Trans-Canada Highway Wildlife Monitoring and Research

Final Report 2014

Part B: Research

Conservation Science for the Management of Transportation Systems and Fragmentation-sensitive species in the Canadian Rocky Mountain Parks

Prepared by the Western Transportation Institute at Montana State University and the Miistakis Institute

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A Report of the Wildlife and Transportation Research in the Rocky Mountains *Project*

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EXECUTIVE SUMMARY

I. Research Background

The Trans-Canada Highway (TCH) is a major transportation corridor traversing Banff National Park with an estimated annual average daily traffic volume of over 17,000 vehicles per day. In the 1970s, the TCH was upgraded from two to four lanes, beginning from the park east boundary and working west. The first 27 km of highway twinning (Phases 1 and 2) included 10 wildlife underpasses and was completed in 1988 (see Figure 1, page 24). Highway upgrades on the next 20 km section (Phase 3A) were completed in late 1997 with 11 additional wildlife underpasses and two 50-m wide wildlife overpasses. The final 35 km of four-lane highway to the western park boundary (Phase 3B) includes 21 crossing structures, including four, 60-m wide wildlife overpasses and was completed in late 2013. The Phase 3B twinning and installation of mitigation measures progressed over a 5-year period (2008-2013).

Seventeen years is longer than most research projects are conducted. The value of long-term research and monitoring is indisputable among scientists and natural resource managers. Our research evolved from the initial basic questions of:

- Whether fencing and wildlife crossing mitigation reduce road-related mortality of wildlife?
- If wildlife use the crossing structures? And if so, what species and how often?
- Are there differences in species use?
- Last, can these data be used to plan and design crossing structures for future mitigation projects on the TCH in Banff (Phase 3B)?

We answered all of these questions in a 2002 final report to the Banff Field Unit of Parks Canada. We then asked: what more can we learn? And what additional information will be gained by continuing monitoring and research?

By 2002, monitoring data confirmed that the Banff crossing structures were regularly used by all large mammal species. However, there was uncertainty whether the crossings provided for demographic and genetic connectivity i.e., males and females were able to cross and their young able to disperse. These fundamental questions were addressed in our research from 2005-2009, which was funded by our first public-private-academic partnership. A second report was prepared for this phase of research in 2009.

As the previous partnership concluded, the last phase of the twinning project (Phase 3B) began on the TCH in Banff National Park. This phase was the first major transportation corridor project in North America to provide crossings for wildlife across the Continental Divide. Different from previously mitigated sections, the focus was on rare, higher elevation, fragmentation-sensitive species: wolverines and lynx. This phase of the research project was branded "Highway Wilding" and partners included Parks Canada Agency, Western Transportation Institute - Montana State University (WTI), Miistakis Institute, Woodcock Foundation, and Wilburforce Foundation.

II. This Report

Our final report consists of published and submitted journal articles, technical reports, and simple data summaries. This document constitutes the final reporting requirement for the 5-year project. As in previous final reports, we address key management objectives of Parks Canada Agency and have analyzed data from the final research segment (2009-2014) and for some analyses and reporting, included data for the entire length of the research project (1996-2014). This Executive Summary is not comprehensive, but summarizes what we consider to be the key sections of the final report.

III. Effectiveness of Phase 3A and 3B Mitigation to Reduce Wildlife Vehicle Collisions

Previously we evaluated the mitigation measures aimed at reducing mortalities on TCH Phases 1 and 2; however, Phase 3A was not included. The final 35 km of four-lane highway to the western park boundary (Phase 3B) was completed in late 2013. We analyzed Phase 3B as sub-phases (3B-1, 3B-2) due to different completion dates. Phase 3B-3 was only completed in November 2013 and is not included in our analyses. Findings include:

- We found a substantial decline in the number of wildlife-vehicle collisions (WVCs) after each mitigation phase was completed despite annual increases in traffic volumes (see Figure 2, page 35). Although fencing effectively reduced road-related mortality of wildlife on Phases 3A and 3B, higher levels of WVCs were found to be associated with fence ends.
- Highway mitigation significantly reduced WVC rates on all phases combined (Phases 1, 2, 3A, 3B). WVC rates decreased on average by 80% (range 66-87%) for the combined mitigated sections over a 24-year period. Rates of ungulate mortality were reduced by 88%; however, carnivore mortality decreased only 18% when coyotes were excluded.
- When comparing WVCs two years pre-mitigation with two years post-mitigation there were significant reductions in WVC rates on Phase 3A and 3B, from 33 to 5 (85% reduction) and 12 to 5 (58% reduction), respectively.
- A total of 73 fence intrusions, where animals breached the fence to gain access to the TCH, were recorded from 1998-2013. More than half of these intrusions were

carnivores, and coyotes were responsible for two-thirds of all carnivore intrusions. Ungulates accounted for slightly more than one-third of fence intrusions.

- Monitoring of access preventive measures (Texas gates and electro-mats) showed they performed poorly.
- Monitoring of access roads to determine the number and types of wildlife gaining access to the TCH can be improved by using "animal recognition software", digital signature technology, microwave detection systems and more sophisticated camera technology.

IV. Summary Data: Wildlife Crossing Structure Use by Phase, 1996-2014

Monitoring of the Banff wildlife crossing structures began in November 1996 and continued year-round until April 2014. Our 17-year data set represents the world's longest and most consistent effort to monitor wildlife use of highway crossing structures.

- A total of 152,154 crossing detections of 11 species of large mammals were recorded at the Phase 1, 2, 3A and 3B crossings structures during the 17 years of monitoring (Table 1). Deer made up 48% of all animal crossings, while elk comprised 35% of the detected crossings. Large carnivores made up 13.5% of the detections in the following descending order: coyotes, wolves, black bears, cougars and grizzly bears.

Table 1. Summary of wildlife crossing use, 1996-2014.

Species	No. Crossings
Bear spp.	71
Black bear	1663
Grizzly bear	1549
Cougar	1627
Lynx	18
Coyote	8749
Wolf	6826
Wolverine	10
Deer	72,857
Elk	53,251
Moose	534
Bighorn sheep	4999
Grand total	**152,154**

- Nearly two-thirds of all wildlife crossings (n=107,664 detections of 11 species) occurred on Phases 1 and 2. This is largely due to the longer monitoring time period and more abundant wildlife populations year-round in the lower portion of the Bow Valley.
- Completed in late 1997, Phase 3A had nearly one-third of all the detected crossings, a total of 39,582 passages by wildlife.

- Phase 3B monitoring began in 2007, but most crossings were not completed until 2011. A total of 4908 passages by wildlife were documented on this new and final phase. Grizzly bears used the Phase 3B crossings comparatively more than on other phases and appeared to have adapted to them sooner than the Phase 3A crossings.
- Monitoring has provided crucial information on the presence of rare-occurring species (Figure 3) and their reproduction (timing, litter size, offspring survival). It has assisted resource managers, conservation officers and human-wildlife conflict specialists by providing locations and movement of specific targeted individuals.
- We recommend monitoring continue at all crossing structures. Monitoring a subset of wildlife crossings for all structures is not recommended.

Figure 3. Lynx detected crossing Redearth Overpass, March 2012.

V. Analysis of Long-term Data to Identify Spatial and Temporal Effects on Large Mammal Movement Through Wildlife Crossing Structures

Little is known regarding effective monitoring durations to identify species' response to wildlife crossing structures. This is particularly important in light of the need for rigorous evaluations in a time of agency budget reductions. The long-term data set was used to: 1) identify whether explanatory variables influencing passage were consistent between models through time. Species models were fitted to the first two years of data, the first four years, the first eight years, and the entire 16 years of data and 2) test the generality of our Phase 3A models and apply them to separate but adjacent mitigated sections of the TCH (Phases 1 and 2, and Phase 3B).

- A total of 859,880 track pad- and camera-days (Figure 4) were logged monitoring Phase 3A year-round since November 1997. We modeled the response of 7 of 8 species using the full 16-year dataset, while for one species we used a 15-year dataset.

Figure 4. Cougar family crossing through Morrison Coulee underpass, May, 2011.

- Over long time periods there was marked variation in key drivers of models explaining species' response to crossing structures. The importance of covariates changed considerably over time for some species (cougar, coyote, grizzly bear, elk), while for others there were only slight changes (deer, wolf).
- *Deer* reacted positively to the openness of crossing structures and the effect increased over time. *Elk* preferred crossing structures with high openness values, i.e., overpasses and large open-span underpasses; however, this preference diminished slightly over time. Previous research suggests a strong tendency for *moose* to nearly exclusively use overpasses. Moose had high fidelity to few crossing structures and the proximity to favored habitat may influence selection.
- Season, year, and crossing structure type were the most important covariates determining *grizzly bear* crossing numbers. Overpasses were preferred in the 7-year and 15-year models. Over time underpasses were more widely used by grizzly bears. Model results also suggested that grizzly bears became less selective in crossing structure use over time. *Black bears* preferred long crossing structures over time. They preferred narrow underpasses to more open underpasses. Black bears utilized more crossing structures as time progressed. *Wolves* consistently used large structures and maintained a preference for certain crossing structure types, i.e., large underpasses. *Cougar* crossings were best explained by time, season, structure type, and the percentage of shrub and grass cover around the structure. Underpasses were used most

in the 4-year and 8-year models, but then reversed in the 16-year model with greater use of overpass structures. *Coyotes* utilized a wide variety of crossing structure types and even some of the larger drainage culverts.

- Some species became more specific to crossing structure types over time (deer, wolf), while others were less selective (elk, black bear, coyote). Grizzly bears, cougars, elk and moose initially used specific crossing structure types, but over time used a greater variety of crossing types and sizes.
- Increasing the number and type of structures used by a species over time suggests individuals may learn that certain crossing structures are safe passages and adapt to them. Cougars, and to some extent black bears, were an anomaly showing no apparent preference for the type of crossing or its location, over time.
- Our results suggest that monitoring based on short time periods will not adequately explain long-term responses of species to crossing structures. In view of these results we recommend monitoring be conducted over longer time periods than the usual 1-3 years as in most highway mitigation studies. Monitoring periods that incorporate adaptation periods for ungulate species should be at least 5 years, while for carnivores a minimum of 7-8 years is recommended.
- We tested the generality of our findings from Phase 3A models on other mitigated sections with four key management species -elk, deer, wolf, and grizzly bear. Some Phase 3A models performed relatively well, while others did not predict well and confidence intervals were extremely large. It is premature to suggest that monitoring a subset of the crossing structures provides robust results that align with previously intensively monitored crossings.
- We recommend continued testing of the predictive ability of crossing structure models using independent data from other species and highway mitigation areas, i.e., grizzly bear use of crossings from other highway projects). This meta-data approach will provide a better understanding of the predictive ability of crossing structure models.
- Only 10 wolverine and 18 lynx crossings were detected after 17 years of monitoring on previous phases (Figure 5). Continued monitoring of Phase 3B crossings will be important given the presence of wolverine and lynx, and current lack of information for these species.

Figure 5. Wolverine crossing at Johnston underpass.

- We recommend Phase 3B monitoring be conducted for a minimum of 10 years. Monitoring should be conducted in conjunction with winter roadside surveys to investigate highway crossings by wolverine and lynx not detected at crossing structures, breaches in fence, and behavior from snow tracking in the highway corridor.

VI. What is More Important for Grizzly Bears - Location or Type of Crossing Structure?

Background

For the past five years, grizzly bears most frequently used the Healy underpass; however, modeling shows grizzly bears prefer overpasses. We examined grizzly bear crossing data between 1996-2013, to help better understand grizzly bear use of Healy underpass and other crossing structure types. We focused particularly on how crossing data are quantified and how grizzly bears respond to newly constructed overpasses and underpasses.

- In our analyses of species response to crossing structures, we used animal *sums*, i.e., the sum of all animals passing through a crossing structure. Another option would have been to use *counts*. Differences in using *sums* vs. *counts* would affect quantifying use by gregarious species and family groups. A family group consisting of four bears (mother and three offspring) routinely using one crossing structure will inflate the importance of this structure if *sums* are used.
- To better understand the family group effect we plotted the annual *sums* and *counts* of grizzly bears at each crossing structure since 2006 (Figure 6). As expected, the most

frequently used crossing structures of Healy, Wolverine overpass (WOP) and Redearth Overpass (REOP) had in certain years much higher *sums* than *counts*.

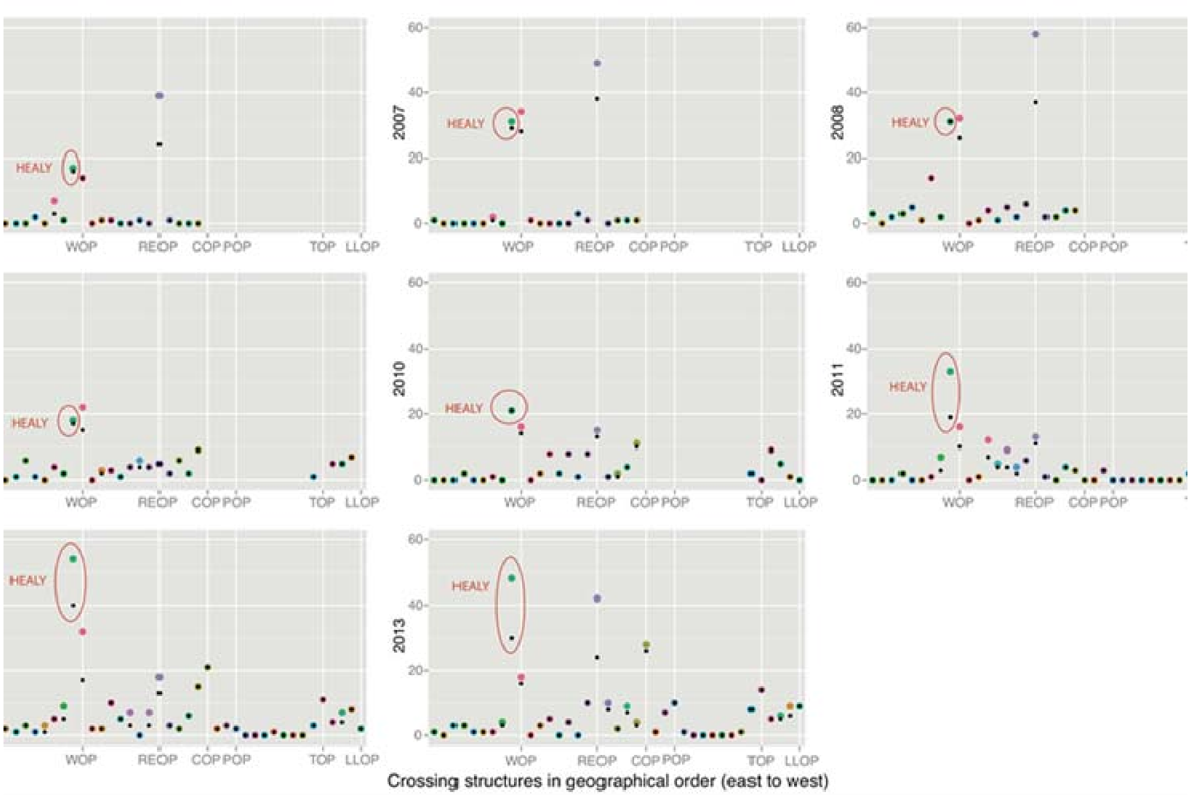

Figure 6. Grizzly bear use of crossing structures, by year, 2006-2013. *Sums* are shown in colour; *counts* are shown in black. Crossing structures are arranged on the X-axis in geographical order from east to west.

- The three underpasses in Phase 3B (Temple, Bow, Island) had relatively high numbers of grizzly bear crossings soon after completion (Figure 7). Throughout this 3-year period, few if any of the small corrugated steel and concrete box culverts had grizzly bear crossings, despite being in the area between the overpass structures.
- We compared grizzly bear use of three Phase 3B overpasses with their adjacent underpasses. There was a dramatic increase in annual use by grizzly bears at all overpasses after their completion (Figure 7).

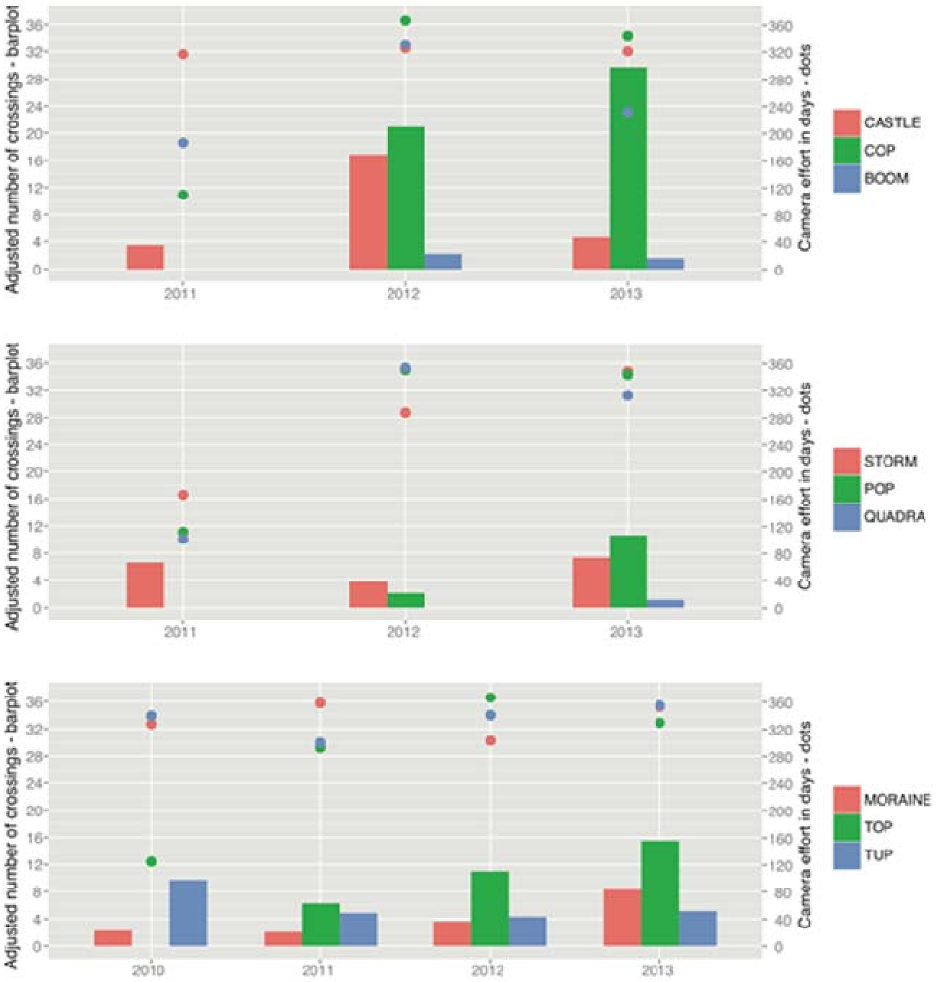

Figure 7. Pair-wise comparisons of annual grizzly bear crossings at newly constructed overpasses and adjacent underpasses on Phase 3B of the Trans-Canada Highway, Banff National Park.

- *Castle Overpass (COP)*: Castle underpass (built in 1992) had fluctuating numbers of grizzly bear crossings from 2011 to 2013. Once Castle overpass (COP) was completed in 2012, grizzly bear use shifted from underpass to overpass.
- *Panorama overpass* (POP) was completed in 2012. The first year there were slightly more grizzly bear crossings at Storm underpass compared to the overpass. The following year, overpass use more than tripled and outnumbered use at Storm underpass.
- *Temple overpass* (TOP): Temple underpass was used almost exclusively by grizzly bears the first year (2010). When Temple overpass was built in 2011, use

at Temple underpass diminished over time, while use at the overpass increased nearly exponentially each year. Crossings at Moraine underpass increased from 2010-2013, but were a fraction of use at Temple overpass.

- Despite the site attributes favourable to grizzly bears at the Healy underpass, the adjacent Wolverine overpass saw similar frequency of use in all years but 2012 and 2013, particularly if *counts* are used. From 2006 to 2008, female grizzly bears nearly exclusively used overpasses and large open span structures.
- There was an apparent trend towards increasing overpass use over time by grizzly bears on Phase 3B. This trend occurred at all three overpasses, despite two of the three overpasses not being built in the optimal location.
- Grizzly bears (especially males) appear to have adapted to and eventually used all types of crossing structures, yet the smallest crossing structures remain virtually underutilized 17 years after construction.
- There is a clear threshold for what crossing structure type grizzly bears will use and not use. Overpass and large span structures are preferred structures, while smaller structures (4 x 7 m and smaller) are underutilized and of little conservation value.
- In absence of preferred structure types we predict that sex-biased dispersal across the TCH will result, i.e., primarily male dispersal and no or limited female dispersal across the highway. Sex-biased dispersal has been found among grizzly bears on highways with no mitigation measures in place.
- Our results provide evidence that effective mitigation strategies for grizzly bears for future TCH projects will consist of large crossing structures, preferentially overpasses and secondarily, large open span underpasses. The locations should be in areas known to be critical cross-highway dispersal corridors. Failing to do so will likely result in filtered and sex-biased movement of grizzly bears across the TCH. These non-lethal effects could affect demographic connectivity (e.g., access to critical habitats), reproduction, and survival.

VII. Anthropogenic Effects on Activity Patterns of Wildlife at Crossing Structures

We evaluated whether existing crossing structures mitigate the effects of anthropogenic disturbance on wildlife activity. We predicted that activity patterns of wildlife at crossing structures should be similar to areas characterized by little or no human disturbance, e.g., backcountry sites.

- There was marked variation in the effect of anthropogenic disturbances on wildlife, including changes to the timing of interspecific interactions and the allocation of activity over daily cycles.

- We found wildlife adjusted their behaviour in response to variation in human activity, and the response depended on baseline levels of human activity in the area.
- Human use of crossing structures affected wildlife activity, yet we found congruent overall activity patterns for most species between crossing structures and backcountry sites (Figure 8). Wildlife can habituate to some types of disturbances (e.g., vehicle traffic), but remain sensitive to others (e.g., pedestrian traffic using structures).

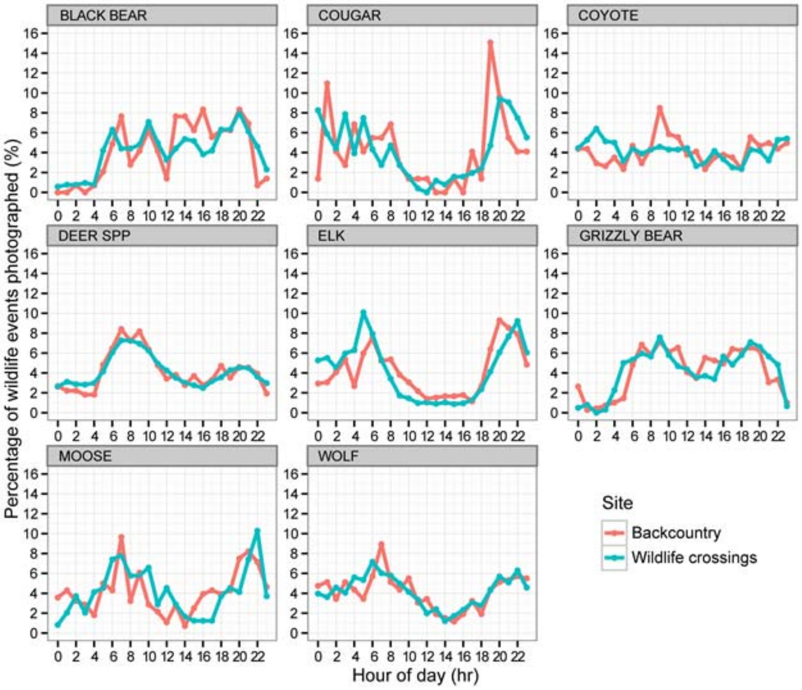

Figure 8. Diel activity patterns of large mammals at wildlife crossings and backcountry sites in Banff National Park, Alberta. Activity is based on the percentage of wildlife events photographed at wildlife crossings (turquoise solid line) and at backcountry sites (red solid line).

- Co-use by humans and wildlife can adversely affect movement of certain species at crossing structures.
- Continued information on the relationship between wildlife and human-related disturbance at crossing structures will aid management in assessing the performance of mitigation efforts.

VIII. Wolverine Genetics and Distribution

Effects of transportation infrastructure on fine-scale genetic structure

The purpose of our research was to collect information on wolverine occurrence in the Canadian Rocky Mountains and examine whether transportation corridors affect their movements and gene flow. Hair and camera traps were used to sample wolverine occurrence and genetics in an 8000 km^2 area of Banff, Yoho and northern Kootenay National Parks and part of the Columbia Valley near Golden, B.C.

- A total of 2563 hair samples were collected between 2010 and 2013; 31% (n=793) of the samples were analyzed, from which 40% (n=314) produced multi-locus genotypes. A total of 64 unique individuals (25 females, 39 males) were detected.
- Out of 75 hair trap locations sampled, 60 (80%) produced at least one individual identification (Figure 9). More than one individual was detected at 39 of the 75 sites (52%).
- Many female and male wolverines reside in the study area, but the two sexes were affected differently by transportation infrastructure. We detected ample male movement across the TCH and a lack of genetic differentiation. However, we detected relatively strong genetic differentiation in females on either side of the TCH (Figure 10).
- We detected 7 wolverines that crossed the TCH (2 females, 5 males), possibly one of the females at a wildlife crossing structure.
- Evidence suggests that females may be starting to use wildlife crossings. For example, a female wolverine, F015, may have been the wolverine detected crossing northward at Castle Underpass in February 2011.
- We strongly recommend Parks Canada continue monitoring wildlife crossing structures on the TCH, particularly the newly constructed Phase 3B crossings. Monitoring should be conducted in conjunction with winter roadside surveys to help understand the number of highway crossings by wolverines not detected at crossing structures, breaches in fences, and behaviour from snowtracking in the highway corridor.
- Parks Canada should consider snow tracking to collect hair from wolverines that use wildlife crossing structures. Gender information can be used to evaluate different crossing structure types and determine the preferred designs for increasing female movement.

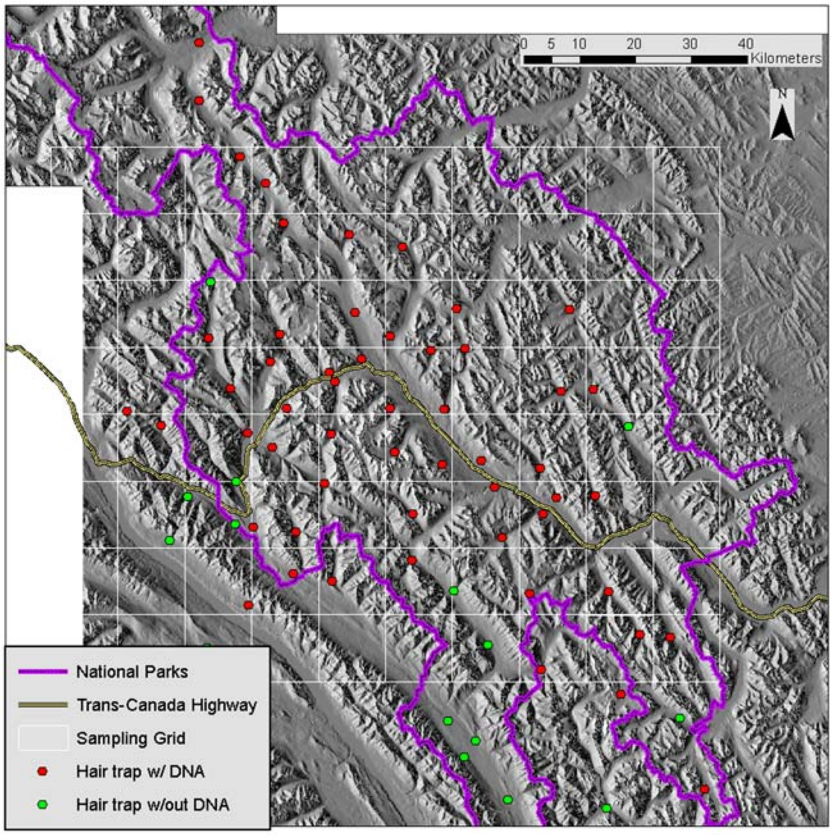

Figure 9. Wolverine hair trap and genotyping success in parks complex between 2011 and 2013.

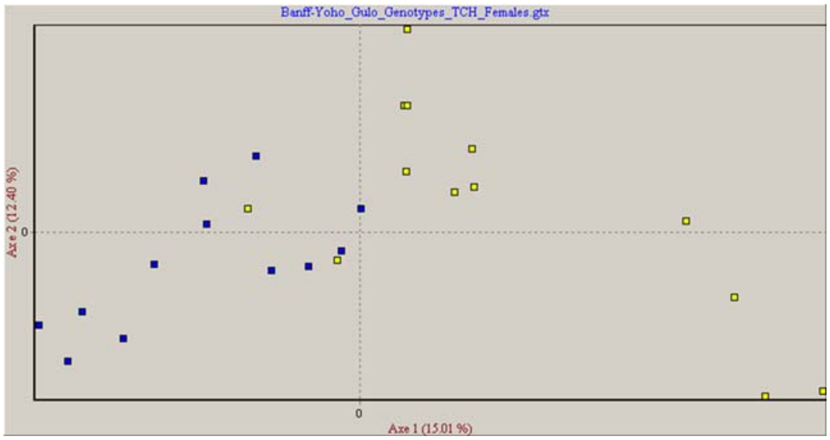

Figure 10. Factorial Correspondence Analysis plot showing 25 female wolverines detected to the north (yellow) or south (blue) of the Trans-Canada Highway in the parks complex between 2011 and 2013.

