fences spanned distances of more than 1 km, 2.6 m vertical jump-out structures were installed to allow for the escape of animals caught inside the fencing along the highway right-of-way. In some locations with no wildlife fencing, these gaps were mitigated with wildlife guards, similar to cattle guards, or metal gates (Hardy et al. 2007).

In addition to the five extended sections of fencing connecting 21 crossing structures, approximately 100 m long wing fences, extending at approximately 45 degree angles from the openings of ten additional, independent crossing structures to funnel animals to these structures were installed (Hardy et al. 2007). Wildlife fencing was not installed at five crossings, such as at bridges, culverts for aquatic passage alone, or where natural features of the landscape, such as drainages, were expected to lead animals to the crossings. A buried apron was added to fencing sections in areas where burrowing or digging animals were a concern.

A six-year, post-construction wildlife-vehicle collision and wildlife crossing monitoring and research project is currently underway with an expected completion date of 2015 (Huijser et al. 2009a). The monitoring and research project is centered on three main subjects: 1) improvement in human safety through a reduction in wildlife-vehicle collisions; 2) maintaining habitat connectivity for wildlife (especially for deer (white-tailed deer [Odocoileus virginianus] and mule deer [O. hemionus] combined) and black bear through the use of the wildlife crossing structures; and 3) a cost-benefit analyses for the mitigation measures.

U.S. Highway 64 – Eastern North Carolina

U.S. Highway 64 (U.S. 64) is an important route in eastern North Carolina. In 1992, the North Carolina Department of Transportation (NCDOT) began planning for improvements to 45 km stretch of U.S. 64 between the towns of Plymouth and Columbia to accommodate expected increased traffic volumes from tourism and economic development promotions (Jones et al. 2010). Improvements included expanding the two-land, rural road to four travel lanes and installing a 14 m grass median, cable guardrails, and right-of-way fencing. New roadway footprints were proposed to improve driver safety and increase speed limits from 55 miles per hour and lower speeds in developed areas to 70 miles per hour.
NCDOT and North Carolina Wildlife Resources Commission (NCWRC) staff applied lessons learned from wildlife crossing structures installed for black bears along a new section of Interstate Highway 26 (I-26) in the southern Appalachian Mountains beginning in 1991. NCDOT settled on structures that could be accommodated within the existing I-26 roadway design because crossing structure planning began after construction was initiated. The two structures were 2.4 by 2.4 m concrete box culverts that were 47.3 and 42.7 m in length. NCWRC staff suspected these underpasses were too small and did not have an adequate openness ratio (0.12 and 0.13) for most large mammals. These openness ratios were notably smaller than the 1.5 ratio recommended by Iuell et al. (2003). Jones (2008) concluded human use of the passageways, high traffic levels of I-26, small structural design, and lack of appropriate fencing negatively influenced wildlife use.

The U.S. 64 project area was topographically flat (elevation range 4.6 to 15.2 m above sea level); contained a mixed land use of agriculture, silviculture, and small residential areas; and included habitat supporting populations of American black bears, white-tailed deer, red wolves (*Canis rufus*), and bobcats. The viability of black bear and federally-endangered red wolf populations, and the hazard posed by white-tailed deer to driver safety were important causes for concern within the project area.

NCDOT agreed to build three fenced wildlife underpasses along a 24.1 km section of U.S. 64 that diverted from the original highway. The underpass and fencing designs were patterned after structures built on I-75 in south Florida (Evink 1997, Jansen et al. 2010) because of similar taxa, geography, and habitats between the two areas. Two underpasses were 29.1 m wide by 3.0 to 3.2 m high and extended the length (12.2 m) of both east-bound and west-bound traffic, and one underpass was an open-to-sky 10.7 m grass median, making the total length of all three 35.1 m. Three meter high chain-link fencing extended at least 800 m in both directions from each underpass structure to guide wildlife to the underpasses. Scheick and Jones (1999), constrained by construction deadlines, conducted a ten-month study using track surveys, ditch crossing surveys, remotely-triggered camera surveys, and land cover maps to determine optimal location for the wildlife underpasses. The focal species was black bears; however, white-tailed deer, red wolves, coyotes, and several medium-sized mammals were considered. Subsequent research using radio-telemetry locations from 35 black bears confirmed the underpasses were located in areas important for habitat connectivity (Kindall and van Manen 2007).