Modeling Wolverine Distribution

We asked whether wolverine occurrence within the national parks complex was affected by natural and/or anthropogenic features, and whether these differed from the features known to affect occurrence outside of protected areas. We used the same study area and sampling method as described in the genetics section above. Explanatory variables used in our analysis described biophysical attributes and human development.

- Our results are consistent with research primarily conducted in the contiguous United States inferring that wolverines are obligate habitat specialists that require areas with spring snow cover.
- Wolverines also were strongly associated with areas of shrub cover, and this supports previous research documenting a consistent year-round association with avalanche path habitats.
- Neither distance to highways, including the TCH, or any other anthropogenic footprint variable explained wolverine occurrence in our study area. This lack of an effect suggests human impacts may not be spatially extensive or strong enough to affect wolverine distribution in our largely protected study area.
- Although we were unable to detect a highway effect on wolverine distribution or habitat selection, we have shown that the TCH has affected dispersal and gene flow among female wolverines.

I. INTRODUCTION

Context and Background

Canada's Rocky Mountain front harbors the richest diversity of large mammals remaining in North America. This landscape is among the continent's last remaining undisturbed natural areas, and provides a critical trans-boundary linkage with the United States (Weaver 2013). Maintaining landscape connectivity throughout the ecoregion has been the vision of the Yellowstone to Yukon (Y2Y) Conservation Initiative. At the ecoregion-scale this has occurred through land securement and managing existing lands for regional scale connectivity (Graumlich and Francis 2010). However, securing local-scale connections will be equally important for mitigating continental-scale bottlenecks (Clevenger 2012).

Roads and increasing vehicle use present some of the most severe human-caused impacts in the Y2Y region. Compared to other sources of habitat fragmentation, roads not only fragment habitat and sever wildlife populations (genetic consequences), they are also an important source of wildlife mortality (demographic consequences). Understanding these two forces and developing science-based solutions to mitigate them will be central to large-scale landscape connectivity efforts in the Canadian Rocky Mountains and landscapes elsewhere impacted by a growing transportation network.

Ecological connectivity at a landscape scale is becoming increasingly important in the face of a changing climate (Heller and Zavaleta 2009). Local-scale corridors such as wildlife crossing structures may play an important role in allowing animals to adapt and respond to a warming climate. Wildlife crossing structures combined with exclusion fencing are one solution to keeping animals off roadways while maintaining or restoring animal movements (Huijser et al. 2007), but the ability of wildlife crossings to provide connectivity for populations fragmented by roads has yet to be properly evaluated (Lesbarrieres and Fahrig 2012, VanderGrift et al. 2012).

Research that identifies important attributes of wildlife crossing structures that facilitate connectivity and dispersal for key fragmentation-sensitive species is needed to ensure local-scale habitat linkages will be able to mitigate continental-scale bottlenecks, such as the Trans-Canada Highway (TCH; Clevenger 2012). Science-based research focused on transportation infrastructure will have significant implications for achieving the necessary science to effectively design highway mitigation and provide necessary evidence for new policy decisions regarding wildlife crossing infrastructure on North American highways.

Trans-Canada Highway Phase 3B Mitigation

The TCH in the Canadian Rocky Mountains has long been recognized as a lethal barrier to wildlife and an acute fracture zone for population connectivity at local and trans-boundary scales (Apps 1999, Gibeau 2000, Sawaya et al. 2014). Mitigation efforts over the past 30 years have essentially restored habitat connectivity across large sections of this major transportation corridor in Banff National Park, Alberta (hereafter referred to as Banff; Clevenger et al. 2002, 2009; Sawaya et al. 2014). This has been accomplished through the construction of 22 wildlife crossing structures during highway reconstruction (Phases 1, 2, and 3A; Figure 1). Wildlife monitoring is conducted through the use of 49 cameras, which are operating on all the constructed crossing structures built by the end of 2011.

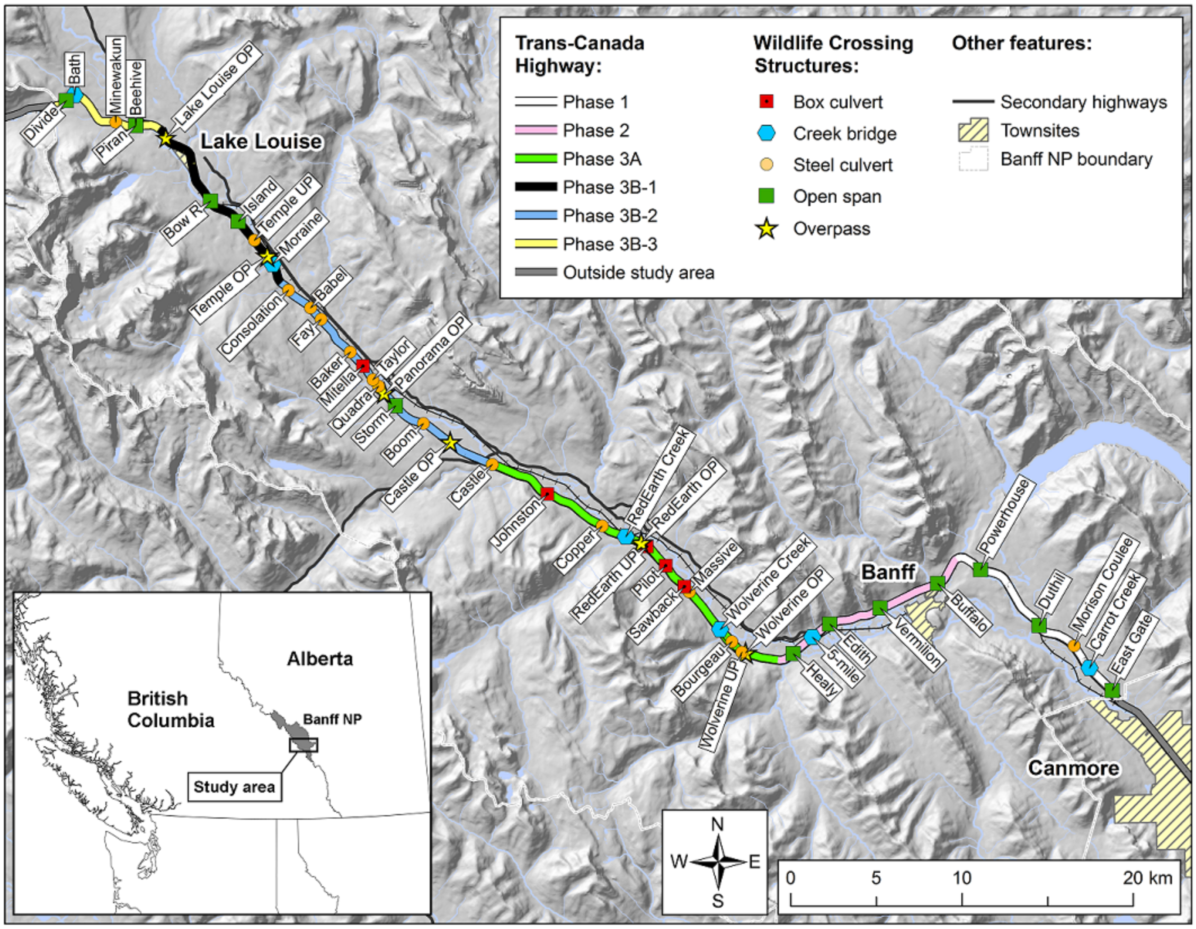

Figure 1. Map of Trans-Canada Highway study area and wildlife crossing structures, types and respective mitigation phase in Banff National Park, Alberta. There are no data from Cascade and 5-Mile underpasses since they were not monitored consistently throughout the project. Castle underpass was built separately from Phase 3A and 3B.

In 2009, construction of an additional 35 kilometers of twinned TCH (Phase 3B) was initiated, including a short section leading into Yoho National Park, British Columbia. Additional lanes for traffic and increased vehicle use threaten to fragment and isolate trans-boundary populations of wide-ranging, fragmentation-sensitive species residing in the heart of the Canadian Rocky Mountains.

Parks Canada Agency has been a world leader in efforts to mitigate the TCH in Banff. Between 2008 and 2013, Parks Canada Agency and the Highway Service Centre built environmental mitigation designed to enhance ecological connectivity throughout the Phase 3B project area. The scale and magnitude of the new twinning and its mitigation measures are unprecedented. A total of 21 new crossing structures (including four 60-m wide wildlife overpasses) were designed to mitigate its impacts by enhancing ecological connectivity throughout the project area by linking habitats for multiple species and ecological processes over time. The desired ecological condition consists of reducing risks of road-related mortality of wildlife, improving the permeability of the highway for all organisms, and providing for the long- term sustainability of populations in the area (Golder Associates 2004).

Background and History

Our highway mitigation research in Banff spans over 17 years and has evolved from the basic questions of: Do wildlife crossing structures provide safe passage and increase motorist safety and highway permeability for a range of wildlife species? Our research has documented 11 species of large mammals traveling safely under or over the TCH more than 150,000 times. This number is not simply 6-digits, but remarkably compelling and capable of changing preconceived ideas of transportation practitioners, as well as politicians and other decision and policy makers. The Banff mitigation has become recognized as a model for transportation planning and the overpasses are an icon for other aspiring wildlife crossing infrastructure projects in North America. Examples include Highway 3 Crowsnest Pass (Alberta, British Columbia), Highway US93 (Montana), Interstate-70 Vail Pass (Colorado), Interstate-90 Snoqualmie Pass (Washington), Highway 69 (Ontario) and Highway 175 (Quebec).

The *Wildlife Monitoring and Research Collaborative in the Canadian Rocky Mountains* was formed in 2010 to provide solutions that help reduce conflicts between transportation corridors, wildlife conservation, and large-scale landscape connectivity. Collaborative partners include the Western Transportation Institute (WTI) at Montana State University, Miistakis Institute, Woodcock and Wilburforce Foundations, and Parks Canada. Our goal was to gather the essential scientific information and to develop the appropriate tools to address current and future ecosystem management priorities as they relate to maintaining landscape-scale connectivity across transportation corridors and changing climates. A Contribution Agreement between Parks Canada and the Miistakis Institute was prepared to implement a 5-year project monitoring wildlife and transportation in the Canadian Rocky Mountain national parks. Parks Canada requested that WTI develop a monitoring and research plan for the project. Resource Conservation Manager for the LLYK Field Unit, Bill Hunt, signed the contribution agreement in February 2010.

The purpose of the multiyear project was to implement a wildlife monitoring and research plan to guide the evaluation of the TCH Phase 3B Project's goals and objectives – reducing wildlife-vehicle collisions and improving habitat connectivity and genetic interchange for key species. Annual work plans were created by WTI and approved by Parks Canada to meet the requirements of both wildlife crossing structure-specific monitoring as well as the broad, landscape-based ecological objectives.

Our report summarizes the research and monitoring results, describes the Phase 3B mitigation measure performance, and discusses the effects of TCH on population connectivity of a wide-ranging fragmentation-sensitive species. The report consists of published and submitted journal articles, technical reports that will eventually be prepared as manuscripts for journal submission, and simple data summaries. This document constitutes the final reporting requirement for the 5-year project. As in previous final reports we have prepared for Parks Canada, we address key management objectives of Parks Canada and have analyzed the response of wildlife populations to the TCH mitigation measures using data from the Contribution Agreement period (5-year; 2009-2014) and the entire length of our research project (17-year; 1996-2014).

II. WILDLIFE-VEHICLE COLLISIONS: MITIGATION MEASURES EFFECTIVENESS AND CONTEXT-DEPENDENT EFFECTS INFLUENCING DEER-VEHICLE COLLISIONS IN THE CANADIAN ROCKIES

1. Effectiveness of Phase 3B Mitigation to Reduce Wildlife-Vehicle Collisions

Authors: Ben Dorsey and Anthony P. Clevenger

Introduction

Most developed nations today have an extensive network of transportation infrastructure (Davenport and Davenport 2006). This infrastructure and the vehicles that travel on them can have pronounced impacts on the physical and biological processes in nearby ecosystems (Forman et al. 2003). One of the more obvious impacts of roads arises from wildlife-vehicle collisions (WVCs). For example, there are an estimated 1.5 million collisions per year between vehicles and wildlife in the USA (Conover et al. 1995, Tardiff and Associates 2003, Huijser et al. 2007). Not surprisingly then, much effort has been made to ensure motorist safety and the persistence of wildlife in areas where large, free-roaming animals occur near roads (Beckmann et al. 2010, Cushman et al. 2013).

Transportation engineers and land managers have created an array of mitigation measures to meet these safety goals, including wildlife-exclosure fencing, wildlife crossing structures (WC), early warning systems (e.g., animal-detection systems) and citizen scientist monitoring (Huijser et al. 2007, Lee et al. 2006, Paul et al. 2014). These measures are increasingly becoming a part of standard transportation practices when motorist safety and wildlife conservation interests are of concern. The cost of mitigation is a concern for agencies as the measures can be expensive if relying on WC and fencing. Of paramount importance is that measures need to be effective at meeting their intended objective or management role in the project (van der Grift et al. 2012).

Road mitigation measures are designed to reduce mortality of wildlife, increase motorist safety, and facilitate safe wildlife movement across roads. There are many ways to assess performance of these measures, but there is no standard method (Clevenger and Huijser 2011). Evaluating their function or conservation value depends largely on their intended purpose, the taxon of interest and biological level of organization most relevant to answering monitoring and research goals (Noss 1990, Clevenger 2005, Roedenbeck et al. 2007). If the primary objective is to reduce road-related mortality, there needs to be a biological basis for the desired change in WVC rate. To restore movements and population connectivity, evaluations preferably should compare movement rates pre-mitigation compared to post-mitigation (Roedenbeck et al. 2007, McCollister and VanManen 2010, Van Manen et al. 2012). Reducing mortality will have greatest effect on population viability over the long term (Forman et al. 2003). Thus, in many cases reducing mortality will be the most logical and effective conservation strategy for most land managers and transportation agencies.

One of the most expensive and well-documented efforts to mitigate road disturbances to wildlife occurs in Banff National Park, Alberta, consisting of a series of fences and WC designed to facilitate large mammal movement across the Trans-Canada Highway (TCH) and reduce wildlife-vehicle collisions (WVC; Ford et al. 2010). In spite of this major highway, numerous wildlife crossings have been recorded along these structures (Clevenger et al. 2009; see Chapter III.1.), rates of WVC have dropped off (Clevenger et al. 2001), and demographic and genetic connectivity continues across the highway (Sawaya et al. 2013, 2014).

Mitigating the TCH in Banff National Park began over 30 years ago and has followed sequential twinning phases with associated mitigation of fencing and WC (See Chapter I, Figure. 1; Ford et al. 2010). Since 1996, mitigation assessments have been conducted using a range of methods on multiple large mammal species (Clevenger et al. 2002, 2009; Sawaya et al. 2013, 2014). Clevenger et al. (2001, 2002) reported on the efficacy of wildlife fencing and WC at reducing WVCs on Phase 1 and 2; however, Phase 3A was not included due to a lack of post-mitigation data at that time. The final Phase 3B was recently completed between 2009 and late 2013 and consists of 30 km of fencing and WC. Although mortalities of carnivores on these two phases have been summarized as part of a larger report covering the entire TCH in Banff (Kinley et al. 2013), Phase 3A and 3B changes in road-kill rates have not been analyzed using statistical methods.

The purpose of our analysis was to:

1. Summarize mortality data for large mammals in mitigated Phases 3A and 3B of TCH in Banff National Park;
2. Estimate WVC rates of large mammal species in mitigated Phases 3A and 3B of TCH in Banff National Park;
3. Evaluate rates of WVC pre-mitigation vs. post-mitigation to evaluate efficacy of the mitigation phases at reducing mortalities;
4. Summarize fence intrusions by large mammal species on mitigated Phases 3A and 3B of TCH and determine the effect of “access points” on WVC locations.

Methods

Study Area

Our study was carried out in Banff National Park, Alberta (hereafter referred to as Banff) approximately 150 km west of Calgary (see Chapter I, Figure 1). The study area is characterized by continental climate with long winters and short summers (Holland and Coen 1983). Vegetation characteristic of the montane and subapine ecoregions consists of open forests dominated by lodgepole pine (*Pinus contorta)*, Douglas-fir (*Pseudotsuga menziesii)*, white spruce (*Picea glauca)*, Englemann spruce (*Picea englemannii)*, trembling aspen (*Populus tremuloides)*, and natural grasslands. The geography of the central and eastern portions of the study area is dictated by the geology of the Front ranges of the Rocky Mountains.

The TCH is the major transportation corridor through Banff currently carrying an estimated annual average daily traffic volume of over 17,000 vehicles per day, with peaks of more than 30,000 vehicles per day during summer (Highway Service Center, Parks Canada, unpublished data). Traffic volumes in Banff are highest at the east gate and gradually decline westward through Banff and Yoho National Parks. In the 1970s, safety issues compelled planners to upgrade the Trans-Canada Highway (TCH) within Banff from two to four lanes, beginning from the eastern boundary and working west (Ford et al. 2010). Large animals were excluded from the road with a 2.4-m-high fence erected on both sides of the highway, and underpasses were built to allow wildlife safe passage across the road. The first 27 km of highway twinning (Phases 1 and 2) included 10 wildlife underpasses and was completed in 1988 (Figure 1 in Chapter I). Fencing and WC on the next 20 km section (Phase 3A) were completed in late 1997 with 11 additional wildlife underpasses and two 50-m wide wildlife overpasses (Clevenger and Waltho 2000, 2005). The Castle wildlife underpass was constructed independent of Phase 3A or Phase 3B in 1990-91. The final 35 km of four-lane highway to the western park boundary (Phase 3B) includes 21 WC, including four, 60-m wide wildlife overpasses and was completed in late 2013. The Phase 3B twinning and installation of mitigation measures progressed over a 5-year period (2008-2013) and for the purpose of this paper we refer to the completed sub-phases as Phase 3B-1, and 3B-2 (Figure 1). Phase 3B-3 was only completed in November 2013 and is not included in our analyses.

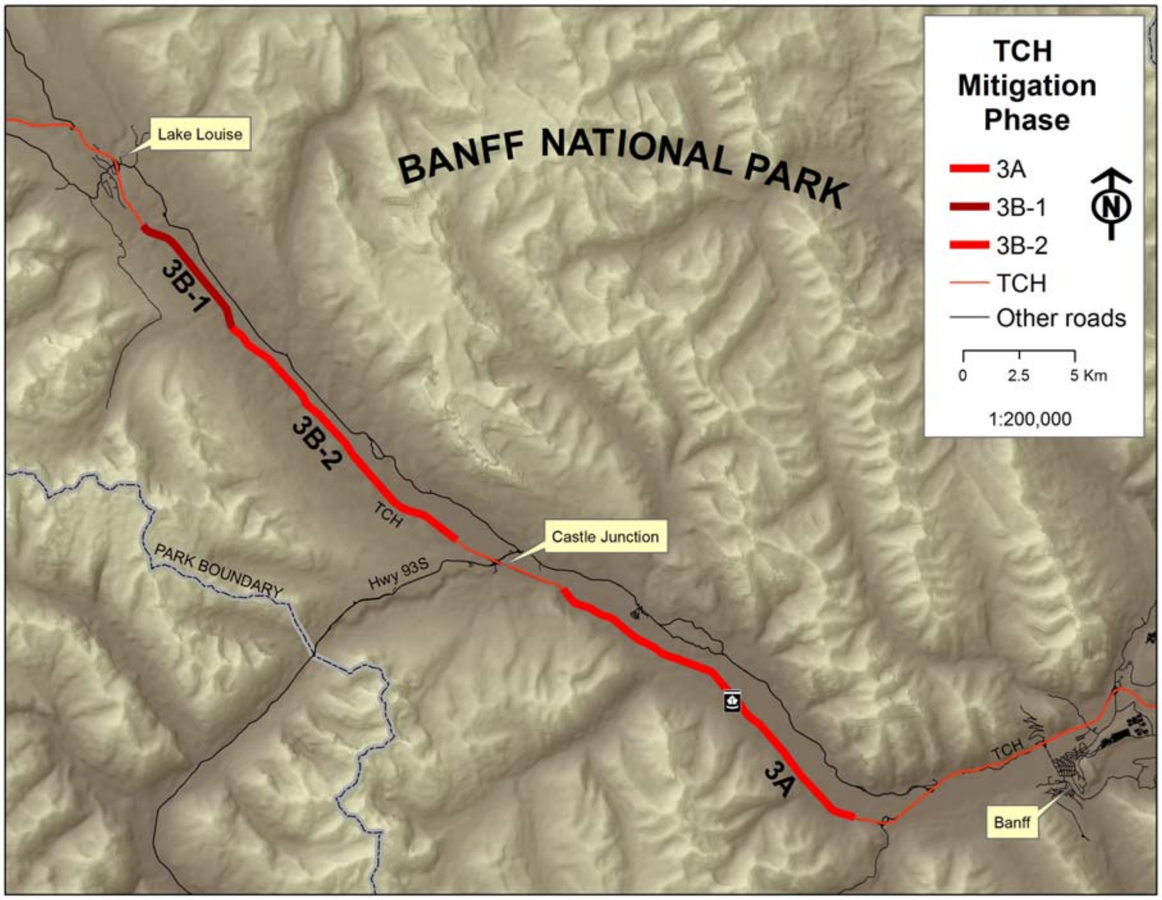

Figure 1. Phase 3A and 3B mitigation study areas of the Trans-Canada Highway (TCH) in Banff National Park, Alberta. Castle Junction was constructed independent of Phase 3A and 3B in 1990-91.

Where wildlife fencing intersects access roads leading to the TCH, cattle guards (Texas gates) and electrified mats have been placed in the road to keep wildlife from entering right-of-ways (Belant et al 1998, Seamans and Helon 2008, Allen et al. 2013). The TCH runs along the floor of the Bow Valley sharing the valley bottom with the Bow River, the Canadian Pacific Railway, outlying commercial areas, and towns of Banff and Lake Louise.

Data Collection

Wildlife-vehicle collision (WVC) data were collected year-round in the study area as part of routine wildlife observation reporting by Banff park staff. Each accident site was visited and the date of the WVC was recorded along with information about the species and the number of individuals. For each WVC location a Universal Transverse Mercator (UTM) coordinate was obtained using a handheld, global positioning system (GPS) unit accurate to <5 m (Clevenger et al. 2002, Gunson et al. 2009).

On an annual basis, observations of wildlife entering highway rights-of-way were opportunistically recorded by Banff park staff as fence intrusions. Date, time, species observed, number of individuals, and estimated location were recorded for each intrusion using UTM coordinates. All UTM coordinates are assumed to be accurate to ≤5 m. We assigned UTM coordinates for all potential access points for wildlife onto the highway right-of-way. Banff park staff reported into the observation database all WVCs in the park; however, for this analysis we focus on primarily large mammal species and those with large enough sample sizes to make statistical inference.

Data Analysis

We analyzed 24 years of spatial data recorded along Phases 3A, 3B-1 and 3B-2 of the TCH totaling 37.3 km for 11 large mammal species (Figure 2). Data were extracted from databases maintained by Parks Canada that stored all known wildlife mortalities and fence intrusions (S. Wrazej and T. Gui, Parks Canada). These data were recorded with a GPS unit or digitized in a GIS on a 1:30,000 topographic map when animals were removed from the highway. WVC data were limited to those directly attributable to collisions that occurred between 1990 and 2013. For the same time period, data were also extracted for fence intrusions and traffic volume. Fence intrusions occurred when wildlife were documented entering an area with wildlife exclusion fencing regardless of whether a road-kill occurred, i.e., post-mitigation road-kills were considered fence intrusions. Data were cross-referenced and corrected based on methods developed by Kinley et al. (2013). Mitigation status was defined for all WVC and intrusions as before mitigation construction started (=pre-mitigation), during construction of highway fencing (=during), or after completion of all fencing to a point where fencing was considered operational (=post-mitigation). We considered fencing operational after the fence was completely attached to a buried apron and supports. A buried apron was present along all mitigation phases considered in this analysis. All fence openings were treated with a mechanism designed to exclude wildlife, e.g., Texas gate or electrified mat.

WVC rates were compared across the entire 24-year period to mitigation status and traffic volume. For calculation of percent change, WVC rates were standardized for length of highway and years of data. We evaluated if WVC counts decreased for each phase, using data occurring two years pre and post highway mitigation with chi-squared tests for consistency (Clevenger et al. 2001). We then used a mixed-design ANOVA, because the data are from a longitudinal study (Underwood 1997). For these tests the null hypothesis was: WVC counts are independent of highway mitigation. A significant test statistic would mean we reject the null hypothesis and thus conclude WVC counts were not independent of highway mitigation. An alpha level (P-value threshold) of 0.05 was used for all hypothesis testing.

To evaluate the effects of fence ends we evaluated if WVC were completely spatially random (CSR), using Ripley's *K* function modified for linear networks (Ripley 1976, 1977; Okabe 2001). This method does not depend on a required minimum number of WVC to identify a cluster but looks for clusters at a range of distances (multi-scale). The *K* function evaluation was limited to distances less than 5 km because clustering or dispersion at larger distances can be affected by changing intensity, e.g., species abundance (Diggle 2003). Clustering was determined by comparing linear K function estimates for the observed WVC points (K_L) to 999 simulated CSR point patterns (K_L) along a GIS layer representing the TCH. Simulations were generated with the same number of points as the data. To determine if any spatial deviations in randomness coincide with fence ends a linear cross K function was used (Diggle 1983, Cressie 1993).

Last, we assessed trends in fence intrusions for the same area and evaluated whether the spatial distribution of fence intrusions coincided with access points for Phase 3B-1 only (east and west ends). Access points included access roads with Texas gates and traditional swing gates, (e.g., Km 69 pit, Mannix pit, Whitehorn Road, Highway 93N, Highway 93S). All analyses were conducted in R 3.0.1 (R Core Development Team 2014) and spatial analyses with the "Spatstat" library (Baddeley and Turner 2005).

Results

Status and Trends of WVC and Traffic Volume

Between 1990 and 2013, there were 298 WVC along three mitigated phases of the TCH: Phase 3A, 3B-1, and 3B-2. Elk, mule deer, white-tailed deer and unidentified deer were the most commonly killed species and made up 93% of all WVC (Table 1). Moose and bighorn sheep (n=16 and n=1, respectively) made up only 7% of all ungulate road-kills. Coyote and wolves were the most commonly killed carnivores (n=37 and n=14, respectively) making up 85% of all carnivore road-kills. Seven black bears and one cougar mortality were recorded during the 24-year period. Only one grizzly bear mortality occurred, although other grizzly bear road-kills occurred along nearby Phase 1 and 2 (Parks Canada, unpublished data). The number of WVCs declined after mitigation fencing was implemented despite annual increases in traffic volumes (Figure 2). This pattern was consistent for all 3 phases while motor vehicle traffic increased 66% from 11,500 AADT to 19,086 AADT along the TCH.

Table 1. Total number of wildlife-vehicle collisions involving large mammal species on Phase 3A and 3B in Banff National Park, Alberta between 1990-2013.

	1990	**1991**	**1992**	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**Total**
Deep sp.	0	0	0	0	0	0	0	1	2	0	1	0	0	0	0	0	1	0	0	1	1	0	0	0	**7**
Elk	22	11	10	8	8	6	1	0	0	5	7	4	2	0	0	1	1	2	1	2	0	0	0	0	**91**
Moose	1	0	0	1	1	1	0	0	0	0	0	2	0	1	0	0	2	1	4	1	0	0	0	1	**16**
Mule deer	10	4	0	9	6	3	2	5	3	1	3	1	0	1	1	4	2	0	3	1	1	0	0	0	**60**
Sheep	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	**1**
White-tailed deer	3	3	5	3	6	3	2	2	0	2	4	4	2	3	3	4	6	2	0	2	2	1	0	1	**63**
Black bear	0	1	0	1	0	0	1	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	**7**
Cougar	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**
Coyote	1	1	1	3	2	0	2	3	2	2	1	2	0	2	1	0	2	2	1	5	0	1	3	0	**37**
Grizzly bear	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	**1**
Wolf	1	1	0	0	1	0	5	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	2	0	**14**
Total	**38**	**21**	**16**	**25**	**25**	**13**	**13**	**11**	**7**	**13**	**17**	**13**	**4**	**7**	**5**	**9**	**16**	**7**	**10**	**13**	**4**	**4**	**5**	**2**	**298**

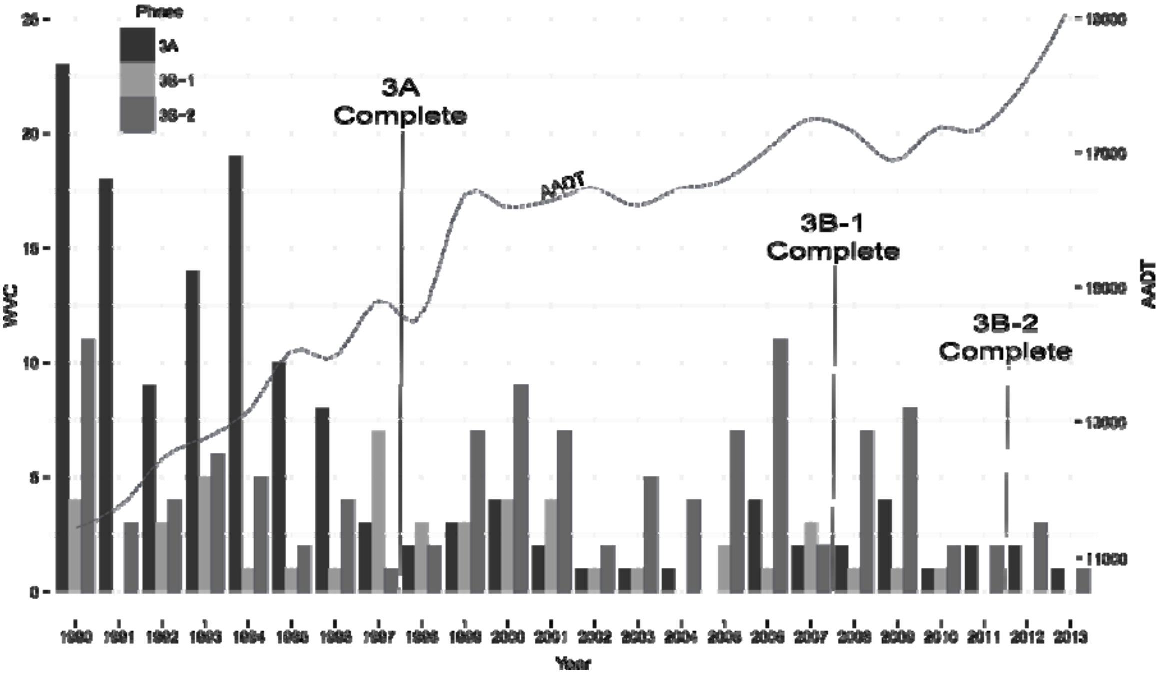

Figure 2. Annual frequency of wildlife–vehicle collisions (WVC) during a 24-year period along phase 3A, 3B-1 and 3B-2 of the Trans-Canada Highway, Banff National Park, Alberta. The year of fence completion is shown for both phases and annual mean daily traffic volume (AADT). Traffic volume was estimated for each year based on traffic counter located at Castle Junction.

WVC rates decreased 79.9% overall for the combined three mitigated sections (Table 2). When considered individually, WVC rates decreased the most along Phase 3A (87.2%) followed by Phase 3B-1 (75.7%) and Phase 3B-2 (66.1%). There was an 89% reduction in ungulate-vehicle collision rates, individually: elk (93%) and deer species (86%). Carnivore mortality rates decreased 10.6 %. Coyotes accounted for most carnivore collisions and their collision rates increased 174.7% on average. For all other species sample sizes were low (n<10), thus making individual assessments difficult. Percent decrease was based on pre-mitigation and post-mitigation mortality rates, excluding WVC that occurred during construction.

Table 2. Rate of wildlife-vehicle collisions by large mammal species on Phases 3A and 3B, Banff National Park, Alberta.

	Phase 3a			**Phase 3B-1**			**Phase 3B-2**			**All phases (averaged)**		
	Pre	**During**	**Post**	**Pre**	**During**	**Post**	**Pre**	**During**	**Post**	**Pre**	**During**	**Post**
Elk	43	6	3	11	1	0	25	2	0	79	9	3
Moose	0	0	0	4	1	1	8	1	1	12	2	2
Sheep	0	0	0	0	0	0	1	0	0	1	0	0
Deep sp.	0	1	1	2	0	0	1	2	0	3	3	1
Mule deer	17	4	2	13	0	0	23	1	0	53	5	2
White-tailed deer	11	4	3	8	1	2	31	3	0	50	8	5
Black bear	2	0	2	0	0	0	3	0	0	5	0	2
Cougar	1	0	0	0	0	0	0	0	0	1	0	0
Coyote	7	3	18	3	0	0	3	1	2	13	4	20
Grizzly bear	0	0	0	0	0	0	0	1	0	0	1	0
Wolf	2	3	3	0	0	0	5	0	1	7	3	4
Ungulates	71	15	9	38	3	3	89	9	1	198	27	13
Carnivores	12	6	23	3	0	0	11	2	3	26	8	26
TOTAL	**83**	**21**	**32**	**41**	**3**	**3**	**100**	**11**	**4**	**224**	**35**	**39**
Years of data	5.40	2.40	16.20	17.60	1.10	5.30	19.50	2.20	2.30	42.50	5.70	23.80
Km of road	17.00	17.00	17.00	6.40	6.40	6.40	14.03	14.03	14.03	37.43	37.43	37.43
Mortality Rate (WVC/yr/km)	**0.904**	**0.515**	**0.116**	**0.364**	**0.426**	**0.088**	**0.366**	**0.356**	**0.124**	**0.545**	**0.432**	**0.110**
Ungulate mortality rate	0.773	0.368	0.033	0.337	0.426	0.088	0.325	0.292	0.031	0.479	0.362	0.051
Carnivore mortality rate	0.131	0.147	0.084	0.027	0.000	0.000	0.040	0.065	0.093	0.066	0.071	0.059
Overall % decrease			**87.15**			**75.70**			**66.09**			**79.89**

Did WVC Decrease After Fencing?

When we compared the number of WVCs two years pre-mitigation with two years post-mitigation on all three phases we found no statistically significant difference in number of collisions with wildlife (X_3^2 (2, n=55) = 2.619, p = 0.27). However, for all three phases there were reductions in the number of WVCs from pre- to post-mitigation. Further testing was done because the result appeared be biased by the low response size (Table 3). A mixed-design ANOVA test showed that the effect of highway mitigation was significant in reducing WVC rates on all phases (*F*(2,4) = 14.05, *p* = 0.015). These findings were confirmed by visual inspection of a medians and variability shown in a box plot (Figure 3).

Table 3. Wildlife-vehicle collision data for two years pre- and post-mitigation for three phases of the Trans-Canada Highway, Banff National Park, Alberta.

	pre	post
3A	33	5
3B-1	3	2
3B-2	9	3

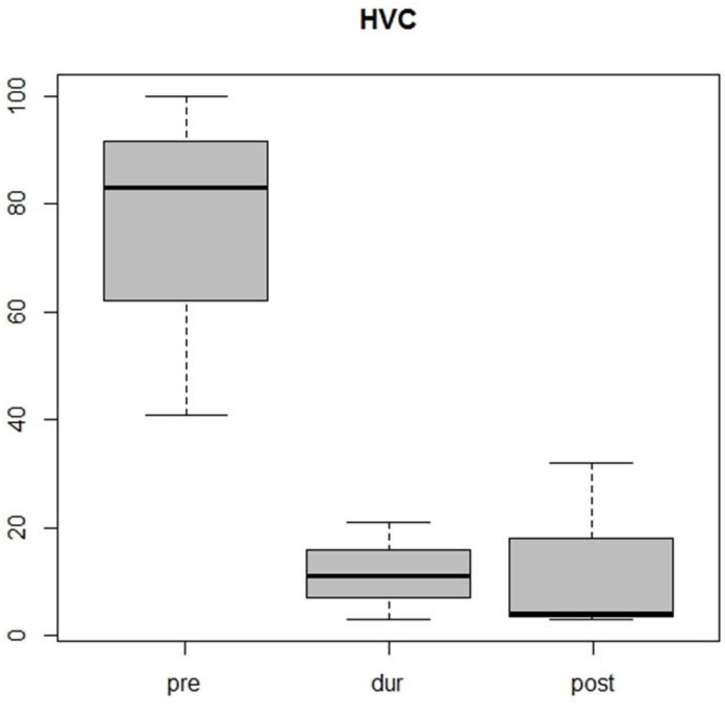

Figure 3. Boxplot of wildlife-vehicle collisions by mitigation status on Phase 3A and 3B. Pre = before mitigation, post=after mitigation, dur=during mitigation construction.

Status and Trends of Fence Intrusions

Fence intrusion data were reported after at least one section was mitigated (Phase 3A starting late 1997) and over time included data from wildlife intrusions on Phases 3B-1 and 3B-2 (Table 4). Intrusion rates were standardized by years of data and kilometers of highway. In total 73 fence intrusions were recorded, 61% (n=45) from carnivores, while ungulates accounted for 39% (n=28). Coyotes made up 38% of all wildlife intrusions and 62% of all carnivore intrusions. Grizzly and black bears were recorded inside mitigated areas 7 and 5 times, respectively. Fewer ungulates entered a fenced area compared to carnivores.

Table 4. Fence intrusions occurring on mitigated sections of Phase 3A, 3B-1 and 3B-2 on the Trans-Canada Highway, Banff National Park, Alberta, 1998-2013.

	1998	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**TOTAL**
Elk	0	0	1	0	1	0	0	0	1	0	0	0	0	1	0	1	**5**
Moose	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	**2**
Sheep	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Deep sp.	0	0	1	0	0	0	0	0	2	0	0	0	0	0	1	0	**4**
Mule deer	0	0	1	0	0	0	0	0	2	1	1	1	1	1	0	0	**8**
White-tailed deer	0	0	0	0	0	0	0	0	4	0	1	2	1	0	0	1	**9**
Ungulates	**0**	**0**	**3**	**0**	**1**	**0**	**0**	**0**	**9**	**1**	**3**	**3**	**2**	**2**	**1**	**3**	**28**
Cougar	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
Coyote	2	1	1	2	0	1	1	0	2	2	1	5	0	2	4	4	**28**
Black bear	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1	**5**
Grizzly bear	0	0	0	0	0	0	0	1	0	2	0	0	1	2	1	0	**7**
Wolf	0	0	0	0	0	0	0	0	0	0	1	0	0	1	2	1	**5**
Carnivores	2	3	1	2	0	1	1	1	2	5	3	5	1	5	7	6	**45**
Grand Total	**2**	**5**	**4**	**2**	**1**	**1**	**1**	**1**	**11**	**6**	**6**	**8**	**3**	**7**	**8**	**9**	**73**

Intrusion rates differed by phase with Phase 3A the highest (0.26) followed by Phase 3B-2 (0.14) and Phase 3B-1 (0.09; Table 5). Ungulate intrusion rates (0.03) were less than carnivores (0.06), but this changed when coyotes were removed (0.02) from the comparison. Mule deer and white-tailed deer accounted for 75% of all ungulate intrusions, and all but two of these occurred along Phase 3A. The more westerly located Phase 3B recorded two moose intrusions. The average intrusion rate (0.09) equals roughly one intrusion per year for every 10 km of mitigated highway.

Table 5. Fence intrusion rates after mitigation, along phase 3A, 3B-1 and 3B-2 of the Trans-Canada Highway, Banff National Park, Alberta.

		Phase 3A	Phase 3B-1	Phase 3B-2	All phases (mean)
Fence Intrusions	Deep sp.	4	0	0	4
	Elk	5	0	0	5
	Moose	0	1	1	2
	Mule deer	8	0	0	8
	White-tailed deer	7	2	0	9
	Ungulates	**24**	**3**	**1**	**28**
	Black bear	5	0	0	5
	Coyote	26	0	2	28
	Grizzly bear	7	0	0	7
	Wolf	4	0	1	5
	Carnivores	**42**	**0**	**3**	**45**
	TOTAL	**66**	**3**	**4**	**73**
	Years of Data	15.00	5.00	2.00	22.00
	Km of road	17.00	6.40	14.03	37.43
	Intrusion Rate (intrusion/yr/km)	**0.26**	**0.09**	**0.14**	**0.17**
	Ungulate intrusion rate	0.09	0.09	0.04	0.07
	Carnivore intrusion rate	0.16	0.00	0.11	0.09
	Carnivore intrusion rate (without coyote)	0.06	0.00	0.04	0.03

Spatial Analysis of WVC and Fence Intrusions

We found the spatial distribution of WVC was clustered. The average nearest neighbor distance was 64 m, compared to 36 m for a simulated CSR pattern with equal intensity. A plot of the K function indicated that clustering was apparent for all distances greater than 300 m and less than 3500 m based on where the observed pattern fell outside the 95% quantile for a simulated CSR pattern (*K*theo) (Figure 4). We proceeded to test if fence ends or access points were related to the clustering of WVC and fence intrusions. A cross K function plot indicated that the two sets of locations (WVC and fence ends) were not spatially independent (Figure 5), with evidence of clustering below 1200 m. Likewise when fence intrusions were compared to access points there was evidence of fence intrusions being clustered around access points when distances less than 3200 m were considered (Figure 6). This trend held true regardless of whether fence ends were included.

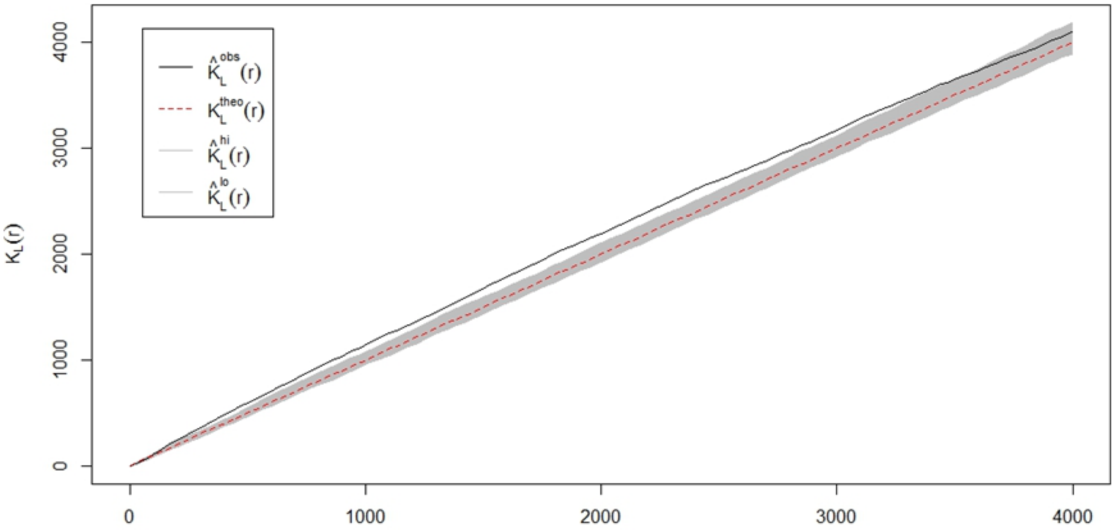

Figure 4. Linear K function for WVC and simulation envelope from 999 simulated CSR spatial patterns.

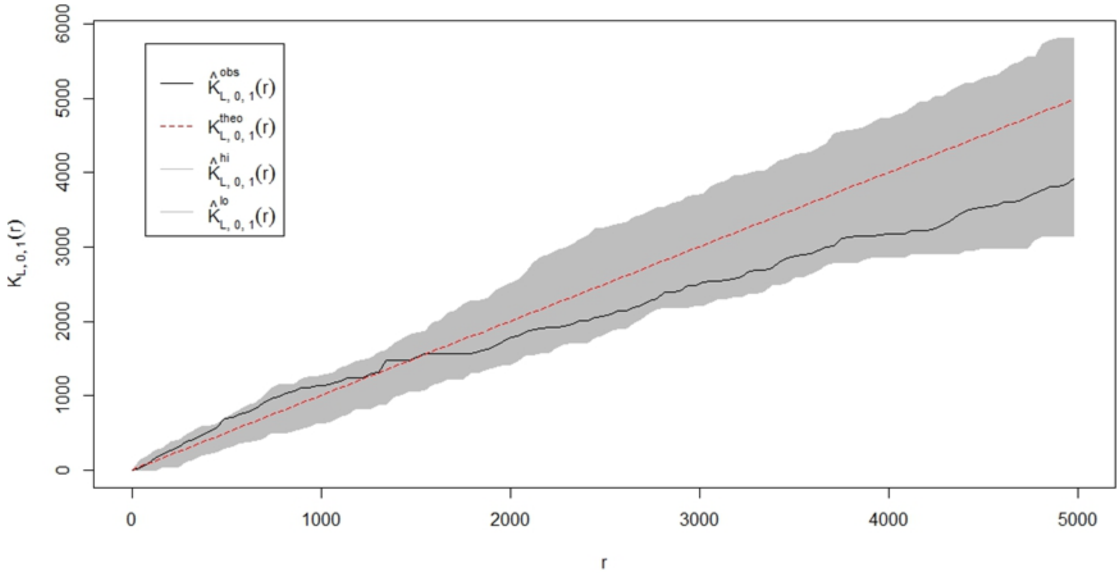

Figure 5. Cross K function plot demonstrating a small indication of interaction between WVC location and fence ends. X-axis is in metres.

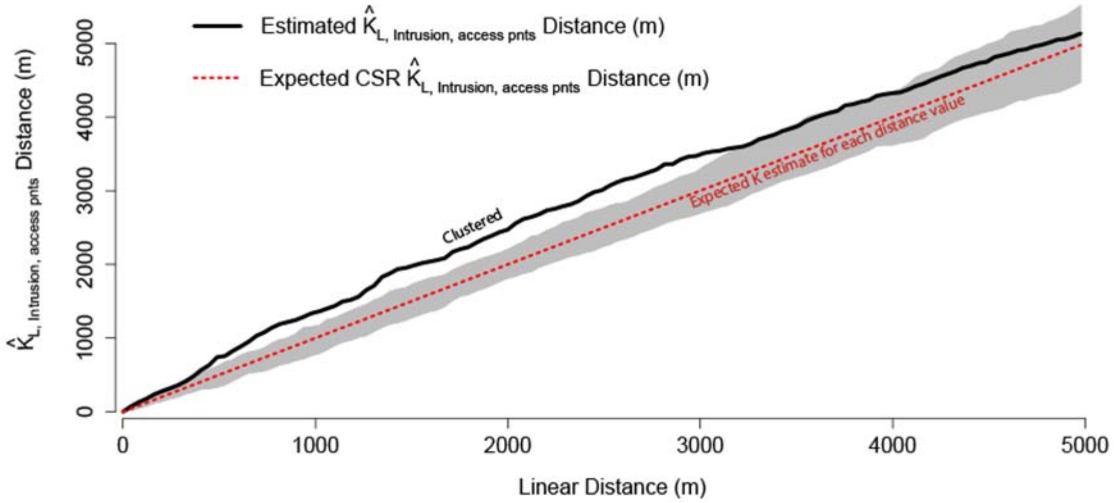

Figure 6. Cross K function plot showing clustering of WVC to intrusion access points. The effect diminishes at scales larger than 3200 m. The horizontal axis shows the scale considered (r in metres). The vertical axis shows the estimated K function for the observed spatial distribution (K^{obs}_{L}).

Discussion

We found a substantial decline in number of WVCs after each mitigation phase was completed despite annual increases in traffic volumes. Much of our evaluation of highway mitigation measures reducing WVCs supports findings from other studies on large mammals (Huijser et al. 2007, Gagnon et al. 2010, Sawyer et al. 2012), including previous research from Phase 1 and 2 in our study area (Clevenger et al. 2001). Although fencing effectively reduced road-related mortality of wildlife on Phases 3A and 3B, WVCs were found to be associated with fence ends. We also found this result in our previous evaluation of Phase 1 and 2 mitigation (Clevenger et al. 2001).

Significant declines in WVCs due to fencing and crossing structures have been reported elsewhere. On a 21-km section of US Highway 30 in Wyoming, fencing and underpass installation reduced deer-vehicle collisions by 81% (Sawyer et al. 2012). McCollister and Van Manen (2010) reported a 58% reduction in WVCs (primarily white-tailed deer) on 17.3 km section of highway in North Carolina. Huijser et al. (2007) summarized numerous studies finding reductions in WVC from 80-97% from fencing mitigation. The collective results of these research projects provide continuing support and science-based evidence that fencing and crossing structures can effectively reduce collision rates with large mammals.

WVC rates decreased 79.9% overall for the combined three mitigated sections when analyzing WVC data over a 24-year period. Ungulate-vehicle collision rates were reduced by 88%; however, carnivore mortality rates decreased only 17.6 % when coyotes were excluded from the analysis. The results of this pre- vs post-mitigation comparison should be taken with caution because the sampling periods between pre- and post-mitigation and among phases are not equally distributed. Slightly more than two years of data were available for post-mitigation Phase 3B-3 and nearly 20 years pre-mitigation. Similarly on Phase 3A, only five years pre-mitigation data were used, while there were 16 years post-mitigation. Further, there was no means of controlling for changes in population abundance over the 24-year time frame.

A more accurate assessment of the efficacy of fencing to reduce WVCs is to test for differences pre- vs. post-mitigation using short time frames in order to control for any changes or fluctuations in population size. We found the effect of highway mitigation was significant in reducing WVC rates on all phases. The chi-square test is a weak test, and the mixed-design ANOVA is the more appropriate statistical test for small sample sizes such as ours (Underwood 1997).

There were a total of 73 fence intrusions recorded from 1998-2013; more than half of those were from carnivores, while ungulates accounted for slightly more than one-third. Coyotes were responsible for two-thirds of all carnivore intrusions and slightly more than one-third of all wildlife intrusions. The relatively small body size of coyotes allows them to easily find gaps in fence material due to fence damage, erosion or other defects in installation. Coyotes are often seen within the TCH corridor; therefore, the number reported is likely an underestimate of the actual number that gains access to the highway right-of-way. Further, during winter we have observed tracks of coyotes in the snow passing through the wildlife fence, indicating that the fence mesh is large enough for some individuals to pass through it (AP Clevenger, personal observation). Our previous study of Phase 1 and 2 fencing highlighted the ineffectiveness of fencing for keeping coyotes off the TCH right-of-way (Clevenger et al. 2001). Future evaluations of fencing for large mammals based on wildlife intrusion reports should be assessed without coyotes because despite the fence, most times coyotes are able to access the right-of-way.

Ungulate intrusion rates were less than carnivores, but once we removed coyotes from the data set the intrusion rates of ungulates and carnivores were nearly equal. Fence ends and access points were not spatially independent, suggesting that ungulate intrusions were most likely associated with fence ends. Access points at Texas gates and electro-mats are weak points among the TCH mitigation measures. Access during winter is facilitated by snow build up under Texas gates and snow cover on electro-mats. Data summarized from monitoring of Texas gates and electro-mats suggests the need for a more effective method of preventing animal access to the TCH right-of-way (see Chapter VI "Assess the effectiveness of Texas gates"). Future monitoring of Texas gates and electro-mats is needed to better understand how effective these measures are in preventing wildlife intrusions and potentially road-related mortalities. Monitoring up until now has been conducted using a relatively ineffective method that could be improved by investment in the emerging systems that utilize "animal recognition software" using digital signature technology, micro-wave detection systems and camera technology (still or video) that more accurately detect and track animal movement and behaviour within the vicinity of Texas gates and electro-mats.

2. Context-dependent Effects on Spatial Variation in Deer-Vehicle Collisions

The results of this research have been prepared as a manuscript for submission to a journal for publication. The abstract is included here, and the full text is included as Appendix A.

Abstract

Identifying strategic locations for mitigating highways has been a key focus of road ecologists. Generally areas with the highest probability of wildlife-vehicle collisions (WVC) are targeted for mitigation measures like warning signs or crossing structures. These high-risk areas arise because of correlated processes that affect the probability of collisions. There are few generalities stemming from studies identifying the landscape and road-related factors contributing to WVCs. The incorporation of large-scale biophysical variables into predictions of WVC locations s remains a significant knowledge gap, principally because data collection efforts are often constrained by political boundaries. Such boundaries encompass landscapes with different biophysical characteristics, masking important large- and local-scale processes affecting the probability of WVCs. We contrasted variables explaining WVCs between five contiguous study areas defined by biophysical boundaries. Our goal was to quantify the extent to which localized processes are general both among and within study areas. We used long-term data from spatially-accurate WVCs locations collected over an 11,400 km^2 area. The factors predicting WVC occurrence varied greatly between and within individual study areas, suggesting that factors explaining WVCs are context dependent, with a strong interaction between local- and large-scale biophysical processes. The lack of generality in our models suggests that efforts to better understand the causes and consequences of WVCs may require field data derived from individual road sections. For transportation and land managers to effectively mitigate highways for wildlife, will require an understanding of the mechanisms giving rise to WVCs. Until these mechanisms are better addressed through additional field studies and meta-analytical methods, additional tools will be required to best identify where to mitigate highways for wildlife.

III. SPECIES RESPONSE TO CROSSING STRUCTURES AND ATTRIBUTES THAT INFLUENCE WILDLIFE MOVEMENT

1. Summary Data: Summary Tables for a) 2009-2014 and b) 1996-2014 by Phase

Introduction

For over 30 years, large mammals have safely crossed a major 4-lane highway bisecting Banff National Park approximately 150,000 times. By ensuring that key ecological processes are connected, highway mitigation is arguably one of Canada's greatest conservation success stories. The details of this story are borne out of data obtained by long-term monitoring. The long-term data has been the basis from which we have gained an understanding of how species use the crossings, what attributes facilitate passage (Clevenger and Waltho 2000, 2005; Gloyne and Clevenger 2001), whether species are able to adapt to them (Clevenger et al. 2009, this report), and ultimately how their populations benefit by having these mitigation measures in place (Sawaya et al. 2013, 2014). The long-term research has significantly advanced our understanding of the science of wildlife crossings and their practical application to highway mitigation projects throughout North America today (Evink 2002, Beckmann et al. 2010).

Given the importance of the long-term data and critical role of wildlife crossings in Banff as a conservation tool, this section constitutes the largest part of the report. The section begins by describing the methods used to quantify animal movement at the crossing structures and how these methods have changed in the last 17 years. Summaries are provided for the period of the Contribution Agreement (2009–2014) and the entire length of our research project (>17 years, 1996–2014).

Methods

All WC wildlife crossing structures in Phases 1, 2 and 3A have been continuously monitored for large mammal use since 1996 using track pads (Clevenger and Waltho 2000, 2005; Clevenger et al. 2002). Monitoring consisted of checking the crossing structures and recording animal movement across raked track pads. Track pads spanned the width of the wildlife underpasses and were set perpendicular to the direction of animal movement. Most track pads had a ≈2-m-wide tracking surface, however, at the wildlife overpasses only a single, 4-m-wide track pad was set across the center. Tracking material consisted of a dry, loamy mixture of sand, silt and clay, 1–4 cm deep (Bider 1968). Each crossing structure was visited every two to four days throughout the year. The quality of tracking medium to detect tracks at each visit was classified as good, fair, poor or "inoperable," the latter generally caused by accumulation of flooding, ice or snow drifts on the track pads.

We identified tracks to species, estimated the number of individuals, their direction of travel and whether they moved through the crossing structure. Species consisted of wolves (*Canis lupus)*, coyotes (*C. latrans)*, cougars (*Puma concolor)*, lynx (*Lynx canadensis)*, black bears (*Ursus americanus)*, grizzly bears (*U. arctos)*, wolverine (*Gulo gulo)*, deer (*Odocoileus* sp*.)*, elk (*Cervus elaphus)*, bighorn sheep (*Ovis canadensis)*, and moose (*Alces alces)*. We also recorded the amount of human activity (travel on horses, bikes or by foot) at each crossing structure check. After collecting species movement data from the track pads they were raked smooth for the next visit.

Since 2005, motion-sensitive digital cameras (Reconyx Inc., Holmen, Wisconsin) have been used to supplement track pads to monitor species use of the WC (Ford et al. 2009). WC cameras were located within or adjacent to (<10 m away) wildlife underpasses and on top of and at the center of wildlife overpasses. All cameras used in this study provided metadata on date, time and ambient temperature during each crossing/passage event (Barrueto et al. 2014). Once set up, all cameras were running 24 hrs/day, year round, but with occasional periods of camera malfunctioning and/or premature battery failure. Cameras were checked for operation (battery life) and CF/SD cards were switched out every 2-3 weeks year-round. Photos were classified using Microsoft Access software and our project's customized image classification form that inputs wildlife crossing data directly into our Microsoft™Access database (Barrueto et al. in press). The image classification allows us to quantify (1) baseline data on species passage/avoidance at the wildlife crossing structures and (2) species behaviour and response to crossing structures types of same design on new and old sections of highway. All camera data collected at crossing structures were stored in Microsoft™ Access and Excel databases on the Parks Canada server in Banff National Park, Alberta.

During the project's fourth year we spent a significant amount of time reconciling data in our long-term database obtained from two detection methods (track pads, cameras) during a period where they overlapped in data collection at the crossing structures between 2005 and 2010. During this overlap period, we collected movement data at the crossing structures from track pads, but also from cameras at a subset of those crossing structures. From 2005 to 2010, we incrementally began to use more cameras at the crossing structures. By November 2010, all crossing structures had cameras in place; therefore we stopped collecting data using track pads. As a result of this overlap, and before we could perform any multivariate analysis of the crossing data planned for this report, we needed to reconcile data obtained from the two field methods. This consisted of determining which method gave the most accurate number of crossings for a given species, at a given crossing structure, and at a given crossing check, during this 5-year period of overlapping (duplicate) data.