Post-construction monitoring (July 2006-July 2007) of underpass use by wildlife using remotely-triggered camera and track-count surveys identified at least 20 different species (McCollister 2008). Nicholson (2009) concluded the documented use of the underpasses by ten bears suggested sufficient demographic and genetic exchange, thus reducing the barrier effects of the highway. Wildlife mortality surveys post-construction revealed no difference in the frequency of mortalities between the three sections of highway with the underpasses and fencing and four adjacent unfenced sections (McCollister 2008). Many of the recorded mortalities were of animals that could pass under or through the fence, which likely influenced this result. Additionally,
collection of these data less than one year post-construction may not have allowed sufficient time for individuals of some species to learn to use the underpasses (Foster and Humphrey 1995, Lotz et al. 1996, McCollister 2008).

Considering focal species individually, collision frequencies involving white-tailed deer were lower within compared to outside the project area. However, radio-collared bears that crossed the highway did not regularly use the underpasses, possibly increasing their risk of collision with vehicles. At least eight bears were killed on the highway between May 2007 and November 2008. Seven of these collisions occurred within unfenced sections of the highway and three were near the edge of the fencing associated with the wildlife underpasses. Jones et al. (2010) concluded the underpasses were not necessarily ineffective in preventing bear-vehicle collisions, rather bears were more likely than deer to climb over or crawl under fencing and additional mitigation measures may be needed to reduce bear-vehicle collisions.

Based on their experience on the U.S. 64 project, Jones et al. (2010) suggest a minimum design criteria of 3 m vertical clearance and a 36.6 m opening for large mammal underpasses. Following the findings of Clevenger and Waltho (Clevenger and Waltho 2000) and the impacts of human activity impacting underpass use by wildlife, NCWRC staff purchased 2 ha easements to protect each underpass entrance from human disturbance and development. Wildlife-vehicle collision data in the project area suggested fencing may be more effective if it were continuous throughout the project area, barbed-wire outriggers were added to the top of fencing to deter animals from climbing over fencing (Clevenger et al. 2001), and buried aprons were added to deter animals from crawling under fencing (Jones et al. 2010).

**Summary**

Roads affect wildlife populations and their ability to persist at local and landscape scales. Roads and associated traffic impose direct and indirect impacts to wildlife, including habitat loss and fragmentation, disruption of demographic and genetic connectivity, and road-related mortality. Large mammalian carnivores are particularly vulnerable to these impacts, owing to their large area requirements, low densities, and slow population growth rates. Wildlife crossing structures and associated exclusion fencing, although relatively novel to the North American transportation infrastructure, are maintaining and improving habitat, demographic, and genetic connectivity, and reducing road-related mortality. Integrating crossing structures and exclusion fencing into transportation systems through collaborative, interdisciplinary planning, design, placement, construction, and monitoring may prove to be a key element in maintaining and improving connectivity for movement of jaguars, thereby increasing the long-term survival of subpopulations.

Genetic variation among jaguar subpopulations has shown little evidence of significant geographical partitions and barriers to gene flow range-wide. Given this, and the demographic benefits of connectivity, maintaining connectivity between jaguar breeding areas is a vital
component in conservation planning for the species. Several models of jaguar corridors among subpopulations throughout their distribution have been developed. Considering existing and proposed improvements of transportation infrastructure throughout the northern distribution of the jaguar and the impacts roadways pose to the persistence and recovery of large carnivores, incorporating wildlife crossing structures throughout the Northwestern Recovery Unit will likely have lasting conservation benefit.

Natural resource and transportation agency personnel experienced with wildlife crossing structures have used systems-level assessments of wildlife habitat linkages and movement corridors to identify and prioritize segments of transportation networks with high levels of wildlife-road conflict over a large area. Specific placements of wildlife crossings are determined at the project level or after a thorough field survey as part of a larger system-level assessment. Species-specific preferences are key considerations in planning, locating, designing, and building wildlife crossing structures and exclusion fencing. Jaguar use of wildlife crossing structures remains unknown, given these structures are largely absent or unstudied throughout the jaguar’s range. Large carnivores exhibit species-specific tendencies in their use of overpasses and underpasses. Pumas and other large carnivores tend to use a variety of crossing structures, provided they are well fenced to guide animals to the crossing structures and prevent animals from climbing over or digging under the fencing; have suitable levels of concealment cover; are suitable distances away from development, human activity, and artificial light sources; are built at-grade level; and provide an unobstructed view of the habitat on the far side of the structure. Monitoring wildlife movements pre- and post-construction is a key element in selecting optimal crossing structure locations and evaluating their success.

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Figure 1. The 226,826 km² Northwestern Jaguar Recovery Unit (NRU) straddles the United States-Mexico border with approximately 29,021 km² in the United States and 197,805 km² in Mexico (Sanderson and Fisher 2013).