The work led to significantly more time investment than anticipated, some discoveries of missing data (not photo-classified) and also duplicate data from the same method that were in the database. We worked with Parks Canada's Tao Gui and Ben Dorsey to resolve this problem; we were also assisted by Adam Ford (project research associate who managed database from 2007-2009).

From this comprehensive and time-consuming effort, which included numerous checks and rechecks of the data in our database, we discovered that the "Grand Total" of wildlife crossings by large mammals was significantly lower than the estimated 200,000+ crossings we had reported up until that time - approximately 80,000 fewer crossings. We revisited annual reports and their general summaries from 2008 forward. We checked, double-checked, and triple-checked tables and previous Microsoft™ Access database queries to try and discover where this discrepancy came from.

We found the inflated number of total crossings was attributable to over-calculated white-tailed deer counts during the preparation of the 2009 Final Report to Parks Canada (Clevenger et al. 2009). In preparing the query, the white-tailed deer counts were erroneously multiplied by 3. The crossing amounts for all the other mammal species, however, were not affected in any way.

We report on data collected from 49 cameras being used to monitor 39 wildlife crossing structures (see Chapter I, Figure 1). For this report we divided our data set into two periods and summarized movement of wildlife at the Banff crossing structures by TCH construction phase: (1) 2009-2014: the period of the Contribution Agreement, and (2) 1996-2014: the entire 17-year period that we have monitored wildlife use of the crossing structures.

Results

Summary Data, 2009 – 2013

The summary data presented in the following three paragraphs always consists of number of through-crossings by the animal species, and does not include attempted but aborted crossings. The number of humans is calculated differently: We present the number of people detected by the crossing structure cameras (which were either situated in or at the entrance of crossing structures) regardless of whether they passed through crossing structures.

Phases 1 and 2

From April 1, 2009 to February 28, 2014, a total of 51,246 passages of coyote sized and larger mammals were detected crossing the nine wildlife underpasses of Phase 1 and 2 (Table 1.a.). In addition to that, 9717 humans were also detected either crossing through the structures, or approaching the entry close enough to be detected by the cameras. Deer were the most frequently detected species, accounting for 54.2% of all detected animal crossings (n=27,758). Elk were the second most frequent species, making up 38.0% of all crossings (n=19,466). The number of bighorn sheep detected was much lower, they were detected only 526 times (1.0%). The number of moose was lower still, with 36 detected passages (0.1%).

Of the large carnivores, wolves used the structures 1132 times (2.2%), coyotes 1367 times (2.7%), and cougars 259 times (0.5%). Black bears (n=402) were more frequent than grizzly bears (n=289), with 0.8% vs. 0.6% of all large mammal crossings. Carnivores made up 6.8% of all detected large mammal crossings. Human use was, as in previous years, concentrated at Buffalo underpass (n=6339), but Edith, Powerhouse and Vermilion underpasses also saw substantial human use. No lynx or wolverines were detected at Phase 1 and 2 crossing structures.

Table 1.a: Data summary from wildlife crossing structure monitoring, Phase 1 and 2, April 1, 2009 to March 31, 2014

	GRIZZLY BEAR	BLACK BEAR	BEAR SPP	WOLF	COUGAR	COYOTE	MOOSE	ELK	DEER	BIGHORN SHEEP	WOLVERINE	LYNX	HUMAN	**Total wildlife**
EAST	4	51	2	40	41	41	6	1708	6342	0	0	0	22	**8235**
CARROT	2	35	0	1	27	29	0	243	770	0	0	0	97	**1107**
MC	5	36	0	102	45	48	0	476	4240	0	0	0	43	**4952**
DH	18	96	3	398	53	33	0	2650	5936	0	0	0	122	**9187**
PH	4	82	0	16	33	211	0	1726	859	0	0	0	618	**2931**
BUFF	4	6	0	0	1	529	0	8369	2201	0	0	0	6339	**11110**
V	16	62	1	52	19	127	0	1739	2315	510	0	0	656	**4841**
EDITH	29	20	0	174	13	309	12	1634	3592	16	0	0	1737	**5799**
HEALY	207	14	5	349	27	40	18	921	1503	0	0	0	83	**3084**
TOTAL	**289**	**402**	**11**	**1132**	**259**	**1367**	**36**	**19466**	**27758**	**526**	**0**	**0**	**9717**	**51246**

Phase 3A

We documented 28,559 large mammal crossings and 1736 humans at the 13 crossing structures (two overpasses, 11 underpasses) of Phase 3A (Table 1.b.). By far the most frequently detected large mammal were deer (n=25,146) with 88.0% of all passages. Second to deer, wolves accounted for 3.9% of all crossings (n=1103). Elk were not well represented at Phase 3A structures; they used the crossings only 699 times (2.4%). Moose used all but three structures (Bourgeau, Redearth underpass, Redearth Creek) at least once, with a total of 237 crossings (0.8%). However, moose use was heavily concentrated at the two overpasses. Bighorn sheep were detected only three times.

Large carnivore use combined accounted for 24.8% of all large mammal crossings. Grizzly bears were detected 526 times (1.8%), coyotes 511 times (1.8%), black bears 184 times (0.6%), and the number of cougar crossings was 114. On the rare species' side, seven wolverine and 13 lynx crossings occurred at Phase 3A structures. The wolverines used six different structures, whereas lynx mostly used the two overpasses (n=10), one creek-bridge (Redearth Creek), one large metal culvert (Wolverine underpass), and one small concrete box culvert (Johnston).

Phase 3B

During the project duration, we monitored 18 wildlife crossing structures on Phase 3B. Due to delays in highway construction, however, monitoring at some of the crossing structures of Phase 3B did not start until late fall 2010 (Lake Louise overpass, Temple overpass) or late fall 2011 (all other structures). Also, monitoring of the Piran underpass stopped in April 2011 due to reconstruction and enlargement of this underpass during continuation of Phase 3B construction west of Lake Louise.

In total, we detected 8225 large mammal crossings at Phase 3B, and 3181 instances of human use (Table 1.c.). Most human use of the structures was mostly related to construction and landscaping activity at the new structures. Again, deer were the most frequently detected species using the crossing structures (n=6066, 73.8% of all wildlife crossings). Elk were second-most detected 853 times (10.4%). The "secondary" underpasses of Island and Storm accounted for more than two thirds of all moose crossings (n=246, 3.0%).

Among carnivores (12.9% of all wildlife crossings), grizzly bears used the structures 292 times, wolves 256 times, black bears 61 times, and coyotes 432 times. In 2013, the first cougars were detected using Phase 3B structures: twice at Castle overpass, and once at Moraine creek. One wolverine used Moraine creek underpass, and three times lynx were detected, twice at Moraine Creek and once on Castle overpass.

Table 1.b. Data summary from wildlife crossing structure monitoring, Phase 3A, April 1, 2009 to March 31, 2014

	GRIZZLY BEAR	BLACK BEAR	BEAR SPP	WOLF	COUGAR	COYOTE	MOOSE	ELK	DEER	BIGHORN SHEEP	WOL-VERINE	LYNX	HUMAN	**Total wildlife**
WOP	133	21	1	160	81	99	49	20	7328	0	1	5	760	**7899**
WUP	2	4	0	17	0	14	6	30	522	0	0	1	226	**596**
BOURG	13	19	3	54	0	35	0	0	59	0	0	0	21	**183**
WCR	50	8	0	93	15	13	4	63	1360	0	1	0	73	**1606**
MASS	18	7	0	96	0	35	12	169	1444	0	0	0	38	**1781**
SAW	41	2	0	35	0	21	28	22	263	0	0	0	17	**412**
PILOT	15	17	3	27	0	11	4	8	332	0	1	0	30	**417**
REUP	40	11	0	51	1	50	0	26	68	0	0	0	14	**247**
REOP	106	33	2	196	13	49	102	119	10440	0	0	5	138	**11065**
RECR	18	16	1	100	1	24	0	9	538	3	1	1	216	**711**
COPPER	14	8	1	44	3	31	1	14	740	0	0	0	24	**856**
JOHN	31	32	2	136	0	86	6	5	150	0	1	1	12	**450**
CASTLE	45	6	6	94	0	43	25	214	1902	0	2	0	167	**2336**
TOTAL	**526**	**184**	**19**	**1103**	**114**	**511**	**237**	**699**	**25146**	**3**	**7**	**13**	**1736**	**28559**

Table 1.c. Data summary from wildlife crossing structure monitoring, Phase 3B, April 1, 2009 to March 31, 2014.

	GRIZZLY BEAR	BLACK BEAR	BEAR SPP	WOLF	COUGAR	COYOTE	MOOSE	ELK	DEER	BIGHORN SHEEP	WOL-VERINE	LYNX	HUMAN	**Total wildlife**
COP	49	1	0	47	2	34	8	74	939	0	0	1	181	**1155**
BOOM	3	2	1	4	0	7	0	10	22	0	0	0	47	**49**
STORM	16	3	0	13	0	18	31	119	503	0	0	0	119	**703**
POP	12	2	2	4	0	7	1	33	694	0	0	0	130	**755**
QUADRA	1	1	0	0	0	7	1	2	9	0	0	0	18	**21**
TAYLOR	0	0	0	0	0	2	0	0	0	0	0	0	18	**2**
MITELLA	0	0	0	0	0	0	3	3	7	0	0	0	26	**13**
BAKER	1	2	0	10	0	2	4	0	42	0	0	0	16	**61**
FAY	0	0	0	0	0	0	2	1	18	0	0	0	31	**21**
BABEL	0	0	0	1	0	1	2	0	4	0	0	0	31	**8**
CONSOLATION	1	3	0	6	0	4	1	0	124	0	0	0	24	**139**
MORAINE	20	6	3	52	1	30	11	3	164	0	1	2	192	**292**
TOP	35	3	0	16	0	19	25	12	723	0	0	0	361	**833**
TUP	41	0	0	14	0	78	12	10	165	0	0	0	110	**320**
ISLAND	40	5	4	38	0	68	140	165	1327	0	0	0	222	**1787**
BOW	49	10	2	32	0	39	0	323	804	0	0	0	1430	**1259**
LLOP	11	22	1	5	0	65	5	95	491	0	0	0	194	**695**
PIRAN	13	1	0	14	0	51	0	3	30	0	0	0	31	**112**
TOTAL	**292**	**61**	**13**	**256**	**3**	**432**	**246**	**853**	**6066**	**0**	**1**	**3**	**3181**	**8225**
GRAND TOTAL	**1107**	**647**	**43**	**2491**	**376**	**2310**	**519**	**21018**	**58970**	**529**	**8**	**16**	**14634**	**88030**

All Wildlife Crossing Structures

Since April 1, 2009, a total of 88,030 large mammal crossings and 14,634 humans were detected at the Phase 1, 2, 3A and 3B crossing structures. Deer accounted for 67.0% of all wildlife use (n=58,970), while elk accounted for 23.9% (n=21,018). The share of large carnivore use was 7.9%. Wolves ranked first, coyotes second, and grizzly bears third (Table 1.c.).

Summary Data, 1996-2013

Phases 1 and 2

Long-term monitoring began in November 1996 and was focused the first year solely on Phase 1 and 2 wildlife underpasses. Since November 1996, there have been a total of 107,664 detections of 10 species of large mammals, and 131,460 including humans at these underpasses (Table 2.a.). Elk were detected 43.9 percent of all recorded passes (n=47,309) followed by deer (n=42,493; 39.5%) and bighorn sheep (n= 4958). Among large carnivores, coyotes were detected using the crossings 5517 times, wolves 4354 times, cougars 1229 times, black bears 1190 times, and grizzly bears 520 times. Human use continues to be high on this phase and ranks third overall with 23,796 passes recorded since 1996. Carnivores accounted for 11.9% of the detected animal crossings.

Phase 3A

Monitoring of Phase 3A wildlife crossing structures began soon after their completion and installation of the wildlife fence in November 1997. Since then there have been 39,582 passages by wildlife and 2486 by humans detected at 13 Phase 3A-crossing structures (Table 2.b.). Deer were most frequently detected using the crossings structures (n=27,208, 68.7% of all large mammal crossings). Second to deer, elk were detected using the crossing structures at only 13.2% of all large mammal crossings (n= 5223). Among carnivores, coyotes used the structures 2918 times, wolves 2260 times, grizzly bears 800 times, cougars 395 times and black bears 414 times. Human use continues to be low, a fraction of the use on Phases 1 and 2 (n= 2486 crossings vs. 23,796 crossings). Carnivores accounted for 17.3% of the detected animal crossings.

Table 2.a. Data Summary from Wildlife Crossing Structure Monitoring, Phase 1 and 2, November 7, 1996 to March 31, 2014.

	Type	Grizzly Bear	Black Bear	Bear Spp	Wolf	Cougar	Coyote	Moose	Elk	Deer	Bighorn sheep	Wolverine	Lynx	Human	Total	**Total wildlife**
East	Open span	9	80	2	188	166	377	7	3502	8355	9	0	0	54	12749	**12695**
Carrot	Creek bridge	4	89	0	152	114	237	0	798	977	9	0	0	254	2634	**2380**
MC	Culvert-lg	7	168	0	300	116	248	0	1422	5157	18	0	0	95	7531	**7436**
DH	Open span	25	326	6	1417	237	340	0	6323	6077	45	0	0	200	14996	**14796**
PH	Open span	13	180	5	278	125	473	2	4124	1763	30	0	0	2214	9207	**6993**
Buff	Open span	8	11	0	254	46	1104	0	14662	2876	53	0	0	9880	28894	**19014**
V	Open span	57	72	3	256	129	845	1	5834	2165	1257	0	0	1784	12403	**10619**
Edith	Open span	39	47	0	350	141	602	12	3675	4446	211	0	1	6629	16153	**9524**
*5Mile	Open span	26	29	2	222	51	665	10	3553	7960	3301	0	1	2505	18325	**15820**
Healy	Open-span	332	188	6	937	104	626	36	3416	2717	25	0	0	181	8568	**8387**
TOTAL PHASE 1 & 2		**520**	**1190**	**24**	**4354**	**1229**	**5517**	**68**	**47309**	**42493**	**4958**	**0**	**2**	**23796**	**131460**	**107664**

* Not monitored after fiscal year 2009-10.

Table 2.b. Data summary from wildlife crossing structure monitoring, Phase 3A, November 7, 1996 to March 31, 2014

	Type	Grizzly Bear	Black Bear	Bear Spp	Wolf	Cougar	Coyote	Moose	Elk	Deer	Bighorn Sheep	Wolv-erine	Lynx	Human	Total	**Total wildlife**
WOP	Overpass	246	47	4	364	91	211	74	298	7004	0	1	5	851	9196	**8345**
WUP	Culvert-lg	2	15	0	67	42	110	4	182	652	0	0	1	135	1210	**1075**
BOURG	Culvert-med	13	57	4	37	21	142	0	7	102	0	0	0	25	408	**383**
WCR	Crk bridge	45	19	1	114	72	255	5	340	948	2	1	0	123	1925	**1802**
MASS	Culvert-lg	18	14	0	129	18	264	10	422	1545	0	0	0	66	2486	**2420**
SAW	Box	37	8	0	66	3	125	25	132	254	0	0	0	46	696	**650**
PILOT	Box	18	49	5	95	15	157	4	164	331	0	1	0	63	902	**839**
REUP	Box	44	37	0	137	25	263	0	234	158	0	0	0	64	962	**898**
REOP	Overpass	267	51	9	520	15	222	112	1128	10906	0	0	4	231	13465	**13234**
RECR	Creek bridge	22	23	1	187	33	164	0	240	1039	29	2	1	474	2215	**1741**
COPPER	Culvert-lg	15	18	1	116	26	326	1	341	1986	8	1	0	43	2882	**2839**
JOHN	Box	30	48	2	192	24	393	6	43	176	0	1	1	28	944	**916**
CASTLE	Culvert-lg	43	28	5	236	10	286	27	1692	2107	2	2	2	337	4777	**4440**
TOTAL PHASE 3A		**800**	**414**	**32**	**2260**	**395**	**2918**	**268**	**5223**	**27208**	**41**	**9**	**14**	**2486**	**42068**	**39582**

Phase 3B

A total of 18 Phase 3B wildlife crossing structures have been monitored since 2007, including the Piran culvert, which was being replaced by a large span (primary) underpass in 2013. Since 2007, we have documented 4908 passages by wildlife and 1934 by humans at these crossings structures (Table 2.c.). Human use was mostly due to construction workers and landscapers. Similar to Phase 1, 2, and 3A, deer were most frequently detected using the crossings among the large mammals (n=3156, 64.3% of all large mammal crossings). Again, similar to Phase 1, 2, and 3A, elk were second to deer (n=719, 14.6% of all large mammal crossings). Among the carnivores, coyotes used the structures 314 times, grizzly bears 229 times, wolves 212 times, and black bears 59 times. Cougars have been detected three times, lynx twice, and wolverines once, using the Phase 3B crossings.

All Wildlife Crossing Structures

A total of 152,154 crossing detections of large mammals, and 28,216 of humans have been recorded at the Phase 1, 2, 3A and 3B crossings structures during the 17+ years of monitoring (Table 2.c.). Consistent with the latest summary of wildlife crossing use (Clevenger et al. 2009), deer made up 47.9% of all animal crossings detected, while elk were only detected 35 percent of the time (Table 2.c.). The proportion of large carnivore detections was 13.5%, coyotes ranking first, wolves second, black bears third, followed by cougars and grizzly bears (Table 2.c.).

Table 2.c. Data summary from wildlife crossing structure monitoring, Phase 3B, November 7, 1996 to March 31, 2014.
Phase 3B

	Type	Grizzly Bear	Black Bear	Bear Spp	Wolf	Cougar	Coyote	Moose	Elk	Deer	Bighorn sheep	Wolv-erine	Lynx	Human	Total	**Total wildlife**
COP**	Overpass	48	1	1	44	2	24	7	74	498	0	0	1	113	813	**700**
BOOM**	Culvert-lg	3	2	1	4	0	8	0	10	11	0	0	0	24	63	**39**
STORM**	Open span-lg	13	3	0	10	0	17	26	97	250	0	0	0	93	509	**416**
POP**	Overpass	12	2	2	4	0	7	1	33	356	0	0	0	94	511	**417**
QUADRA**	Culvert-lg	1	1	0	0	0	7	1	2	5	0	0	0	9	26	**17**
TAYLOR**	Culvert-med	0	0	0	0	0	1	0	0	0	0	0	0	10	11	**1**
MITELLA**	Box	0	0	0	0	0	0	2	3	4	0	0	0	20	29	**9**
BAKER**	Culvert-lg	1	2	0	10	0	2	4	0	17	0	0	0	8	44	**36**
FAY**	Culvert-lg	0	0	0	0	0	0	2	1	8	0	0	0	10	21	**11**
BABEL**	Culvert-med	0	0	0	1	0	1	2	0	2	0	0	0	1	7	**6**
CONSOL**	Culvert-lg	1	3	0	6	0	4	1	0	63	0	0	0	20	98	**78**
MORAINE	Creek bridge	16	4	2	45	1	21	10	3	85	0	1	1	113	302	**189**
TOP	Overpass	30	3	0	14	0	18	25	12	363	0	0	0	224	689	**465**
TUP	Culvert-lg	27	0	0	10	0	65	12	8	88	0	0	0	56	266	**210**
ISLAND	Open span-lg	31	5	3	40	0	32	102	132	508	0	0	0	164	1017	**853**
BOW	Open span	30	9	2	14	0	55	0	232	635	0	0	0	857	1834	**977**
LLOP	Overpass	11	20	2	4	0	44	3	81	237	0	0	0	84	486	**402**
PIRAN*	Culvert-lg	5	4	2	6	0	8	0	31	26	0	0	0	34	116	**82**
TOTAL PHASE 3B		**229**	**59**	**15**	**212**	**3**	**314**	**198**	**719**	**3156**	**0**	**1**	**2**	**1934**	**6842**	**4908**
GRAND TOTAL COUNTS		**1549**	**1663**	**71**	**6826**	**1627**	**8749**	**534**	**53251**	**72857**	**4999**	**10**	**18**	**28216**	**180370**	**152154**

2. Species Interactions at Wildlife Crossing Structures

The eight large mammal species subject to this analysis are interconnected in an intricate web of predator-prey and competitor relationships (Hebblewhite et al. 2005, Kortello et al. 2007, Ford and Clevenger 2010). Some of these interactions may have influenced their use of and behaviour at wildlife crossing structures (WC) and therefore needs to be examined before analysis of the factors that influence species use of WC (Clevenger et al. 2009). This analysis focused on a time-scale of seasons, we were therefore only able to detect general effects of species on each other. For example, we repeatedly observed avoidance of WC by smaller ungulate species (mule deer and white-tailed deer), while elk were using the WC. However, these interactions only lasted minutes and thus were not expected to affect WC use on the time-scale of this analysis. Similarly, while prey species probably avoided WC if a predator was in the area, such an effect would likely only last minutes to days and would not be reflected in this data set.

We considered three broad categories of interactions: Competition, predation, and a combination of the two. Interactions between competitors can either result in differential habitat use, or aggregation in suitable habitats. In both cases, non-use and increased use of certain WC could be explained by appropriate habitat variables. As the habitat along the TCH in our study area was relatively uniform, however, we did not expect strong habitat effects between competitors. Predator-prey interactions between the monitored species were potentially more important. The two main potential effects were general avoidance of certain WC by prey species because of frequent use by predators (negative correlation), and increased use of WC by predator species because of frequent use by prey species (positive correlation). This study was not designed to distinguish whether animals avoided a whole area around a WC, or merely the WC itself.

Previous research was unable to find evidence that WC in this study area acted as prey traps (Little et al. 2002, Ford and Clevenger 2010). The main predators in the study area, wolves, cougar and grizzly bears, all have large territories and range widely and thus occur at relatively low densities. For these reasons we did not expect them to utilize certain WC frequently enough to repel their prey species from using them. An exception might be if a wolf den was close to a WC and the den was routinely used over a number of years. On the other hand, however, predators, especially wolves, actively seek out prey species (Hebblewhite et al. 2002). It is therefore expected that they should be frequenting areas with higher prey densities. Whether these interactions are better explained by habitat variables, or actual prey presence at WC, or whether the temporal scale of these patterns is not congruent with the scale of the analysis, is part of this study. Table 1 gives an overview of the general interaction patterns between the species assembly in our study. Information on interactions in Table 1 were vetted with Parks Canada biologists, Jesse Whittington and Steve Michel.

The third category to be considered was the competitive/predatory relationship between wolves, cougars and grizzly bears. In a study on interactions between wolves and cougars, while wolves may drive away cougars from certain areas, no effect was found in the other direction (Kortello et al. 2007). The avoidance interactions between grizzly bears and wolves in the study area were not expected to be strong on a seasonal scale. Also, while they may opportunistically prey on each other, the rarity of such events was likely too great to be reflected in our data.

Before proceeding with the multivariate WC analysis, we had to determine to what extent species interactions had to be taken into account. To test the above basic assumptions, we calculated Pearson's product moment correlation coefficients for each species pair, using the number of crossings per season (64 seasons), at each of 13 WC of phase 3A (Table 2). No correlation coefficient was higher than 0.65. The strongest correlations were between wolf and grizzly bear, grizzly bear and deer, and wolf and deer. They were positive correlations and thus indicated either shared preferences (wolf – grizzly), predatory intentions (wolf-deer) or, in the case of grizzly-deer, most likely shared preferences of either habitat or WC. While grizzly bears prey on deer, they do not regularly hunt them (Mattson et al. 1991, Hobson et al. 2000). Surprisingly, wolf-elk did not show any correlation. Wolf-moose also had significant correlation, but a small coefficient/effect size. No negative correlations were found, indicating that avoidance behaviour was not likely to be a strong factor in WC use.

We took the results of these exploratory tests as evidence that, while some correlation was apparently present, it was neither strong nor widespread. We concluded that use of multi-response models in the framework of generalized linear or additive mixed modelling was not warranted by the observed interaction directions and effect sizes. Generalized linear and additive mixed models are already complex, and adding more complexity without strong evidence than was necessary was undesirable. For the following analysis of long-term WC data (Chapter III.3.), we decided to include the prey (ungulate) species in the models for wolves as covariates, and add the number of wolves as a covariate in the cougar models, based on the correlation coefficients and previously-mentioned ecological knowledge.

Table 1. Overview of predominant inter-specific interactions between study species. P-P = predator-prey interactions; Comp = competition for resources; na = species generally lacking inter-specific interactions. For some species pairs these interactions may change depending on size, age and sex of individuals, as well as time of year. This is reflected in combinations of interactions in the table.

Cougar	na	-	-	-	-	-	-
Coyote	na	P-P	-	-	-	-	-
Deer spp	P-P	P-P	P-P	-	-	-	-
Elk	P-P	P-P	P-P	na	-	-	-
Grizzly	P-P	na	P-P	P-P	P-P	-	-
Moose	P-P	P-P	na	na	na	P-P	-
Wolf	P-P	Comp/P-P	P-P	P-P	P-P	P-P	P-P
	Black bear	**Cougar**	**Coyote**	**Deer spp**	**Elk**	**Grizzly**	**Moose**

Table 2. Pearson`s correlation product moment correlation coefficient. Data was the number of crossings per season (64 seasons) and wildlife crossing structures (n=13). * For bear species, only spring, summer and fall data were used.

	Species1	Species2	Correlation	t	df	P value	Lower CI	Upper CI
1	wolf	deer	0.406	12.381	778	0.000	0.345	0.463
2	wolf	elk	0.002	0.067	778	0.947	-0.068	0.073
3	wolf	coyote	0.059	1.646	778	0.100	-0.011	0.129
4*	wolf	grizzly	0.572	16.8505	583	0.000	0.515	0.624
5	wolf	moose	0.196	5.568	778	0.000	0.127	0.262
6*	wolf	black bear	0.024	0.5714	583	0.568	-0.058	0.105
7	wolf	cougar	0.012	0.337	778	0.736	-0.058	0.082
8*	grizzly	black bear	0.217	5.368	583	0. 000	0.138	0.293
9*	grizzly	deer	0.634	19.800	583	0.000	0.583	0.680
10*	grizzly	elk	-0.009	-0.214	583	0.831	-0.090	0.072
11*	grizzly	moose	0.245	6.102	583	0.000	0.167	0.320
12*	cougar	grizzly	0.001	0.031	583	0.975	-0.080	0.082
13	cougar	deer	0.093	2.611	778	0.009	0.023	0.162
14	cougar	elk	-0.023	-0.651	778	0.515	-0.093	0.047
15	cougar	coyote	0.074	2.079	778	0.038	0.004	0.144
16	cougar	moose	0.084	2.344	778	0.019	0.014	0.153

3. Analysis of Long-term Data to Identify Spatial and Temporal Effects on Large Mammal Movement Through Wildlife Crossing Structures

Authors: Mirjam Barrueto and Anthony P Clevenger

Introduction

Wildlife crossing structures (WC) and fencing has long been considered one of the more effective means of mitigating road impacts on wildlife populations (Huijser et al. 2007). The first WC were built in North America in the 1960s (Evink 2002) and many more have been constructed since then (National Research Council 2005, Beckmann et al. 2010). Their increased implementation by transportation agencies in the last decade has resulted in growing number of studies of species use, response to crossing designs, and efficacy at reducing barrier effects (Foster and Humphrey 1995, Clevenger and Waltho 2000, Gagnon et al. 2011). However, after nearly 20 years of research, surprisingly little is known regarding whether WC restore movements, reduce mortality, benefit populations and restore genetic connectivity (Corlatti et al. 2009, Sawaya et a. 2013, 2014). Even less is known regarding effective monitoring durations. This gap in knowledge is particularly important in light of the need to perform rigorous evaluations (Lesbarrieres and Fahrig 2012, VanderGrift et al. 2013) in a time of limited agency budgets and cutbacks in research funding.

Banff National Park has the world's longest running program monitoring and evaluating WC for large mammals. For over 17 years WC have been monitored for wildlife use on a consistent year-round basis (Clevenger et al. 2002, 2009, in prep.). The dataset is unique given it spans nearly two decades, contains data from 11 large mammal species, and has been managed by the same researcher since its inception. The dataset has been used to help answer pressing management questions related to species patterns of WC use, species interactions, and anthropogenic effects on wildlife use (Clevenger and Waltho 2000, 2005; Ford and Clevenger 2010, Barrueto et al. 2014). The dataset is uniquely poised to examine questions of species response to WC that short-term datasets are unable to examine (Gagnon et al. 2011).

Despite a growing number of technical reports and published literature on WC use, few have focused on identifying adequate monitoring periods required to identify covariates of WC use. Long-term monitoring has shown that species require time to adapt to new WC before using them on a regular basis (Clevenger et al. 2009, Gagnon et al. 2011). Models have been developed to identify attributes of WC that influence passage of a wide variety of wildlife species (Rodriguez et al. 1996, Cain et al. 2003, Mata et al. 2005, Gagnon et al. 2011); however, key drivers affecting models may change over time. If WC models are dynamic, additional monitoring will be required to capture model variability and better understand the mechanisms that cause changes in species use of WC.

Research results have been used to develop guidelines or best management practices for designing future WC, in situ or in other areas (Huijser et al. 2008, Clevenger and Huijser 2009).

The extent at which research results can be extrapolated to other areas, even in the same transportation corridor, has not been explored. As WC become more prevalent and the monitoring effort and costs increases, it would be beneficial to know whether subsampling is a viable alternative to monitoring a full suite of WC. Recent research using time-series and habitat models may provide a framework for understanding the predictive ability of WC use models (Porzig et al. 2014).

Because there is an inherent tendency for WC to be grouped closely together and connected by fencing there is potential for interspecific interactions to occur at WC that may influence WC selection and usage (Ford and Clevenger 2010). These interspecific interactions may be occurring at WC, however, up until now this has scarcely been addressed. These interactions may result in data that are spatially and temporally auto-correlated. Failure to identify autocorrelation can result in data that lack independence among the values at certain covariates and multivariate normality (Chatfield 1975).

The purpose of this paper was to identify factors affecting movement of large mammals through wildlife WC on the Trans-Canada Highway (TCH) using a long-term data set. Our methodological approach consisted of analyzing the first 16 years of data from Phase 3A for a suite of large mammal species, taking into account species interactions, followed by testing the generality of these findings using data from two separate but adjacent mitigated sections of the TCH, Phase 1 and 2 and Phase 3B.

Methods

Study Area

Banff National Park (hereafter referred to as Banff) is situated approximately 150 km west of Calgary, Alberta, in the Bow River Valley along the Trans-Canada Highway (TCH; see Chapter I, Figure 1). The study area is characterized by mountainous landscapes with a continental climate consisting of long winters and short summers (Holland and Cohen 1983). Vegetation characteristic of the montane and subalpine ecoregions consists of open forests dominated by lodgepole pine *Pinus contorta*, Douglas-fir *Pseudotsuga menziesii*, white spruce *Picea glauca*, Englemann spruce *Picea englemannii*, trembling aspen *Populus tremuloides*, and natural grasslands.

The TCH is the major transportation corridor through Banff currently carrying an estimated annual average daily traffic volume of over 17,000 vehicles per day, with peaks of more than 30,000 vehicles per day during summer (Highway Service Center, Parks Canada, unpublished data). Traffic volumes in Banff are highest at the east gate and gradually decline westward through Banff and Yoho National Parks.

In the 1970s, safety issues compelled planners to upgrade the TCH within Banff from two to four lanes, beginning from the eastern boundary and working west (Ford et al. 2010). Large animals were excluded from the road with a 2.4-m-high fence erected on both sides of the highway, and underpasses were built to allow wildlife safe passage across the road. The first 27 km of highway twinning (Phases 1 and 2) included 10 wildlife underpasses and was completed in 1988. Fencing and WC on the next 20 km section (Phase 3A) was completed in late 1997 with 11 additional wildlife underpasses and two 50-m wide wildlife overpasses (Clevenger and Waltho 2000, 2005). The Castle wildlife underpass was constructed independent of Phase 3A and Phase 3B in 1990-91. For the purpose of this report we include Castle as part of Phase 3A. The final 35 km of four-lane highway to the western park boundary (Phase 3B) includes 21 WC, including four, 60-m wide wildlife overpasses and was completed in late 2013.

Wildlife Crossing Structures

Our analyses involved 39 WC along the TCH, including 17 recently constructed within Phase 3B (Table 1). The WC constituted five different structural designs: 1) open span bridge underpass, 2) creek bridge underpass, 3) elliptical, metal culvert underpass 4) prefabricated concrete box underpass, and 5) wildlife overpass. The age of WC ranged from the oldest built on Phase 1 in the early 1980s to the most recently constructed on Phase 3B between 2008 to 2013.

Table 1. List of wildlife crossing structures (WC) monitored consistently along Trans-Canada Highway in Banff National Park, Alberta, 1996-2014.

	WC name	**Type**	**Dimensions (m; W x Ht x L)**	**Phase**
1	East Gate	open span	9.8 x 2.8 x 63.0	1
2	Carrot Creek	creek bridge	13.4 x 2.5 x 83.2	1
3	Morison Coulee	culvert large	4.2 x 3.5 x 96.1	1
4	Duthil	open span	9.8 x 2.9 x 40.	1
5	Powerhouse	open span	9.5 x 2.9 x 39.7	1
6	Buffalo	open span	10.0 x 3.0 x 27.1	2
7	Vermilion	open span	9.8 x 2.7 x 27.2	2
8	Edith	open span	10.3 x 2.8 x 25.6	2
9	Healy	open span	9.0 x 2.9 x 40.1	2
10	**Wolverine OP**	overpass	50.0 x na x 72.0	3A
11	Wolverine UP	culvert large	7.3 x 3.4 x 62.5	3A
12	Borgeau	culvert medium	2.0 x 1.8 x 170.0	3A
13	Wolverine Creek	creek bridge	11.5 x 2.5 x 83.0	3A
14	Massive	culvert large	7.2 x 3.6 x 51.0	3A
15	Sawback	box	3.0 x 2.4 x 66.0	3A
16	Pilot	box	3.0 x 2.4 x 66.0	3A
17	RedEarth UP	box	3.0 x 2.4 x 78.0	3A
18	**RedEarth OP**	overpass	50.0 x na x 72.0	3A
19	RedEarth Creek	creek bridge	11.4 x 2.2 x 56.5	3A
20	Copper	culvert large	7.2 x 3.9 x 57.4	3A
21	Johnston	box	3.0 x 2.4 x 58.0	3A
22	Castle	culvert large	7.3 x 3.5 x 56.5	- - [1]
23	**Castle OP**	overpass	56.3 x na x 105.0	3B
24	Boom	culvert large	7.1 x 3.5 x 44.0	3B
25	Storm	open span large	19.0 x 5.0 x 46.0	3B
26	**Panorama OP**	overpass	55.1 x na x 117.0	3B
27	Quadra	culvert large	7.1 x 3.3 x 55.0	3B
28	Taylor	culvert small	2.1 x 1.5 x 38.0	3B
29	Mitella	box	3.6 x 2.1 x 57.0	3B
30	Baker	culvert large	7.8 x 2.9 x 59.0	3B
31	Fay	culvert large	7.9 x 3.1 x 57.0	3B
32	Babel	culvert medium	5.8 x 2.2 x 57.0	3B
33	Consolation	culvert large	8.0 x 3.3 x 51.0	3B
34	Moraine	creek bridge	23.0 x 1.6 x 42.0	3B
35	**Temple OP**	overpass	56.0 x na x 123.0	3B
36	Temple UP	culvert large	7.1 x 4.1 x 60.0	3B
37	Island	open span large	24.0 x 4.0 x 47.0	3B
38	Bow River	open span large	85.0 x 6.2 x 39.0	3B
39	**Lake Louise OP**	overpass	58.0 x na x 93.0	3B
	Piran[2]	*culvert large*		3B
	Beehive[2]	*open span large*		3B
	Minewakun[2]	*culvert medium*		3B
	Bath[2]	*creek bridge*		3B

	Divide[2]	*open span large*	3B

[1] Constructed independent of phases in 1990-91. For the purpose of this report it is included in Phase 3A.

[2] Piran was temporarily installed (2007) then removed (2008) and Beehive was built in the same location. Beehive, Minewakun, Bath, Divide were completed in November 2013 and not monitored due to late construction completion.

Data Collection

Systematic year-round monitoring of WC began in November 1996 (Clevenger et al. 2002). Monitoring consisted of checking the WC and recording animal movement across raked track pads (Bider 1968). Track pads spanned the width of the wildlife underpasses, were generally ≈2 m wide, and were set perpendicular to the direction of animal movement. At wildlife overpasses a single, 3-m-wide track pad was set across the center and motion-sensitive cameras were used to supplement track pad data. Tracking material consisted of a dry, loamy mixture of sand, silt and clay, 1–4 cm deep. Each WC was visited every two to four days throughout the year. Observers identified tracks to species, estimated the number of individuals, their direction of travel (northbound or southbound across the TCH) and whether they moved through the WC.

Since 2005, motion-sensitive digital cameras (Reconyx Inc., Holmen, Wisconsin) have been used to supplement track pads to monitor species use of the WC (Ford et al. 2009). WC cameras were located within or adjacent to (10-15 m away) wildlife underpasses and on top of and at the center of wildlife overpasses. All cameras used in this study provided metadata on date, time and ambient temperature during each crossing/passage event (Barrueto et al. 2014). Once set up, all cameras were running 24 hrs/day, year round, but with occasional periods of camera malfunctioning and/or premature battery failure. Cameras were checked for operation (battery life) and CF/SD cards were switched out every 2-3 weeks year-round. Camera data collected at WC were stored in Microsoft™ Access and Excel databases on the Parks Canada server in Banff National Park, Alberta (Barrueto et al. in press).

For this analysis we defined an *event* as a successful passage through a WC by an individual or groups of individuals of one species. An event had to be recorded by cameras greater than or equal to two minutes apart from other events, to take into account large groups or lingering individuals. We determined camera-sampling effort at WC by calculating the number of days that cameras were operational (camera trap-days).

We attempted to identify photographs at WC to species level. With the exception of bison *Bison bison* and caribou *Rangifer tarandus*, Banff retains the full complement of native large mammal species: Wolves *Canis lupus*, coyotes *C. latrans*, cougars *Puma concolor*, lynx *Lynx* *canadensis*, black bears *U. americanus*, grizzly bears *U. arctos*, wolverine (*Gulo gulo)*, mule deer *Odocoileus hemionus*, white-tailed deer *O. virginianus*, elk, and moose *Alces alces*. Because of their similarity in habitat use and life-history, and occasional difficulties in distinguishing these two species from some of the low-quality nighttime photos, we pooled the two *Odocoileus* species. (hereafter referred to as "deer spp."). The analysis was conducted at a species level, pooling data from both sexes and all age classes.

Explanatory Variables

We identified a total of 37 field and geographic information system (GIS)-based variables that have been shown to influence passage by WC in previous research (Ng et al. 2004, Clevenger and Waltho 2005, Gagnon et al. 2011). Variables broadly encompassed three types: structural, environmental and human-related (Table 2). Five covariates used in the models were used to test for an effect of WC, sampling effort, season and time. Of the 31 covariates, 23 were eventually used in model development.

Table 2: Description of data set including covariates used in analysis of long-term data to identify factors affecting movement of large mammals through wildlife crossing structures (WC). Covariates in red were not included in models.

				Comments
Multi-response	Species			8 species (a *Number* for each species). May be **correlated (→ estimate covariance)**, need to allow different responses to most covariates
Response	Number		Count	Number of animals counted per sampling period. Poisson or NB distributed. One number for each species
	Covariates		**Type**	**Definition/Comments**
	Effort	Offset	Continuous	Number of sampling days per sampling period
	WC type	**Random effect**	Factor	(=WC). 13 levels
	Season	Fixed effect	Factor	4 levels (winter, spring, summer, fall). Black bears in winter = 0
	Year	Fixed effect	Continuous	May be **nonlinear**
	SeasID	Fixed effect	Continuous	= Time/sampling period. 64 sampling periods (1997-2014). Used for testing **temporal correlation**

	Structural			
	Openness	Fixed effect	Continuous	Used log(openness)[a]. Interaction with seasID (=time)?
	Length	Fixed effect	Continuous	May not be linear effect. BOURG changed to 100 m
	Noise	Fixed effect	Continuous	Correlated with Distance to water
	Bridge	Fixed effect	Factor	=WC on creek or river
	Config	Fixed effect	Factor	Some correlation with length, noise, Distance to water
	WC Type		Factor	Overpass, underpass
	WC Width		Continuous	Correlated with openness
	WC Height		Continuous	Correlated with openness
	Environmental			
	Distance to Forest	Fixed effect	Continuous	Correlated with openness
	Distance to water	Fixed effect	Continuous	Correlated with noise – one or the other
	Distance to CPR	Fixed effect	Continuous	Distance to CP Railway mainline
	Distance to next WC		Continuous	Correlated with openness
	Distance to town		Continuous	Correlated with openness
	Distance to road		Continuous	Distance to nearest paved road
	Buff1	Fixed effect	Continuous	# of WC within 1-km buffer
	Buff2.5		Continuous	Correlated with openness
	Buff5	Fixed effect	Continuous	# of WC within 5-km buffer. Correlated with “km” -> some sort of proxy for spatial location
	RSF.100m	Fixed effect	Continuous	Mean RSF value with 100-m radius for wolf and grizzly bear only. Grizzly: used seasonal maximum value.
	RSF.1km	Fixed effect	Continuous	Mean RSF value with 1-km radius for wolf and grizzly bear only. Grizzly: used seasonal maximum value.
	100m%forest	Fixed effect	Continuous	Correlated to 1-km values
	100m % shrub	Fixed effect	Continuous	Correlated to 1-km values
	100m %grass	Fixed effect	Continuous	Correlated to 1-km values
	100m %bad	Fixed effect	Continuous	Correlated to 1-km values
	1km%forest	Fixed effect	Continuous	% forest cover in 1-km radius
	1km%shrub	Fixed effect	Continuous	% shrub cover in 1-km radius
	1km%grass	Fixed effect	Continuous	% herb cover in 1-km radius
	1km.%bad	Fixed effect	Continuous	% unsuitable habitat (rock, open water) within 1 km. Correlated to 1

				km % forest cover
	Elevation	Fixed effect	Continuous	
	Rad.100m	Fixed effect	Continuous	Mean solar radiation value within 100-m radius. An outlier, plus the area is very small
	Rad.1km	Fixed effect	Continuous	Solar radiation – relative measure. Proxy for snow cover. In kwh.
	Human-related			
	Human use	Fixed effect	Continuous	Number of humans in period
	Other			
	Coordinates	Correlation structure	Continuous	Test for X,Y Spatial correlation

[a] Openness (= width x length/height) .

Structural variables included WC dimensions: width, height, length (including central median), openness = width x height/length (Reed and Ward, 1985) and type (overpass or underpass). The noise-level data were collected at 38 WC in summer 2012. Sound meters were placed outside either entrance and in the center of WC, resulting in 72 unique WC-side locations sampled. The number of data points collected at each WC ranged from 226 to 918 and a total of 16,270-decibel values were logged at 5-min intervals. The covariate bridge characterized whether WC spanned creeks or rivers. WC type was a factor also: underpass or overpass. Configuration was described as divided (separated structures with central median) or undivided (one structure with no central median).

Environmental covariates included distance to: nearest forest cover, nearest water (drainage), Canadian Pacific Railway (CPR) mainline, nearest WC, nearest townsite, and the nearest road (2-lane paved). Buffers of 1 km, 2.5 km and 5.0 km were created to determine the density of WC within each buffer. Wolf and grizzly bear resource selection function (RSF) maps were used to assess the importance of habitat quality on the two species use of WC (J Whittington, Banff Field Unit, unpublished data). Mean RSF values were calculated in 100 m and 1 km buffers around each WC. For grizzly bears we used the seasonal maximum value. Vegetation attributes were measured as percent forest, shrub, grass/open and unsuitable habitat within 100 m and 1 km buffers at each WC. Solar radiation was measured as a proxy for snow cover, as it takes into account shading, but also is partly associated with elevation. We measured mean solar radiation values in buffers of 100 m and 1 km. Covariate human use was quantified at WC by counts of people on foot, bike, horseback, but not including people servicing the cameras, as this was the same for all cameras. Because of excessive spread of human use numbers, we square-root transformed this covariate to achieve a more even distribution. WC configuration characterized whether lanes of traffic were bundled or separated.

Our study area exhibits distinct seasonal patterns in climate and species biology. An appropriate scale for this analysis was to count crossings by (astrological) season: Spring (Mar-May), summer (Jun-Aug), fall (Sep-Nov), and winter (Dec-Feb). A finer temporal scale may have been possible for some species, but would have resulted in many more seasons with zero crossings (zero inflation). Animal use of WC is relatively consistent over time; however, some of the least used WC may go without crossings by some species for several months.

All species were active throughout the year except for grizzly and black bears. While there were few observations of WC use by grizzly bears during winter, virtually all observations were of large adult males. To remove potential bias due to individual behaviour, and because of the low sample size, we only analyzed spring, summer and fall seasons for both bear species.

We tested all covariates for collinearity. As we were more interested in inference on individual parameters, we only included minimally correlated covariates in all models. We used variance inflation factors (VIF), with a conservative cut-off of 2 (Zuur et al. 2009) to determine the covariates to be used in the analysis. The caveat here, as in all studies with correlated covariates, was that an effect attributed to a certain covariate may not be only caused by that covariate, but also to some part by a correlated covariate. Checking the covariates for outliers showed that the covariate openness was problematic: Because it is a combination of WC dimensions, overpasses scored high: They were by far the widest, and in keeping with practice in previous analysis (Clevenger and Waltho 2005), were assigned a height of two times the height of the highest underpass. To diminish the gap between the openness values of underpasses and overpasses, we log-transformed the openness variable for all further analysis.

Overpasses are inherently different to underpasses. Also, overpasses have much higher openness values than most underpasses, with exception of some large bridges like Bow River. We therefore only used the openness value in the models if exploratory plotting of crossing number against openness had suggested an effect also when only looking at underpass data. Also, we did exploration plots to understand if an effect was driven by length, width or height rather than by the combinatory covariate openness.

Statistical Analysis

The data from Phase 3A WC was the starting point for analyses in this paper. It consisted of a 16-year time-series from 13 different WC since the date of completion of their construction (November 1997). We expected temporal correlation in the WC passage counts, and potentially spatial correlation. Generalized linear mixed modeling (GLMM) is a statistical method that is uniquely suited to analyze nested count data. However, currently there are no readily available statistical packages to analyze nested count data with correlation structures in a frequentist setting. Ignoring dependence structures in the data can lead to biased standard error and spurious results.

Another option, the function gamm() of the package *mgcv* (Wood 2006) would have allowed us to fit generalized additive mixed models (GAMMs) with random effects and correlation structures. One issue with using this function, however, is that it uses penalized quasi likelihood (PQL) to estimate the model parameters. PQL, however, is unreliable in certain cases; for example it has been found to underestimate variance components and regression coefficients in GLMMs (Jang et al. 2009, Woncheol and Lim 2009).

We therefore decided to mainly analyze our data in a Bayesian framework, using Marchov Chain Monte Carlo (MCMC) simulation methods (Ellison 2004). We used the program JAGS and the R package RJAGS to run the models using R (R Core Development Team 2008). This allowed us to address the expected dependence structures in the data more easily. Another benefit of using MCMC methods to develop the models was that they allow for estimation of uncertainty with regards to the variances and correlation factors.

The main drawback to MCMC, however, was that the computation time to fit a single model was such as to make model selection for eight parallel analyses (eight species) impractical. We therefore did not conduct model selection, but presented the results of the full models. In this paper, our main goal was to estimate the effects of different covariates on the number of WC passages, and comparing the magnitude of these effects between models that were fit to different subsets of the data. Fitting full models to the different data sets resulted in unbiased parameter estimates, and thus fulfilled the comparative part of our goal well. However, using full models for inference rather than "best models" derived through an appropriate model selection process, results in inclusion of the effects of non-significant factors, and therefore results in noisy predictions (Whittingham et al. 2006).

Since we worked with count data, we used GLMM with Poisson distribution, or potentially negative binomial distribution if overdispersion was an issue. Both distributions were used with a log-link function. The basic model for the number of crossings (Dij), with the appropriate covariates depending on species, at time *i* and WC *j* is given by:

Dij~Poissonμij
EDij=varDij=μij
or
Dij~NBμij, k
EDij=μij, varDij=μij+μij2k

and

$$\text{log}\mu\text{ij=Yearij+Seasonij+...+log(effort)+ai+}\varepsilon\text{ij}$$
$$\text{ai\textasciitilde N0, }\sigma\text{CS2}$$
$$\varepsilon\text{ij=}\varphi\text{*}\varepsilon\text{i,j-1+}\gamma\text{ij}$$
$$\gamma\text{ij\textasciitilde N(0, }\sigma\text{eps2)}$$

Model Variation Over Time

Our first objective was to identify key factors influencing the number of passages through WC of each large mammal, and whether these effects were consistent between models with differing monitoring periods. We used two methods to address the question of change over time in these factors: First, for each species, we fitted models to the first two years of data (2YR), the first four years of data (4YR), the first eight years of data (8YR), and the entire 16 years of data (16YR). We chose these intervals because most WC monitoring efforts span 1-2 years, some even less than one year in length (Mata et al. 2005, Sawyer et al. 2012), while others may be as long as 3-4 years (Gagnon et al. 2011, Huijser et al. 2013). Often results of these studies are used to formulate WC design. Our analyses allowed us to explore the effect of monitoring duration on model outcomes. We chose covariates to exhibit minimal collinearity and were expected to have some effect on passage count based on previous studies. We fitted the full models for each species and present the resulting estimates.

The above methods allowed for a qualitative description of change in parameter effects over time. We attempted to quantify the expected change of the effect of WC design over time, by introducing an interaction term of the WC design variable and year. We then used the Deviance Information Criterion (DIC) (Spiegelhalter et al. 2002), to determine which model provided better fit while penalizing added complexity: the full model or the full model with a design*year interaction.

Time was expected to show non-linear patterns in some or all of the species. Fluctuations in population numbers were expected in most species, but especially elk, where Parks Canada actively conducted population control during 2000-2001 (B. Fyten, Banff Field Unit, personal communication). Apart from elk, Parks Canada does not track long-term population numbers of large mammal species. The covariate *year* was thus expected to not only capture a change of crossing counts over time due to adaptation, but also due to changes in population size. To determine the pattern of the effect of time on number of WC passage counts, we applied generalized additive mixed models (GAMMs) to determine if adding a smoother for *year* was necessary. We fitted a GAMM (*year* non-linear) as well as a GLMM (*year* linear), using the function gamm() in the package *mgcv* (Wood 2006). We used this approach rather than fitting the GAMMs using MCMC and comparing DICs, because of reduced computing time. We compared the AIC values of the two models. Where warranted, we then added second, and if necessary, third order polynomials for the *year* covariate in the GLMM models. We checked for residual patterns to determine if the non-linear patterns had been sufficiently addressed. We also visually inspected the resulting smoother plots for *year* to gain understanding of the mechanisms that led to the patterns.

Last, we examined the selectivity of certain species to WC types over time by calculating the intraclass correlation (ICC; Zuur et al. 2009). A high ICC score indicates within WC variance is smaller than between WC variance, and the inverse for low ICC scores. Our interpretation is that a high ICC score translates to high fidelity or selectivity of WC that are used, while low ICC scores suggest more widespread use of the available WC types.

Predictive Ability of Phase 3A Models

Our second goal was to test the generality of the model estimates on two data sets from adjacent parts of our study area. We used parameter estimates derived from full models fitted to the data of Phase 3A to generate the predicted values for Phases 1, 2 and 3B, despite the expected noise generated by non-significant covariates. While this approach was not optimal in that respect, it balanced the effort required to analyze complex multi-year data of eight focal species, with the need to effectively summarize and understand these datasets and draw conclusions from the observations. We only tested model predictions for four species of particular management importance: Elk, deer, grizzly bear and wolf.

Two independent datasets were used to test predictive power of Phase 3A WC: 16 years of continuous monitoring data from Phase 1 and 2, and 2-5 years of continuous monitoring data from Phase 3B.

The two main difficulties of this analysis and especially while assessing predictive performance of our models were that firstly, no population estimates of any species but elk were available. Second, the WC in the different phases were not built at the same time. WC on Phase 1 and 2 were completed in 1985, while all but one of the Phase 2 structures were finished in 1987 (Castle UP was finished in 1992). WC on Phase 3B were completed between 2008 and 2012. Thus, age of WC in a given calendar year differed between the phases and within Phase 3B (Table 3).

Table 3. Years since completion of mitigation on phases of the Trans-Canada Highway, Banff National Park, Alberta, 1985-2013. Monitoring of crossing structures began in Year 0 for all phases but Phase 1&2; when it began in Year 13.

Year	**Phase 1&2**	**Phase 3A**	**Phase 3B$_{2008}$**	**Phase3B$_{2010}$**	**Phase3B$_{2011}$**
2013	28	16	4	3	2
2012	27	15	3	2	1
2011	26	14	2	1	0
2010	25	13	1	0	
2009	24	12	0		
2008	23	11			
2007	22	10			
2006	21	9			
2005	20	8			
2004	19	7			
2003	18	6			
2002	17	5			
2001	16	4			
2000	15	3			
1999	14	2			
1998	13	1			
1997	12	0			
1996	11				
1995	10				
1994	9				
1993	8				
1992	7				
1991	6				
1990	5				
1989	4				
1988	3				
1987	2				
1986	1				
1985	0				

Phase 3B$_{2008}$: Moraine, Temple underpass, Bow River, Island
Phase 3B$_{2010}$: Lake Louise overpass, Temple overpass
Phase 3B$_{2011}$: Castle overpass, Boom, Storm, Panorama overpass, Quadra, Taylor, Mitella, Baker, Fay, Babel, Consolation

Previous research in the study area showed a distinct adaptation period with increasing use of WC over time and eventual stabilizing in passage counts and fluctuations around an average value (Clevenger et al. 2009). While this precluded us from testing the full 16YR models with the independent datasets, we were able to assess them in two steps: In a first step, we fit models to the 3A data for the years when adaptation had largely concluded, and tested it with data from Phase 1 and 2. In a second step, we fitted models for the first five years of data of Phase 3A, and assessed the prediction intervals with data from Phase 3B. We used the respective covariates values for the WC at Phases 1, 2 and 3B. We also added the temporal correlation structure to the prediction functions, but did not include random variation.

To determine the onset of the stabilization period (at $year_x$), we assessed the smoother plots for year of the GAMMs that were fitted, determining if the effect of time was linear). We then fitted the two models for each species:

- Model 1: Calculate 95% prediction intervals for the full model for $year_x$ to year 16, from the Phase 3A data, for a specific set of covariate values
- Model 2: Calculate 95% prediction intervals for the full model for years 1 to 5 to the Phase 3A data, for a specific set of covariate values.

We then plotted the prediction intervals along the time-axis, and overlaid the data points of Phases 1 and 2 (combined) and 3B from the same calendar years for a visual assessment.

Results

Wildlife Crossings

We detected 39,582 through-passages by 11 species of large mammals at 13 WC on Phase 3A from November 1997 to March 2014 (Table 4). Ungulates comprised 82% (n=32,740 crossings) of this total, while carnivores 17% (n=6842 crossings). There were a total of 2486 crossings by humans at the WC. Individual WC ranged from 13,465 passages (Redearth Overpass) to 383 passages (Bourgeau). Deer were most frequently detected using the WC (n=27,208, 68.7% of all large mammal crossings). Second to deer, elk were detected using the WC at only 13.2% of all large mammal crossings (n= 5223). Among carnivores, coyotes used the structures 2918 times, wolves 2260 times, grizzly bears 800 times, cougars 395 times and black bears 414 times.

A total of 859,880 track pad- and camera-days were logged monitoring the Phase 3A WC year-round since November 1997. One track pad- or camera-day equals one operative day at one WC using one or both detection methods.

Table 4. Summary of wildlife passage at 13 crossing structures (WC) on Phase 3A of the Trans-Canada Highway, Banff National Park, Alberta, 1997-2014.

	Wolverine overpass	Wolverine underpass	Bourgeau	Wolverine Creek	Massive	Sawback	Pilot	Redearth underpass	Redearth overpass	Redearth creek	Copper	Johnston	Castle underpass	**Total**
Grizzly bear	246	2	13	45	18	37	18	44	267	22	15	30	42	**800**
Black bear	47	15	57	19	14	8	49	37	51	23	18	48	28	**414**
Bear spp.	4	0	4	1	0	0	5	0	9	1	1	2	5	**32**
Wolf	364	67	37	114	129	66	95	137	520	187	116	192	236	**2260**
Cougar	91	42	21	72	18	3	15	25	15	33	26	24	10	**395**
Coyote	211	110	142	255	264	125	157	263	222	164	326	393	286	**2918**
Moose	74	4	0	5	10	25	4	0	112	0	1	6	27	**268**
Elk	298	182	7	340	422	132	164	234	1128	240	341	43	1692	**5223**
Deer	7004	652	102	948	1545	254	331	158	10,906	1039	1986	176	2107	**27,208**
Bighorn sheep	0	0	0	2	0	0	0	0	0	29	8	0	2	**41**
Wolverine	1	0	0	1	0	0	1	0	0	2	1	1	2	**9**
Lynx	5	1	0	0	0	0	0	0	4	1	0	1	2	**14**
Human	851	135	25	123	66	46	63	64	231	474	43	28	337	**2486**
Total	9196	1210	408	1925	2486	696	902	962	13,465	2215	2882	944	4777	**42,068**
Total wildlife	**8345**	**1075**	**383**	**1802**	**2420**	**650**	**839**	**898**	**13,234**	**1741**	**2839**	**916**	**4440**	**39,582**

Exploratory Analysis

Residual patterns

Generally, no problematic residual patterns were detected when plotting residuals against all covariates, also those not included in the models. Exceptions to this can be found in the corresponding results sections.

Spatial residual correlation

None of the models displayed residual spatial correlation. When the WC were built initially, a variety of designs were included. The different WC types were spread relatively equally along the TCH which facilitated statistical analysis. While the structures exhibited spatial clustering, the distribution of design types and the habitat variables were expected to account for any spatial correlation of passage counts.

Species models

Deer

Time, season and openness were the most important factors determining the number of deer crossings (Table 5, Table 6). While time had a linear, positive impact on deer numbers from year 1 to 8 (1998 to 2005), it levelled off and fluctuated around a mean value (Figure 1). Deer passage was highest in summer, followed by fall, spring and winter. Openness had a strong, positive effect on number of deer using WC; deer preferred overpasses and underpasses with high openness values. This effect tended to get stronger over time. Solar radiation had a positive effect in the 4YR model, while in other models it was only a trend. The number of humans had a slight negative impact on deer in the 16YR models. Percentage of tree cover in a 1-km radius around the WC, distance to water and WC density had no impact on deer passage counts. Interestingly, temporal correlation across seasons as well as intra-class correlation increased strongly from the 4YR model (ICC = 0.108) to the 8YR model (ICC = 0.718), and stayed high afterwards.

Table 5. Deer models for 2, 4, 8 and 16 years. Displayed are the means and standard errors of the coefficient estimates. The models have no intercept. The model for 16 years included the interaction between year and openness.

Deer	2 years		4 years		8 years		16 years		16 years INT	
	mean	se	mean	se	mean	se	mean	se	mean	se
Year	0.157	0.276	0.309	0.101	0.292	0.034	0.397	0.055	0.408	0.057
Fall	-5.290	5.218	-5.091	2.598	-5.249	2.464	-5.291	2.541	-5.386	2.560
Spring	-6.313	5.234	-5.941	2.601	-5.907	2.470	-5.928	2.539	-6.027	2.560
Summer	-3.919	5.247	-3.696	2.601	-4.218	2.467	-4.299	2.540	-4.396	2.560
Winter	-7.084	5.227	-7.185	2.601	-7.073	2.467	-7.198	2.540	-7.308	2.560
l.openness	0.935	0.343	0.878	0.168	0.777	0.159	0.908	0.169	0.770	0.190
distwater	0.075	0.584	-0.097	0.300	-0.085	0.296	-0.230	0.291	-0.213	0.298
buff5	-0.105	0.176	-0.037	0.094	-0.039	0.092	-0.051	0.093	-0.051	0.097
tree.1km	0.012	0.055	-0.022	0.029	-0.005	0.028	0.007	0.028	0.007	0.029
rad.1km	0.169	0.264	0.278	0.141	0.217	0.131	0.172	0.136	0.167	0.133
sqrthuman	-0.049	0.145	-0.051	0.096	0.010	0.054	-0.029	0.027	-0.034	0.027
φ	-	-	0.270	0.129	0.821	0.097	0.845	0.048	0.851	0.047
τ_{eps}	-	-	0.989	0.187	12.462	7.388	10.502	3.533	10.356	3.350
σ_{cs}	0.940	0.562	0.351	0.274	0.452	0.270	0.523	0.249	0.518	0.253
size	1.035	0.271	-	-	2.165	0.582	2.384	0.281	2.407	0.282
Year^2	-	-	-	-	-	-	-0.018	0.003	-0.018	0.003
Year*l.open	-	-	-	-	-	-	-	-	0.017	0.011
σ_{eps}	-	-	1.006	-	0.283	-	0.309	-	0.311	-
ICC	-	-	0.108	-	0.718	-	0.742	-	0.735	-

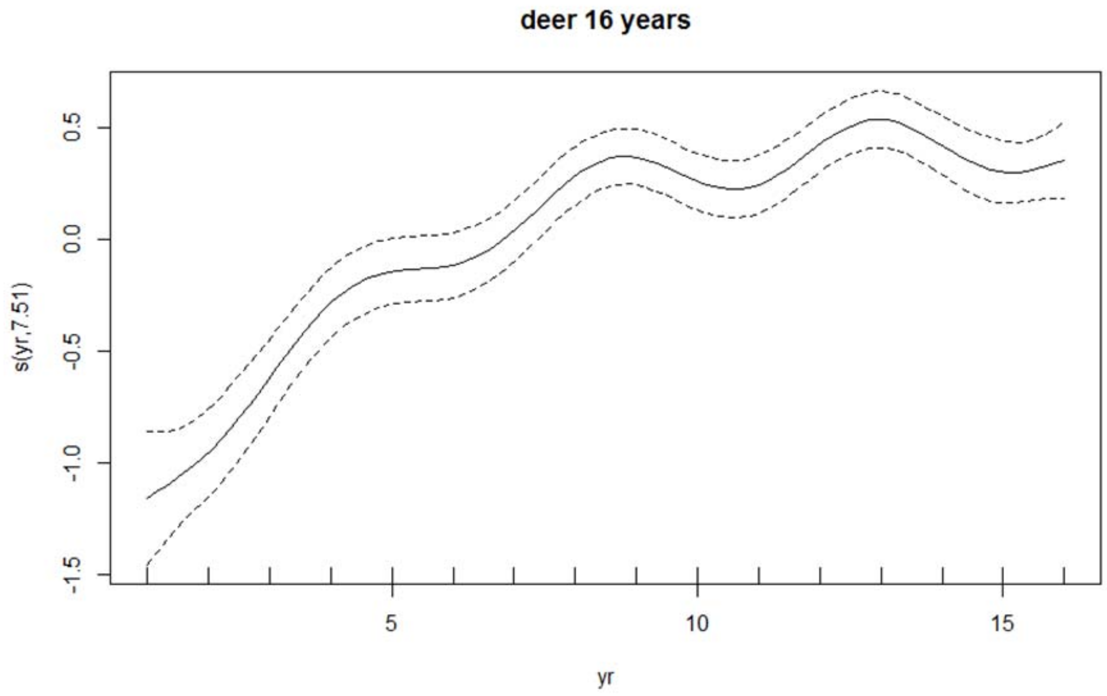

Figure 1. Plot showing the smooth functions for the 16 Year best GAMM models for deer at Phase 3A crossing structures in Banff National Park, Alberta. The x-axes of the smooth function plot shows the covariate time (year) and the y-axis is the covariate effect on the mean response, which is the number of animals using crossing structure. Values on the y-axis are on the linear predictor scale.

Elk

The most important factors determining elk passage counts on Phase 3A were time, season, openness, and solar radiation (Table 6, Table 7). Distance to water and WC density within a 5-km radius also consistently influenced counts. Time had a non-linear effect on elk (Figure 2). Correspondingly, while there was a slight increase in elk crossing numbers from 1998 to 2001, numbers fell for six years, until reaching a low in 2008 (year 10). The number of crossings summed across all structures was 922 in 2001 and 64 in 2008. Since 2008, there has been a slight increase in passage counts. The highest passage counts for elk were in summer, followed by fall, spring and winter.

Table 6. A summary of full model results in analysis of long-term data to identify factors affecting movement of eight species of large mammals through wildlife crossing structures (WC). Direction of positive (+) or negative (-) effect on crossing numbers is provided for each covariate. Covariate categories are colour-coded: structural (grey), environmental (green), and human use (orange).

Covariates[1]	Deer_2	Deer_4	Deer_8	Deer_16	Elk_2	Elk_4	Elk_8	Elk_16	Moose_16	Grizzly_15	Black bear_2	Black bear_4	Black bear_8	Black bear_16	Wolf_4	Wolf_8	Wolf_16	Cougar_4	Cougar_8	Cougar_16	Coyote_2	Coyote_4	Coyote_8	Coyote_16	Total
Openness	+	+	+	+	+	+	+	+							+	+	+								11
WC type									UP -	UP -	UP +							UP +	UP +	UP -			UP +		7
Noise																					-	-			2
Length													+	+											2
Buff1										-															1
Buff5					-	-	-	-			-	-	-		-	-	-				-	-	-	-	14
Rad.1km	+	+	+	+	+	+	+	+																	8
Dist_water					-	-	-	-			+	+	+	+											8
1km%forest																					+	+	+	+	4
1km%grass																		-	-	-					3
Human use				-	-										+	-	-				-	-			7
ICC[2]	-	0.108	0.718	0.742	0.722	0.522	0.439	0.428	0.880	0.572	0.558	0.128	0.128	0.061	0.124	0.086	0.291	0.338	0.169	0.384	0.929	0.147	0.144	0.186	

[1] See Table 2 for description of covariates used in analysis.

[2] ICC: Intraclass correlation coefficient (see Methods).

Table 7. Elk models for 2, 4, 8 and 16 years. Displayed are the means and standard errors of the coefficient estimates. The models have no intercept.

ELK	2 years		4 years		8 years		16 years		16 years INT	
	mean	se	mean	se	mean	mean	mean	se	mean	se
Year	-	-	0.305	0.115	1.321	1.321	1.321	0.298	1.300	0.307
Spring	-9.690	5.301	-	4.290	-9.793	-9.793	-9.793	4.210	-8.676	4.171
Summer	-6.139	5.328	-8.303	4.271	-7.244	-7.244	-7.244	4.206	-9.839	4.174
Fall	-7.309	5.320	-9.550	4.269	-8.648	-8.648	-8.648	4.205	-7.297	4.168
Winter	-10.366	5.280	-	4.291	-	-	-	4.205	-10.571	4.182
Log(Openness)	0.486	0.337	0.536	0.273	0.519	0.519	0.519	0.277	0.628	0.287
distwater	-0.324	0.604	-0.388	0.479	-0.536	-0.536	-0.536	0.496	-0.542	0.495
buff5	-0.212	0.184	-0.203	0.154	-0.226	-0.226	-0.226	0.152	-0.243	0.150
tree.1km	-0.002	0.057	0.007	0.048	0.016	0.016	0.016	0.048	0.022	0.047
rad.1km	0.566	0.264	0.505	0.218	0.471	0.471	0.471	0.220	0.451	0.216
sqrthuman	-0.352	0.104	-0.128	0.085	-0.080	-0.080	-0.080	0.047	-0.061	0.049
pop	-0.001	0.003	0.002	0.001	-0.002	-0.002	-0.002	0.001	-0.002	0.001
φ	-0.006	0.197	0.035	0.107	-0.063	-0.063	-0.063	0.073	-0.063	0.071
τ_{eps}	2.124	0.698	1.281	0.233	0.785	0.785	0.785	0.084	0.751	0.077
σ_{cs}	1.106	0.473	0.923	0.380	0.975	0.975	0.975	0.369	0.953	0.370
$Year^2$	-	-	-	-	-0.367	-0.367	-0.367	0.071	-0.363	0.073
$Year^3$	-	-	-	-	0.029	0.029	0.029	0.007	0.029	0.007
$Year^4$	-	-	-	-	-0.001	-0.001	-0.001	0.000	-0.001	0.000
									-0.015	0.010
σ_{eps}	0.686	-	0.884	-	1.128	1.128	1.128	-	1.154	
ICC	0.722	-	0.522	-	0.428	0.428	0.428	-	0.406	

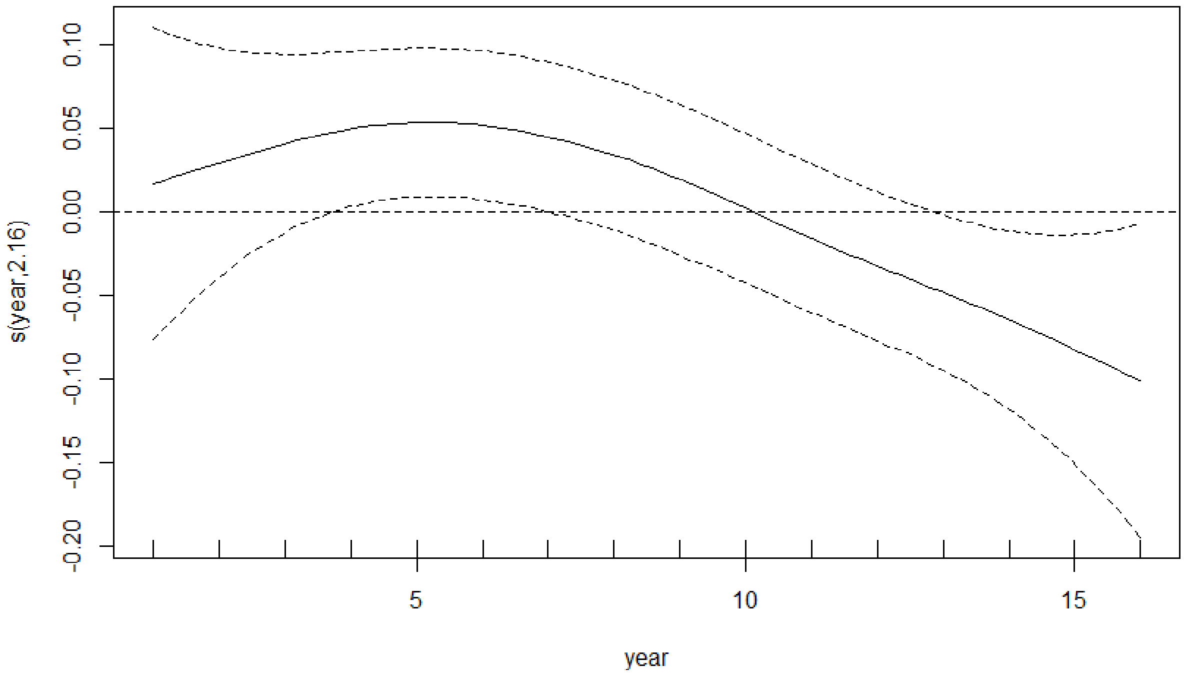

Figure 2. Plot showing the smooth functions for the 16 Year best GAMM models for elk at Phase 3A crossing structures in Banff National Park, Alberta. The x-axes of the smooth function plot shows the covariate time (year) and the y-axis is the covariate effect on the mean response, which is the number of animals using crossing structure. Values on the y-axis are on the linear predictor scale.

Elk consistently preferred WC with greater openness, suggesting overpasses and larger underpasses. The estimate for openness changed slightly between the four year-based models. The interaction term, while its posterior distribution included zero, was negative, suggesting the preference of larger openness decreased over time. WC with higher solar radiation yielded more elk crossings. The mean estimate for distance to water was consistently negative, resulting in more elk crossings if a structure was closer to a river. However, the posterior distribution for this covariate included zero in all models. Similarly, WC density within a 5-km radius consistently had a negative impact on number of passages at a given structure. Population number and time were strongly, albeit non-linearly, correlated. The covariate year appeared to account for most of the effect population size had on crossing numbers. The covariate population had changing effects: in the 2YR model, population had no effect on crossing numbers. In the 4YR model, it had a positive effect. In the 8YR model, the effect was a slightly positive trend. In the 16YR model, the population effect was negative. Number of humans using the WC had a strong negative impact on elk numbers in the first two years of the study. With time, this effect decreased, but stayed negative. Intra-class correlation in elk decreased over time, from 0.722 in the 2YR model, to 0.428 in the 16YR model.

Grizzly bear

Four outliers made it difficult to obtain adequate model fit. All of the data points were collected in the first year of data collection, and likely stemmed from one large adult male, which was killed on the highway in the fall of that year (S Michel, Banff Field Unit, personal communication). We re-analyzed the data without the first year of data. While this significantly improved model fit, it did not alter the pattern of the results, so we proceeded with the truncated data set.

Season, year, and WC type were the most important covariates determining grizzly bear crossing numbers (Table 6, Table 8). There was a continuous increase in passage counts over time, declining slightly at approximately 10 years (2007) (Figure 3). However, the GAMM with a linear time effect had a much lower AIC than the GAMM with a non-linear time effect, and we therefore treated time as linear. The highest number of crossings occurred during summer, followed by spring and fall. Only the 15-year full models had satisfactory mixing of chains. In year 2 (1999), only one crossing took place, at an overpass. From years 2 to 4, 17 the majority of crossings took place on overpasses, while only two occurred at underpasses. We did not attempt to develop a model for years 2 to 4.

Table 8. Grizzly bear models for 7 and 15 years. Displayed are the means and standard errors of the coefficient estimates. The models have no intercept

Grizzly	7 years		15 years		15 years INT	
	mean	se	mean	se	mean	se
yr	0.324	0.108	0.303	0.040	0.174	0.064
distwater	-	-	-0.487	0.581	-0.527	0.606
buff1	-	-	-0.776	0.523	-0.833	0.528
g.1km	-	-	0.268	0.486	0.349	0.509
dist.road	-	-	0.000	0.002	0.000	0.002
sqrthuman	-	-	0.057	0.038	0.068	0.039
Spring	-7.414	1.581	-8.174	4.214	-7.562	4.289
Fall	-7.887	1.578	-8.663	4.216	-8.095	4.289
Summer	-5.779	1.535	-6.546	4.213	-5.962	4.290
typeUP	-3.765	1.726	-3.321	1.123	-5.153	1.404
φ	0.318	0.419	0.851	0.060	0.794	0.085
τ_{eps}	3.405	3.695	3.317	1.045	3.074	0.989
σ_{eps}	0.669	0.226	0.549	-	0.570	-
σ_{cs}	1.502	1.167	0.635	0.464	0.738	0.482
beta.yr	-	-	-	-	0.182	0.077
ICC	0.835	-	0.572	-	0.626	-

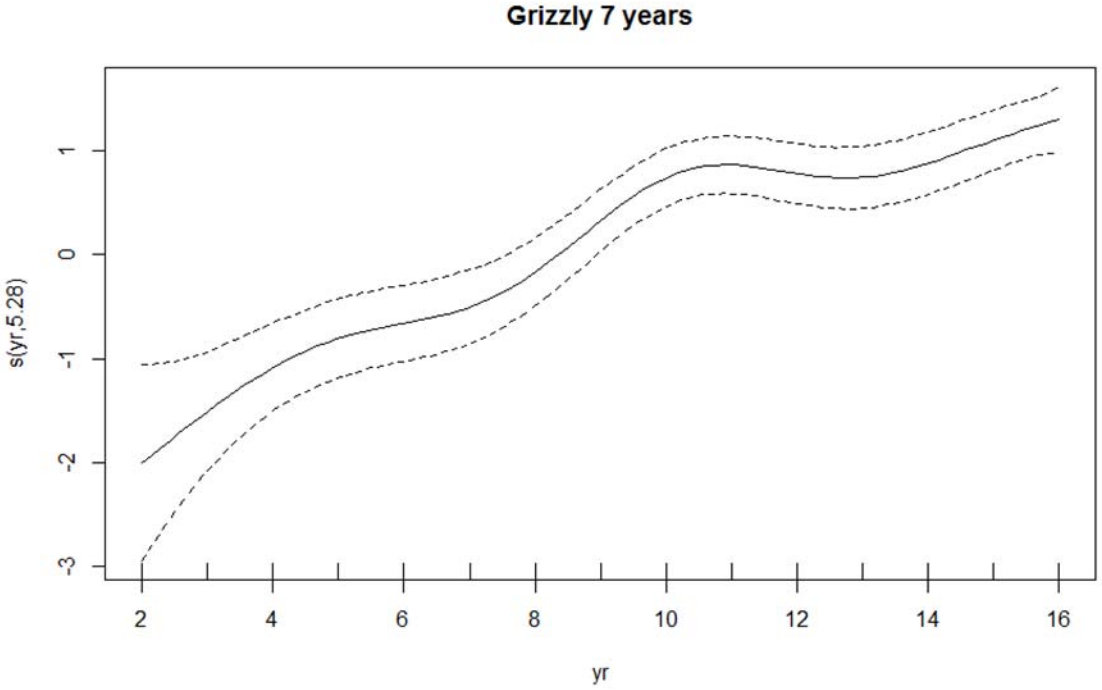

Figure 3. Plot showing the smooth functions for the 15 Year best GAMM models for grizzly bear at Phase 3A crossing structures in Banff National Park, Alberta. The x-axes of the smooth function plot shows the covariate time (year) and the y-axis is the covariate effect on the mean response, which is the number of animals using crossing structure. Values on the y-axis are on the linear predictor scale.

In the 7- and 15-year models, grizzly bears showed a strong preference for overpasses, i.e. the estimate for underpass preference was negative. However, the 7-year full model did not converge – we therefore fitted a model with only the most important covariates from the 15-year model, to the 7-year data, for comparison. In the 15-year models, WC density within a 1-km radius tended to have a negative effect on crossing numbers. The number of humans had a slight positive effect on grizzly bear passage counts, but the 95% posterior distribution interval included zero. Distance to road, distance to water and general habitat quality within a 1-km radius around a WC (RSF model) did not have an effect on passage counts. The interaction term between time and underpass preference was clearly positive, and the DIC of the model with the interaction was lower than the model without, suggesting that over time, underpasses were more accepted by grizzly bears (Table 9). We used WC type rather than openness to analyze the effect of WC design on crossing numbers, because data exploration had shown that an apparent correlation between openness and number of crossings disappeared when looking at underpass data only. To confirm this, we fitted a GAMM to the 15-year underpass data only, using the gamm() function from the mgcv-package. The estimate for openness was negative (-3.382 with a standard error of 1.089), indicating that grizzly bear use of underpasses increased over time. Intra-class correlation was higher in the 7-year model (0.835) than the full 15-year model (0.626).

Table 9. Model comparisons for all species and years for which models were created.

Species		2 years	4 years	8 years	8 years, s(year)	16 years	16 years, s(year)	16 years, interaction
Deer	DIC:	-	-	-	-	5990.7	-	5935.0
	AIC:	-	-	1194.8	1205.8	2460.9	2302.4	-
	Phi:	1.065	0.435	0.827	-	0.811	-	0.809
	p_B	0.292	0.403	0.377	-	0.316	-	0.312
Elk	DIC:	-	-	-	-	2725.6	-	2674.8
	AIC:	-	-	1448.9	1445.6	4042.2	3497.3	-
	Phi:	0.526	0.358	0.381	-	0.348	-	0.328
	p_B	0.341	0.461	0.477	-	0.266	-	0.195
Grizzly	DIC:	-	-	-	-	1180.4	-	1171.5
	AIC:	-	-	1641.1	1633.3	2635.4	2611.2	-
	Phi:	-	-	0.643	-	0.685	-	0.688
	p_B	-	-	0.459	-	0.486	-	0.454
Wolf	DIC:	-	-	-	-	3923.4	-	4113.5
	AIC:	-	-	1942.6	1972.3	3362.2	3433.7	-
	Phi:	-	0.217	0.347	-	0.746	-	0.746
	p_B	-	0.498	0.368	-	0.398	-	0.402
Coyote	DIC:	-	-	-	-	3446.1	-	3521.4
	AIC:	-	-	1282.6	1284.6	2830.7	2820.3	-
	Phi:	0.347	0.358	0.359	-	0.384	-	0.383
	p_B	0.452	0.396	0.351	-	0.399	-	0.397
Black bear	DIC:	-	-	-	-	1229.8	-	1224.6
	AIC:	-	-	1407.2	1437.3	2888.6	2905.2	-
	Phi:	0.951	0.702	0.739	-	0.711	-	0.725
	p_B	0.300	0.293	0.310	-	0.298	-	0.284
Cougar	DIC:	-	-	-	-	1369.8	-	1372.6
	AIC:	-	-	1810.7	1856.5	3717.3	3719.3	-
	Phi:	-	0.607	0.503	-	0.542	-	0.541
	p_B	-	0.413	0.485	-	0.385	-	0.397
Moose	DIC:	-	-	-	-	811.3		814.6
	AIC:	-	-	2869.4	2871.4	4904.2	5003.2	
	Phi:	-	-		-	0.390		0.472
	p_B	-	-		-	0.404		0.494

Wolf

The main factors affecting wolf passage counts were time, season, openness of the WC, and WC density (Table 6, Table 10). Time was best explained as a linear effect in all models, but its effect, i.e. the increase of crossing numbers per year increment, was largest in the 4YR model, and smallest in the 16YR model. Summer had the highest number of crossings, followed by fall, spring, and winter. Wolves preferred WC with larger openness in all models; the effect was strongest in the 16YR model. An interaction term for openness-preference and time was positive, but its 95% confidence interval included zero. WC density tended to negatively affect the number of crossings in all models.

Table 10. Wolf models for 4, 8 and 16 years. Displayed are the means and standard errors of the coefficient estimates. The models have no intercept. σ_{eps} was calculated as the square root of $(\tau_{eps})^{-1}$. Intra-class correlation (ICC) was calculated as $(\sigma_{cs}^2)/(\sigma_{cs}^2 + \sigma_{eps}^2)$.

Wolf	4 years		8 years		16 years		16 years, INT	
	mean	se	mean	se	mean	se	mean	se
Year	1.101	0.320	0.366	0.061	0.197	0.024	0.206	0.029
Spring	-9.172	4.715	-7.428	2.154	-6.338	1.599	-6.385	1.622
Summer	-8.425	4.708	-6.356	2.160	-5.684	1.598	-5.735	1.621
Fall	-8.887	4.735	-6.468	2.158	-5.993	1.601	-6.040	1.623
Winter	-12.320	4.864	-8.960	2.158	-7.010	1.599	-7.068	1.625
log(Openness)	0.385	0.328	0.359	0.157	0.336	0.116	0.253	0.182
distwater	0.246	0.780	-0.132	0.355	-0.153	0.239	-0.151	0.242
buff5	-0.297	0.249	-0.207	0.111	-0.143	0.088	-0.146	0.087
w.5km	-0.001	0.085	0.023	0.041	0.034	0.030	0.033	0.030
Sqrt(human)	0.359	0.309	-0.084	0.132	-0.065	0.049	-0.070	0.051
τ_{eps}	0.210	0.077	0.429	0.081	4.707	2.799	4.678	2.678
φ	-0.156	0.209	0.140	0.128	0.796	0.087	0.799	0.090
σ_{cs}	0.820	0.699	0.467	0.324	0.296	0.213	0.294	0.219
size	-	-	-	-	0.751	0.131	0.767	0.548
σ_{eps}	2.182	-	1.526	-	0.461	-	0.462	-
Beta.yr	-	-	-	-	-	-	0.009	0.016
ICC	0.124	-	0.086	-	0.291	-	0.288	-

To investigate potential interactions between wolves and their main prey species (see Chapter III.3. [Methods], Table 2), which we expected to be positive (i.e. more wolves with higher prey species numbers) we fitted an alternative "prey" model to the 16YR data set. With the same random effect and correlation structures as all other models, we included the fixed effects season and year, as well as the crossing numbers of the three main prey species elk, deer and moose, as covariates. The prey species numbers were highly correlated with especially the covariates openness, as well as a number of other factors (see results section of the respective species). The resulting DIC value was 3774.5, virtually identical to the DIC value of the full model (DIC = 3775.9; Table 9). However, the coefficient estimates of all three species were centered at zero.

Interestingly, in the 4YR model, number of wolf crossings was positively associated with the amount of human use at WC – this trend switched in the other models to a negative association, which was stronger in the 16YR model than the 8YR model, but stayed a trend. Intra-class correlation, the average correlation of wolf crossing counts from the same WC, was low in all models (Table 6, Table 10).

Coyote

Season was the most important predictor in all coyote models, as was time in the 16YR model (Table 6, Table 11). The time effect was non-linear: for the first 7 to 8YRs, numbers did not change over time, then they started declining, and were still declining at year 16 (Figure 4). WC density at a 5-km radius had a negative impact on coyote crossing numbers in all models, however, the 95% interval of the posterior distribution always included zero (Table 11). The same was true for percentage of forest in a 1-km radius around the WC – it had a positive impact in all models, but the 95% interval of the posterior distribution always included zero. Noise had a clear negative impact on numbers in the 2YR model, a slight negative impact in the 4YR model, and no impact on the 8 and 16YR scale. Solar radiation had no effect, neither did length of the WC. Human numbers only had a slight negative effect in the 8YR model, but otherwise did not impact coyote numbers. In the 2YR and 4YR models, there appeared to be no preference of either over- or underpasses. At 8YR, there was some preference for underpasses. At 16YR, no such preference was found in the full model. We used WC type rather than openness to analyze the effect of WC design on crossing numbers, because during data exploration we found that while there appeared an effect of openness on the underpass data only, there was no effect of openness when overpass data was included. Since type and openness were correlated, we did not want to use both covariates in the same model. To confirm this pattern, we fitted a GAMM using the mgcv function gamm() to the underpass data only.

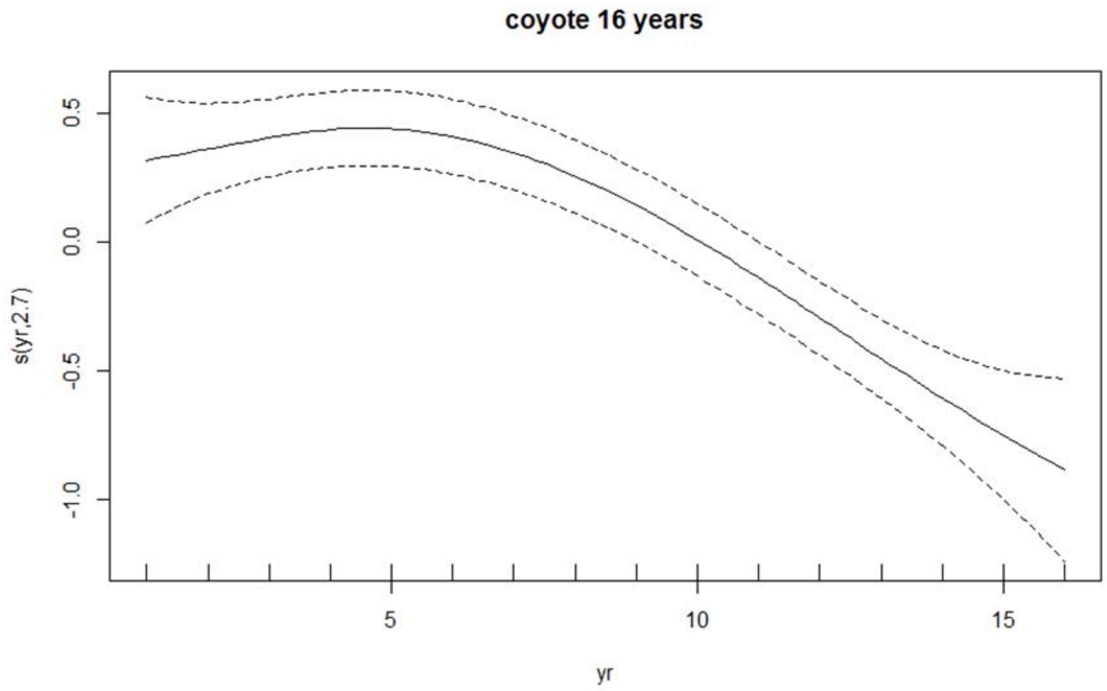

Figure 4. Plot showing the smooth functions for the 16 Year best GAMM models for coyote at Phase 3A crossing structures in Banff National Park, Alberta. The x-axes of the smooth function plot shows the covariate time (year) and the y-axis is the covariate effect on the mean response, which is the number of animals using crossing structure. Values on the y-axis are on the linear predictor scale.

Table 11. Coyote models for 2, 4, 8 and 16 years. Displayed are the means and standard errors of the coefficient estimates. The models have no intercept.

Coyote	2 years		4 years		8 years		16 years		16 years INT	
	mean	se	mean	se	mean	se	mean	se	mean	se
yr	0.249	0.276	0.017	0.080	0.019	0.028	0.069	0.051	0.138	0.058
noise	-0.757	0.349	-0.241	0.310	-0.004	0.247	-0.083	0.282	-0.066	0.290
buff5	-0.160	0.104	-0.144	0.092	-0.083	0.077	-0.117	0.085	-0.115	0.087
tree.1km	0.052	0.028	0.047	0.025	0.034	0.020	0.026	0.023	0.025	0.024
rad.1km	0.020	0.142	-0.030	0.131	0.001	0.106	-0.008	0.123	-0.006	0.121
sqrthuman	0.111	0.136	-0.018	0.089	-0.081	0.062	0.011	0.036	-0.010	0.038
length	0.006	0.007	0.003	0.007	0.000	0.006	-0.001	0.006	-0.001	0.006
Fall	-7.857	2.742	-6.369	2.509	-6.250	2.024	-5.038	2.236	-5.522	2.272
Spring	-8.381	2.756	-6.701	2.513	-6.075	2.024	-5.110	2.239	-5.580	2.273
Summer	-7.410	2.736	-6.249	2.511	-5.468	2.024	-4.509	2.238	-4.983	2.269
Winter	-8.806	2.740	-7.148	2.510	-6.560	2.023	-5.550	2.237	-6.045	2.271
typeUP	0.063	0.626	0.292	0.585	0.430	0.465	0.174	0.549	0.814	0.624
beta.2	-	-	-	-	-	-	-0.010	0.003	-0.010	0.003
φ	0.207	0.162	0.175	0.110	0.239	0.071	0.307	0.053	0.291	0.052
τ_{eps}	1.078	0.271	1.233	0.215	1.324	0.160	1.062	0.095	1.064	0.096
σ_{cs}	0.986	0.125	0.378	0.280	0.356	0.215	0.444	0.236	0.464	0.226
beta.yr	-	-	-	-	-	-	-	-	-0.080	0.034
σ_{eps}	0.273	0.251	0.911	0.078	0.869	-	0.970	-	0.970	-
ICC	0.929	-	0.147	-	0.144	-	0.173	-	0.186	-

Intra-class correlation was high in the 2YR model (0.9), then dropped to 0.15 in the 4YR model and stayed low in subsequent models. All coyote models were somewhat problematic insofar as there was a consistent pattern of only positive residuals for larger fitted values, suggesting a missing, yet important covariate.

Black bear

Time, season and partly distance to water and WC length were the most important factors describing black bear use of WC (Table 6, Table 12). The time effect was not linear across the 16 years (Figure 5). The 2YR model exhibited a trend for underpass preference, as well as a negative impact on crossing numbers with higher WC density. In the 4YR model, however, there was no indication for underpass preference. However, WC density was still negatively impacting black bear numbers. Also, larger distance to water showed a trend to positively influence crossing numbers. In the 8YR model, distance to water still positively influenced crossing numbers, as did increased WC length. In the 16YR model, the distance of water effect was even stronger, as well as the length effect. To assess if openness was influencing underpass use, we fitted a GAMM to the 16YR underpass data only, using all covariates also included in the MCMC model. Openness had a negative coefficient estimate of -2.023 (s.e. = 0.910), meaning that black bears preferred less open underpasses. The interaction between underpass preference and time was relatively clear – over time that preference decreased, at 7.7 years after construction the preference was estimated to have become zero. However, the 95% confidence intervals for the interaction term posterior distribution was large and included zero. Distance to the CPR, forest cover within 1-km of a WC and amount of human use at WC did not impact passage counts. Intra-class correlation was 0.558 in the 2YR model, but sank to 0.128 in both the 4YR and 8YR model, and was low at 0.061 in the 16YR model.

Table 12. Black bear models for 2, 4, 8 and 16 years. Displayed are the means and standard errors of the coefficient estimates. The models have no intercept.

Black Bear	2 years		4 years		8 years		16 years		16 years INT	
	mean	se	mean	se	mean	se	mean	se	mean	se
yr	-0.028	0.398	-0.565	0.199	0.612	0.808	-0.653	0.240	-0.590	0.243
distwater	0.268	0.603	0.616	0.522	0.749	0.384	0.578	0.256	0.559	0.287
buff5	-0.227	0.188	-0.182	0.160	-0.021	0.122	-0.038	0.085	-0.039	0.094
tree.1km	0.001	0.056	0.008	0.047	0.016	0.032	0.020	0.023	0.016	0.025
distcpr	0.226	1.460	-0.114	1.229	0.216	0.943	-0.508	0.628	-0.527	0.655
sqrthuman	0.056	0.192	-0.091	0.190	0.078	0.135	-0.005	0.064	-0.044	0.069
length	0.009	0.012	0.005	0.010	0.009	0.007	0.013	0.005	0.012	0.005
Spring	-6.536	4.447	-5.880	3.742	-8.907	2.802	-7.513	1.825	-7.772	1.957
Fall	-9.331	4.504	-7.005	3.778	-9.681	2.819	-8.185	1.836	-8.430	1.982
Summer	-5.485	4.512	-4.186	3.795	-7.132	2.832	-5.561	1.832	-5.801	1.975
typeUP	1.601	1.220	0.502	0.990	0.133	0.680	-0.043	0.481	0.676	0.719
φ	-0.277	0.572	0.163	0.314	0.287	0.217	0.379	0.170	0.390	0.182
τ_{eps}	3.556	6.026	0.719	0.297	1.035	0.342	1.049	0.278	1.084	0.299
σ_{eps}	0.678	0.249	1.245	0.235	1.020	0.158	1.000	0.122	0.985	0.125
σ_{cs}	0.762	0.556	0.476	0.436	0.392	0.333	0.255	0.225	0.302	0.264
beta.2	-	-	-	-	-0.357	0.207	0.066	0.033	0.068	0.033
beta.3	-	-	-	-	0.036	0.015	-0.002	0.001	-0.002	0.001
beta.yr	-	-	-	-	-	-	-	-	-0.088	0.057
ICC	0.558	-	0.128	-	0.128	-	0.061	-	0.086	-

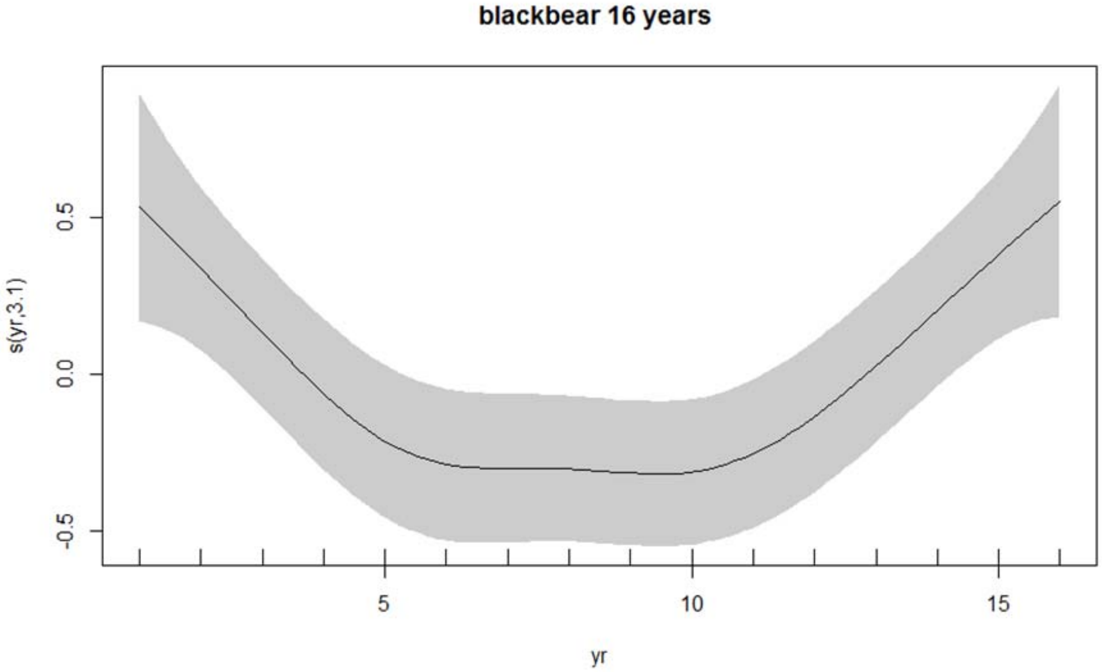

Figure 5. Plot showing the smooth functions for the 16 Year best GAMM models for black bear at Phase 3A crossing structures in Banff National Park, Alberta. The x-axes of the smooth function plot shows the covariate time (year) and the y-axis is the covariate effect on the mean response, which is the number of animals using crossing structure. Values on the y-axis are on the linear predictor scale.

Cougar

The effect of time was highly important for cougars, but not linear: at underpasses, there was a peak in cougar crossings around year eight (2005). After year 10 (2007) numbers decreased to levels well below those of the first year (Figure 6). At overpasses, the number of cougars was low for 10 years, and then started to increase (Figure 7). The key factors predicting number of cougar crossings were time, season, WC type, and the percentage of shrub and grass cover around the WC (Table 6, Table 13). Fall had the highest, winter the lowest crossing numbers, this pattern held true in all models (4YR, 8YR, 16YR). Cougars tended to prefer underpasses to overpasses in the 4 and 8YR models, a trend that was reversed in the 16YR model. When explicitly modeling the interaction of underpass preference and time, we found strong evidence for this pattern: after 6.4 years the initial preference of underpasses reached zero, changing into a preference of overpasses. In all the models, the percentage of shrub or grass cover in a 1-km radius around the WC negatively impacted the number of cougars crossing. We found some evidence that human use negatively impacted cougar crossing numbers in the 4YR model, a trend that was weaker in the 8YR model and absent in the 16YR model. Intra-class correlation was relatively low: 0.338 in the 4YR model, then decreased to 0.169 in the 8YR model, and increased again to 0.384 in the 16YR model.

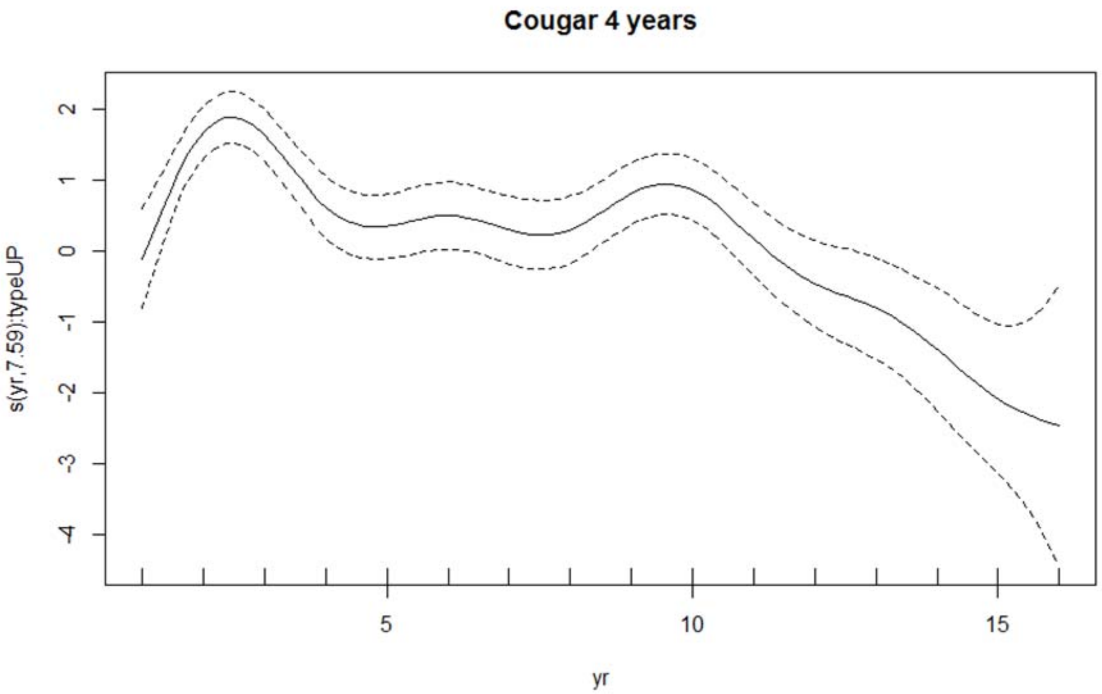

Figure 6. Plot showing the smooth functions for the 16 Year best GAMM models for cougar at Phase 3A underpasses in Banff National Park, Alberta. The x-axes of the smooth function plot shows the covariate time (year) and the y-axis is the covariate effect on the mean response, which is the number of animals using crossing structure. Values on the y-axis are on the linear predictor scale.

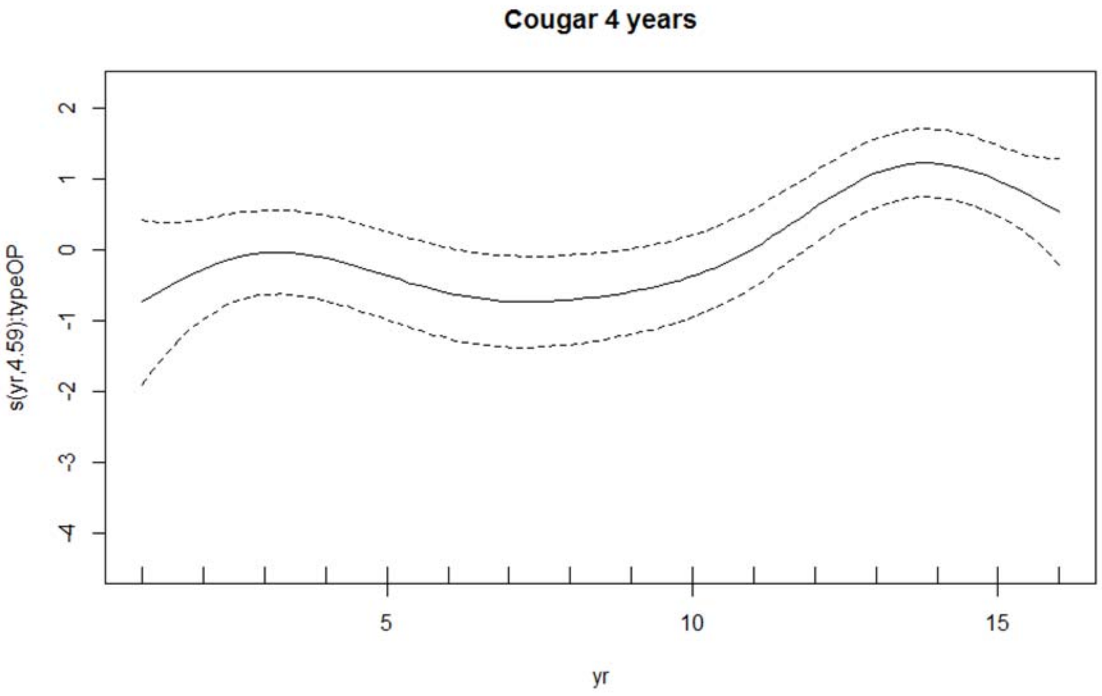

Figure 7. Plot showing the smooth functions for the 16 Year best GAMM models for cougar at Phase 3A wildlife overpasses in Banff National Park, Alberta. The x-axes of the smooth function plot shows the covariate time (year) and the y-axis is the covariate effect on the mean response, which is the number of animals using crossing structure. Values on the y-axis are on the linear predictor scale.

Table 13. Cougar models for 4, 8 and 16 years. Displayed are the means and standard errors of the coefficient estimates. The models have no intercept. The model for 16 years included the interaction between year and typeUP.

Cougar	4 years		8 years		16 years	
	mean	se	mean	se	mean	se
Year	5.079	1.051	0.840	0.377	0.667	0.175
Spring	-12.422	2.496	-7.421	1.757	-7.432	1.782
Summer	-12.941	2.521	-7.565	1.765	-7.446	1.791
Fall	-12.355	2.506	-6.936	1.746	-7.018	1.785
Winter	-13.132	2.504	-7.930	1.763	-8.031	1.793
typeUP	1.153	0.980	0.693	0.796	2.242	1.065
distwater	0.243	0.599	-0.179	0.469	-0.333	0.487
buff5	0.169	0.205	0.067	0.144	0.001	0.143
herb.1km	-0.336	0.158	-0.249	0.126	-0.287	0.128
sqrthuman	-0.223	0.180	-0.099	0.129	-0.031	0.053
$Year^2$	-0.944	0.195	-0.102	0.041	-0.032	0.010
φ	0.496	0.165	0.639	0.099	0.732	0.079
τ_{eps}	1.096	0.415	0.786	0.198	1.319	0.299
σ_{cs}	0.682	0.540	0.508	0.395	0.687	0.393
Year*typeUP	-	-	-	-	-0.350	0.086
σ_{eps}	0.955	-	1.128	-	0.871	-
ICC	0.338	-	0.169	-	0.384	-

Moose

Moose crossings were relatively rare during the 17 years of monitoring. There were no recorded moose crossings at Phase 3A during the first two years after construction. Within the first four years, 10 crossings took place, all at overpasses. Within the first eight years, 48 crossings took place, of which only eight occurred at five different underpasses. The 16YR models had more data -188 crossings at overpasses compared to 85 at underpasses (Table 4). Year had the strongest effect – the data suggested a steady, linear rise in crossing numbers. While season had a distinct effect, too, with most crossings in fall, followed by summer, spring and winter, the posterior distributions of the season levels displayed a large spread –indicating large uncertainty in the probability model. Thus, caution had to be exerted when interpreting the estimates. Moose tended to prefer overpasses to underpasses, and the interaction term between underpass preference and time was negative, indicating a decrease in overpass preference over time (Table 6, Table 14). Intra-class correlation was the highest between all monitored species, at 0.884. No other covariate showed any clear effect. When fitting a GAMM to the underpass data only, no effect of openness on passage counts was detected.

Table 14. Moose models for 16 years. Displayed are the means and standard errors of the coefficient estimates. The models have no intercept.

Moose	16 years		16 years INT	
	mean	se	mean	se
seasonfall	-8.898	12.381	-2.729	13.001
seasonspring	-10.506	12.382	-4.329	13.003
seasonsummer	-9.326	12.385	-3.162	13.007
seasonwinter	-10.648	12.388	-4.424	13.010
typeUP	-4.322	3.985	-4.280	3.562
yr	0.272	0.037	0.222	0.047
noise	-0.684	2.163	-0.861	2.313
buff5	-0.415	0.639	-0.357	0.635
rad.1km	-0.091	0.765	-0.292	1.102
tree.1km	0.072	0.169	0.290	0.765
sqrthuman	-0.008	0.065	0.016	0.065
rho	0.215	0.142	0.182	0.142
taueps	0.683	0.166	0.698	0.171
sigma.eps	1.237	0.149	1.224	0.148
sigma.re	3.347	1.968	3.398	2.340
beta.yr	-	-	0.105	0.067
ICC	0.880	-	0.885	-

Predictive Ability of Phase 3A WC Models

Phase 1 and 2 – Years 10 to 16 Post-mitigation

All of the predictions were generated using the autoregressive (AR1) temporal correlation structures from the models fitted to the Phase 3A data set. However, the predictions did not include random effects of the WC. Therefore the prediction intervals were expected to be at least slightly narrower than had we taken into account the nested nature of the data. Exploratory analysis showed that the effect of solar radiation for deer and elk was found to be non-linear (Figure 8 and 9). For both species the pattern showed the same shape and could be well approximated with a quadratic term. Addition of this term to the models was necessary, as the range of solar radiation values was much wider in Phase 1 and 2 compared to Phase 3A. Ignoring the actual shape of this covariate would lead to inflated predictions at WC with high solar radiation values.

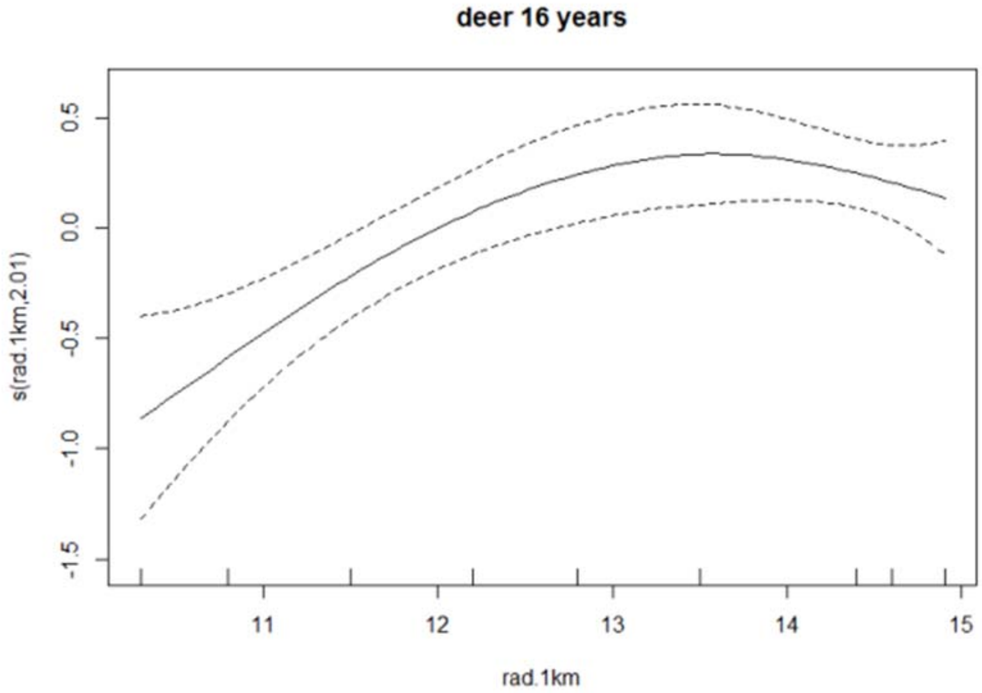

Figure 8. Smoother for solar radiation for deer from exploratory fitting of general additive mixed model (GAMM).

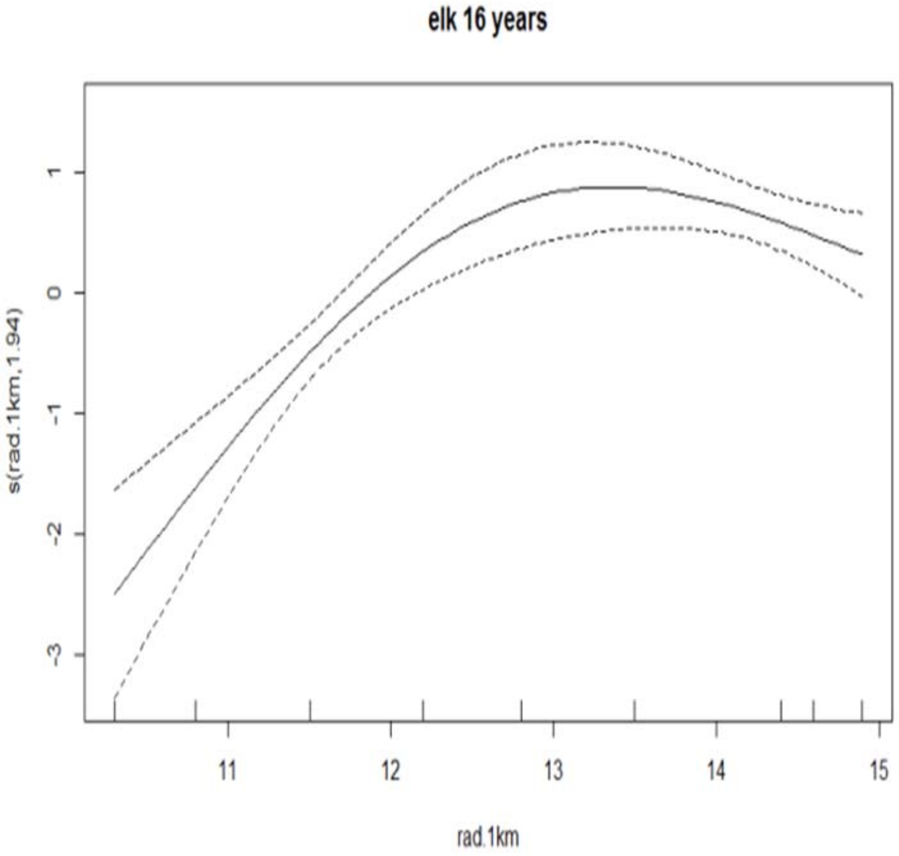

Figure 9. Smoother for solar radiation for elk from exploratory fitting of general additive mixed model (GAMM).

Deer

The observed crossings for deer from Phase 3A did not match predictions for Phase 1 and 2 along the time axis (Figure 10). While we had treated time as linear in the 10-16 year model, exploratory fitting of a GAMM to the data showed that time had a non-linear effect on numbers, most likely due to fluctuations in the deer population (Figure 11). Due to the irregular shape of the time effect, use of second and third degree polynomials did not improve model fit. The next step would consist of adding a smoother for year to the prediction function, and then assess predictive ability of the original model once again.

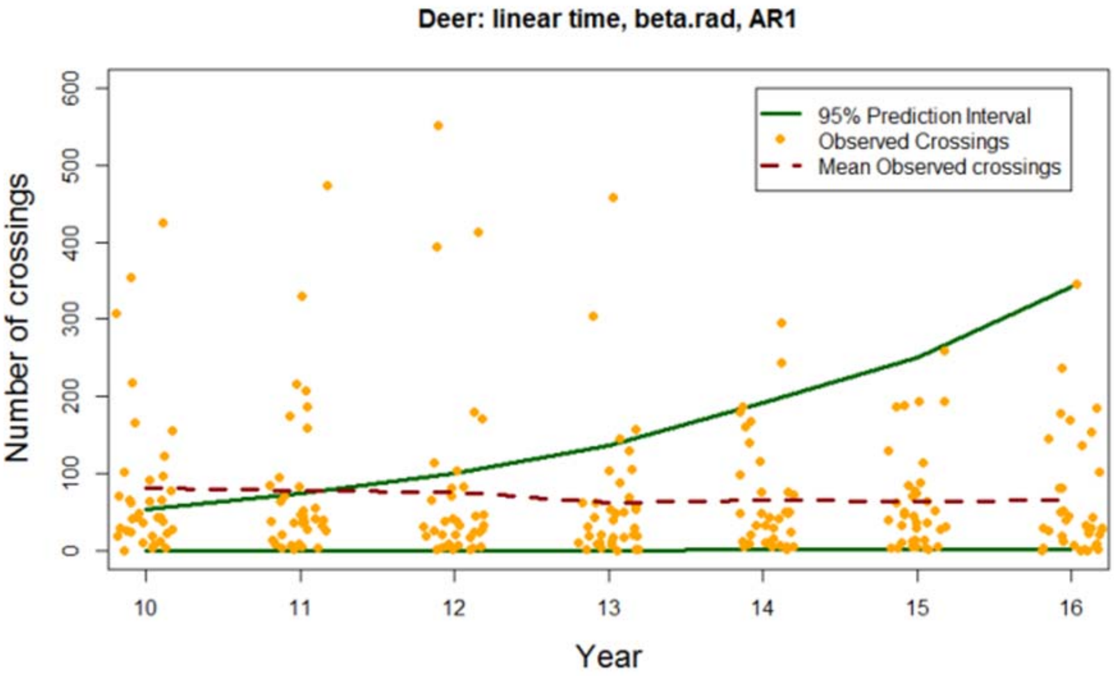

Figure 10. Predictive plots for deer applying Phase 3A model output to Phase 1 and 2.

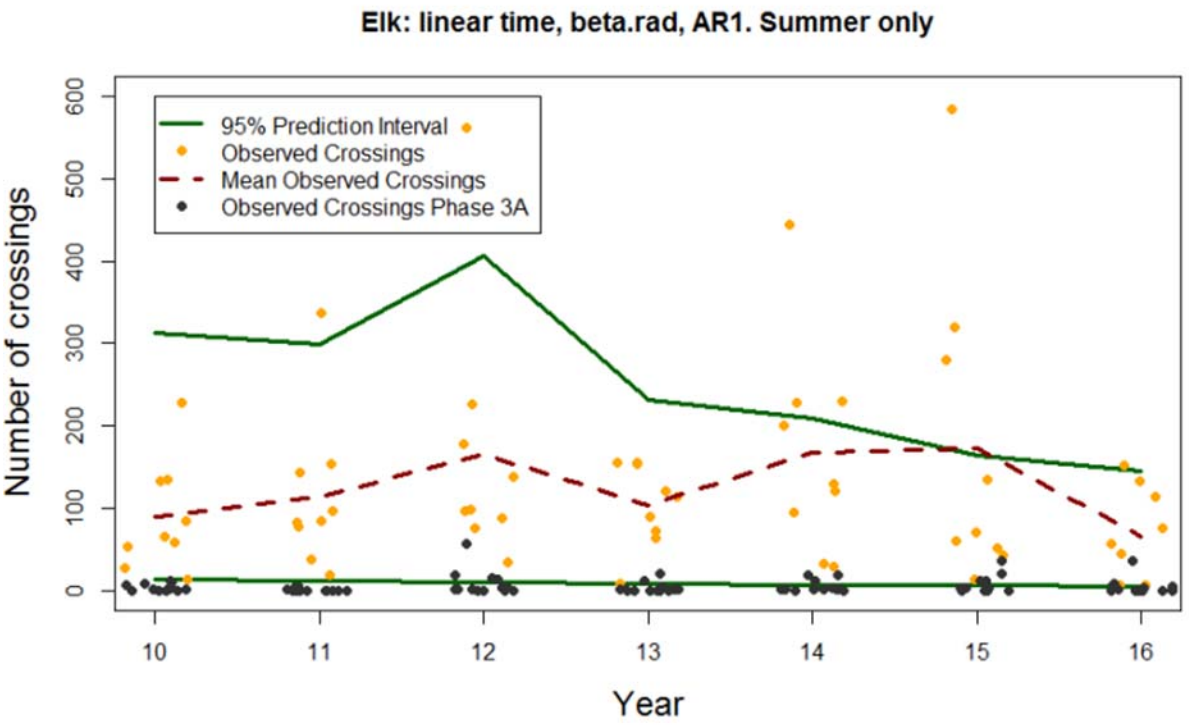

Figure 11. Elk prediction intervals for Phase 3A model output applied to Phase 1 and 2. Figure includes summer data only. In grey are the observed crossing numbers at Phase 3A.

Elk

The observed crossings for elk from Phase 3A matched the predictions for Phase 1 and 2. The prediction interval did not encompass all of the observed values, which may have been partly due to the omission of including random effects, and partly due to a larger elk population in that area compared to Phase 3A. We had used the same population numbers for both models, as they reflect the size of the Bow Valley herd, which is spread out across the entire valley, and centered on the Banff townsite (Hebblewhite et al. 2002, S. Michel, Banff Field Unit, personal communication). Elk crossing numbers at Phase 1 and 2 were an order of magnitude higher than at Phase 3A WC, which was captured well by the prediction interval (Figure 12). The two factors leading to the higher predicted values in these two phases were higher mean openness of WC (-0.51 vs. -1.06 at Phase 3A), as well as higher mean solar radiation values (16.29 vs. 12.96).

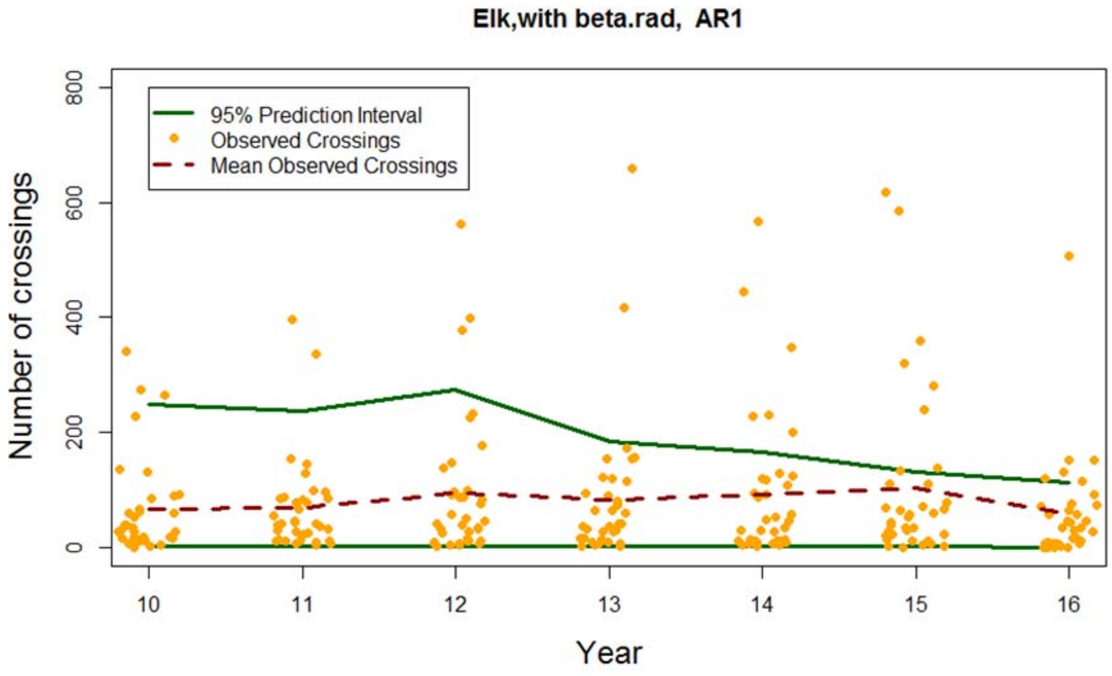

Figure 12. Elk prediction intervals for Phase 1 and 2, both winter and summer data. In grey are the observed crossing numbers at Phase 3A.

Grizzly bear

The chains of a GLMM fit to the data from years 10 to 16 (the stable period) did not converge well. We therefore based the predictions for years 10 to 16 on the full, previously developed 15-year model (see *Species Models* above). The resulting 95% prediction intervals for Phase 1 and 2, however, were large (Figure 13). This reflected the large amount of uncertainty in the model, making it unable to produce useful predictions for other phases. Since we were not able to develop a 4-year model in the previous section, we made predictions for Phase 3B (years 1 to 4) based on the coefficient estimates of the full model. While we had not used year 1 to develop this model, we did allow predictions to be made for year 1. Surprisingly, the 95% prediction interval captured the observed data well (Figure 14). The mean predicted crossings were slightly above the mean observed crossings, which, on closer examination could be attributed to the covariate *sqrthuman*, which had a positive estimate, and which was on average higher at Phase 3B (Figures 15 and 16).

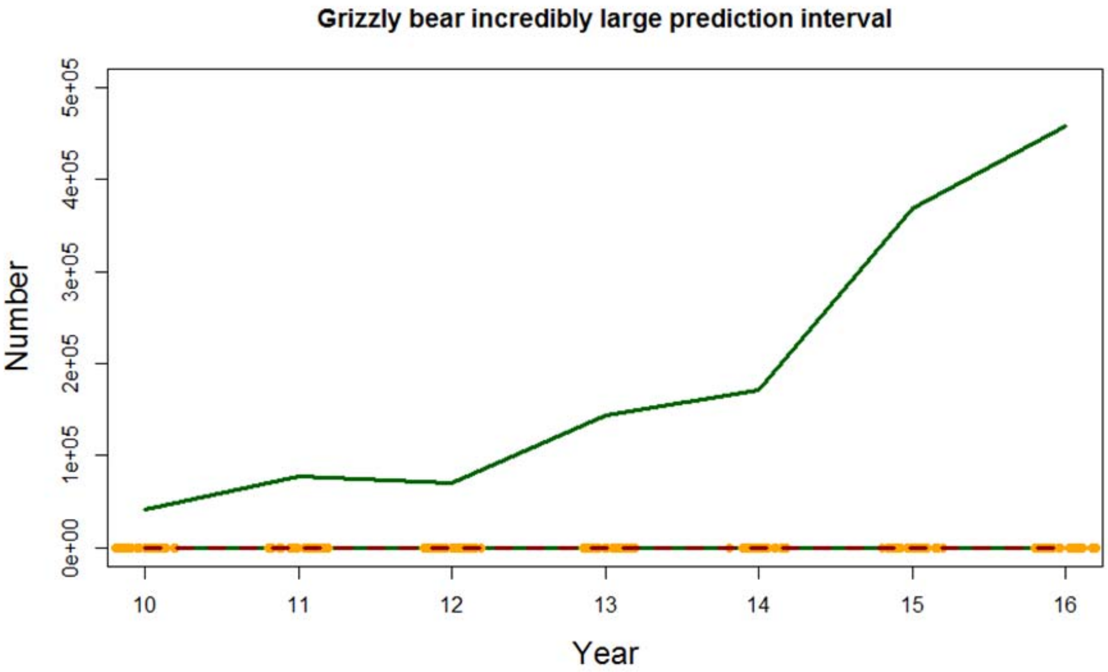

Figure 13. Grizzly bear prediction intervals for Phase 3A model output data to observed data on Phases 1 and 2.

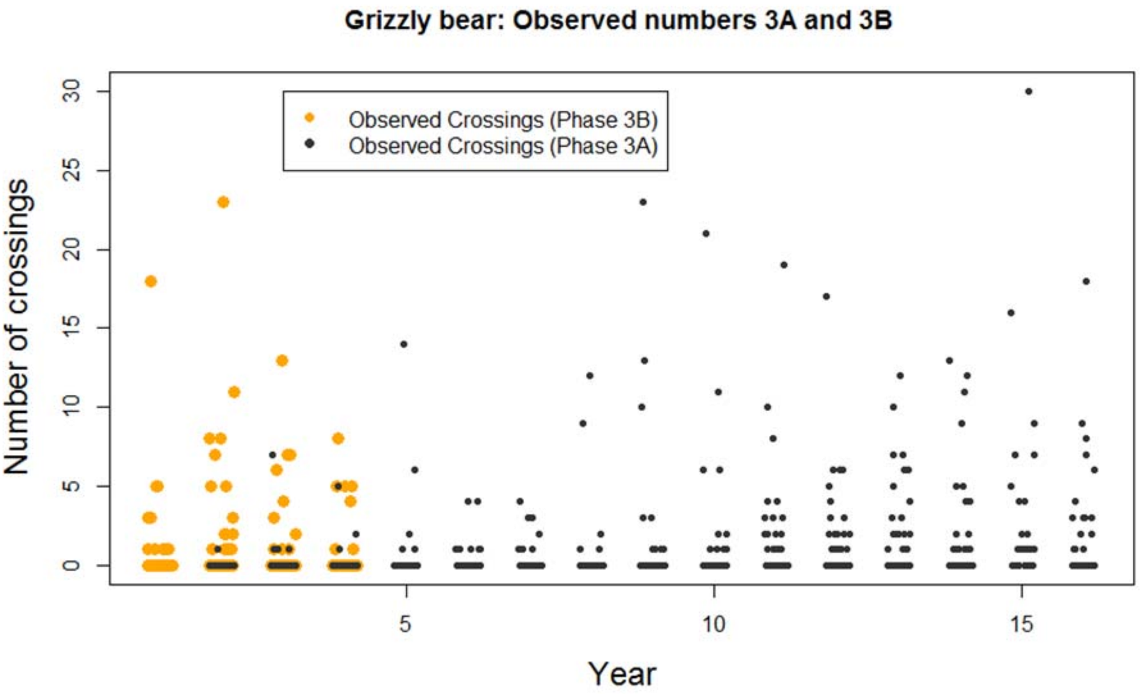

Figure 14. Observed grizzly bear crossings for Years 1 to 16 at Phases 3A and 3B. Note only four years of data for Phase 3B.

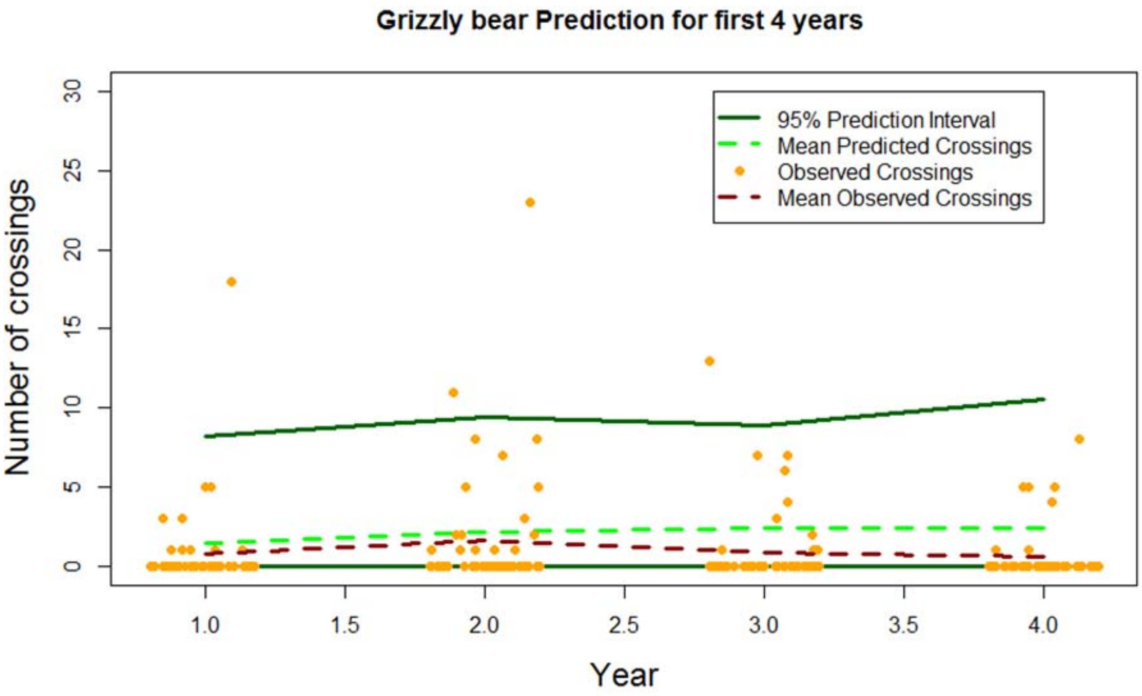

Figure 15. Grizzly bear prediction intervals for Phase 3B. The prediction interval includes the covariate “sqrthuman”.

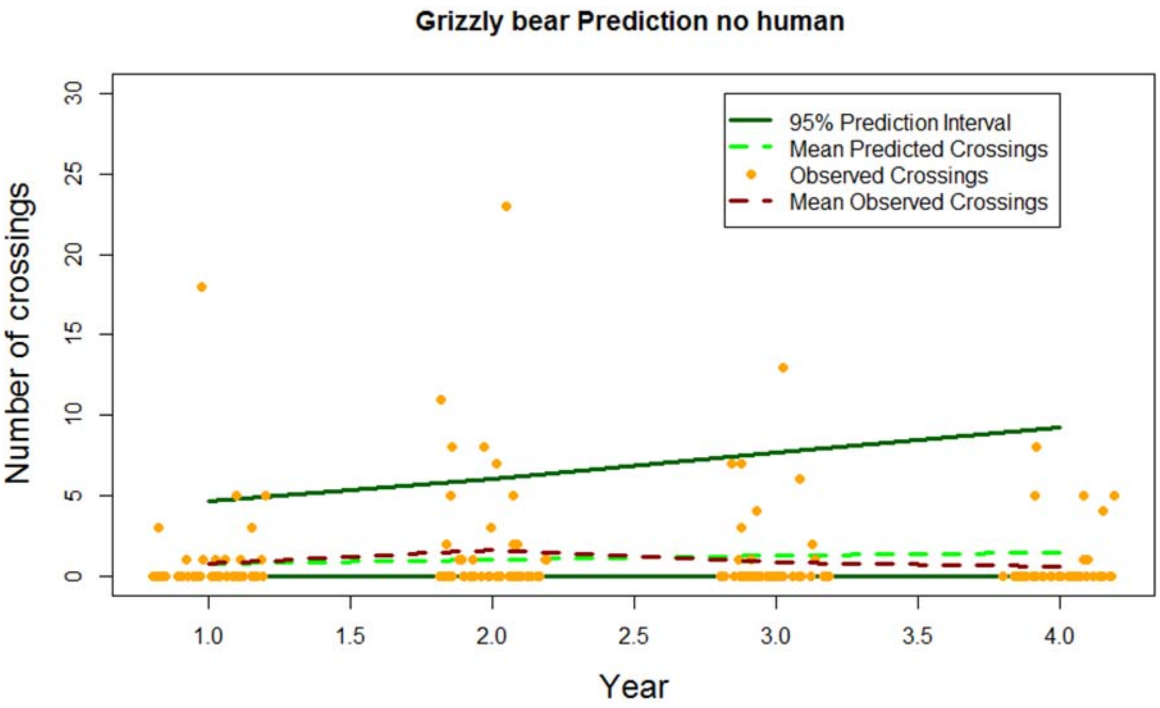

Figure 16. Grizzly bear prediction intervals for Phase 3B. The prediction interval does not include the covariate "sqrthuman".

Wolf

The prediction interval for Phases 1 and 2 fitted the Phase 3A observed data well, when looking at all seasons (Figure 17). Time was treated as a linear effect, which did not quite agree with the observed values. The summer and winter only predictions both yielded slight underestimations, which may be partly due to not having included random effects in the prediction functions. Especially observed, winter use of Phase 1 and 2 WC was higher than expected, with one or two outliers in each year. The prediction interval for Phase 3B, however, strongly overestimated wolf use of the WC (Figure 18). The main covariate that contributed to the large predicted values was openness, with WC in Phase 3B having higher openness values than those in Phase 3A (mean of openness of 0.07 vs. -1.06 at Phase 3A).

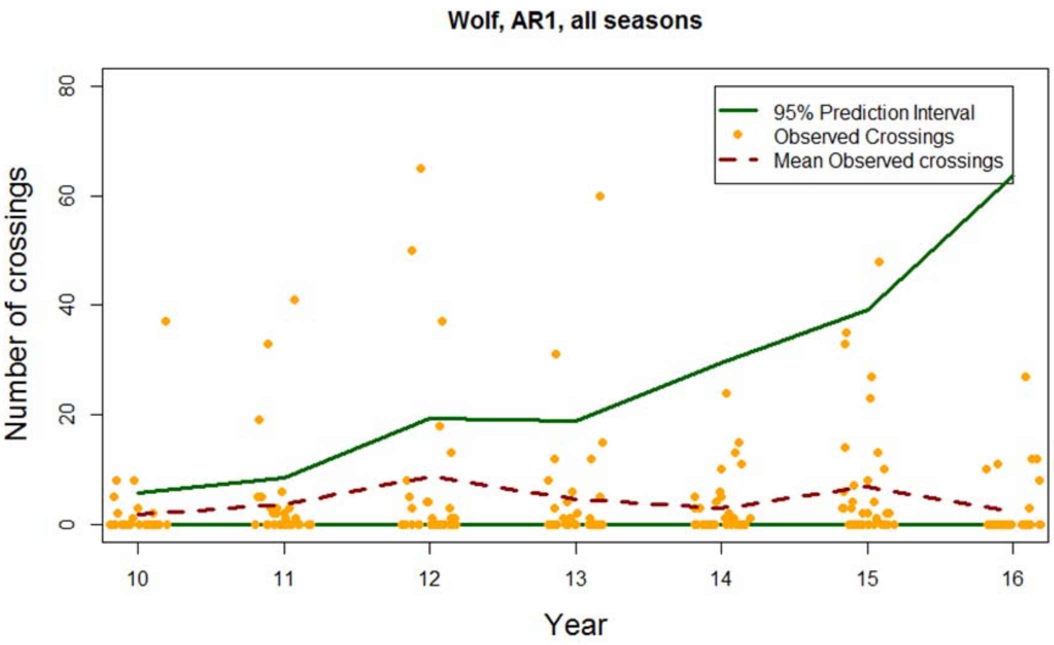

Figure 17. Wolf prediction interval for Phase 3A model output data for all seasons, Phase 1 & 2.

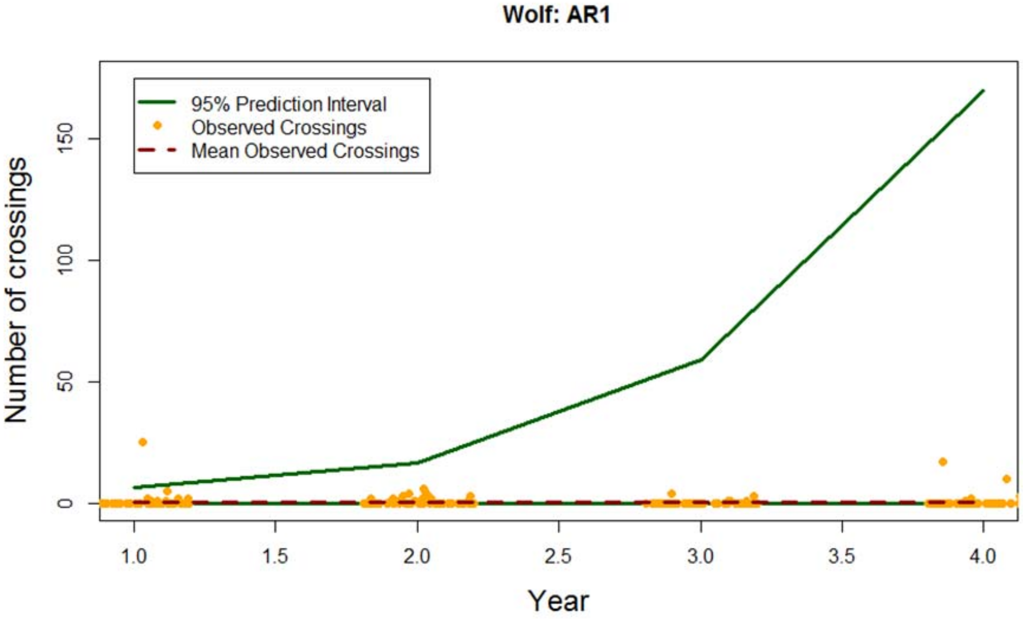

Figure 18. Wolf prediction interval for Phase 3A model output data applied to Phase 3B.

Discussion

Model Variation Over Time

The long-term data has been valuable in allowing for a time-sequenced analysis of the most important covariates explaining species use of WC. We successfully modeled the response of 7 of 8 species using the full 16-year dataset, while for one additional species we were able to model species response from a 15-year dataset. The 2-, 4- and 8-year data subsets were successfully analyzed in some of the species. Our results demonstrated that over long time periods there was marked variation in key drivers of models explaining species response to WC. The importance of covariates associated with the models changed dramatically over time for some species (cougar, coyote, grizzly bear, elk), while for others there were only slight changes, but counterintuitive changes in model predictors over the 16-year period (deer, wolf). This main result provides compelling evidence that short monitoring durations do not accurately reflect long-term responses of species to WC.

Our results imply that there can be substantial differences in how species respond to WC attributes and their surrounding environment over time. It will be important for managers to understand what might explain the underlying causes of model variation over time. Many of the changes in species response to WC we have documented in this analysis appear to be attributed to animals adapting or habituating to newly-constructed Phase 3A WC and increasing their use of those structures over time. This was particularly apparent for grizzly bears, cougars, elk and moose, which initially tended to use a specific WC type, but over time became less exclusive and used a greater variety of WC types and sizes as time progressed. Gagnon et al. (2011) found similar results from long-term monitoring (4-5 years) of elk use underpasses in Arizona. The number of key variables explaining elk passage decreased from year 1 to year 4 and appeared to habituate to underpasses, regardless of attributes, within approximately 4 years. Habituation over time has also been documented for increasing use of squirrel gliders to road crossing structures in southeast Australia (Soanes et al. 2013).

The ICC scores indicate that some species became more specific to WC over time (deer, wolf), while others were less selective and broadened their usage of WC types (elk, black bear, coyote). Consistent use of specific WC and high fidelity over time may be explained by species learning where WC are located and having them become established in routine travel to access food, habitat and/or dens. Incorporating a greater number and type of WC over time suggests individuals may learn that WC are safe passages and incorporate them into their daily and seasonal movements. Cougars were an anomaly with regards to the ICC scores as there was no apparent trend. At 4 years they were less specific than at 2 year and at 16 years they were more specific than at 8 years. We believe this reflects the highly dynamic nature of the cougar population in the Bow Valley, which is strongly influenced by wolf population dynamics and distribution (Kortello et al. 2007).

Species models

A review of the literature indicates that there have been mixed results regarding the relative importance of explanatory variables influencing wildlife movement at WC. The location and placement of a WC with regard to habitat quality have been main drivers in some studies (Yanes et al. 1995, Ng et al. 2004, Grilo et al. 2008, Gagnon et al. 2011). Other studies have shown that the dimensions or structure provide the best explanation for crossings (Reed et al. 1975, Cain et al 2003, Clevenger and Waltho 2005, Mata et al. 2005, Gagnon et al. 2011). Many of these differences in species response to WC have been explained by taxon- and/or habitat-specific factors.

Deer

Models indicated that deer reacted positively to the openness of WC, and this effect increased over time, preferring more open WC as time progressed. They also appeared to increasingly use only certain large structures, in contrast to other species use patterns. The initial eight years of increasing crossing numbers were likely due to an increase in size of the deer population at a time when elk numbers were decreasing in the Bow Valley (S Michel, Banff Field Unit, personal communication). Further, given the relative stability of the other factors in our models, initial acceptance of WC by deer was relatively quick, within only a few years.

Elk

Preferred WC for elk were those with high openness values, i.e., overpasses and large open-span underpasses. This preference diminished slightly over time; however, their preference for specific WC changed as shown by ICC scores decreasing from 0.722 at the 2YR model to 0.428 at the 16YR model. This suggests that while elk continued to prefer more open WC, they expanded the number of regularly used WC. We are unable to attribute this to a specific cause but may be a result of elk expanding their range in the Phase 3A section or habituation to greater number of WC along the TCH. Like deer, elk preferred WC with high mean solar radiation values. We used mean solar radiation as a proxy for snow cover during the year. South-facing slopes with high solar radiation values are regarded as high quality habitat for ungulates in Banff National Park (Woods et al. 1996) and less vulnerable to predation compared to north-facing slopes that are characterized by deep snow (Huggard 1993, Hebblewhite et al 2002). We found that human use had negative effects on elk use of WC, however the effect declined over time, suggesting habituation to this type of disturbance at

WC. This supports results from a previous analysis, where human use did not impact hourly elk crossing numbers between 2008 and 2012 (Barrueto et al. 2014).

Grizzly bear

Season, year, and WC type were the most important covariates determining grizzly bear crossing numbers. Grizzly bear use of WC showed a continuous increase over time with a slight decline at approximately 10 years (2007). The number of crossings was highly seasonal with most crossings occurring during summer. Grizzly bears showed a strong preference for overpasses in the 7YR and 15YR models. The interaction term between time and underpass preference was positive, suggesting that over time underpasses were more widely used by grizzly bears. In the 15YR models, WC density within a 1-km radius tended to have a negative effect on crossing numbers. Few WC have one or more WC within 1-km, the most noteworthy being the two wildlife overpasses (Wolverine, Redearth), each with an underpass $\leq$300 m. The large discrepancy of number of crossings at the overpasses compared to nearby underpasses likely explains this result. Human use had a slight positive effect on grizzly bear passage counts. The wildlife overpasses receive relatively high amounts of human use compared to most of the other WC, mainly people visiting the overpasses for educational purposes, e.g., field trips. We believe the effect is more of a correlation than causation, and the number of human visits (events) and number of people in each event is markedly different from underpasses such as Buffalo or Edith, where there are few recorded grizzly bear crossings. Last, ICC scores suggested that grizzly bears became less selective in WC use over time. However, compared to most other species we analyzed, they displayed relatively high ICC scores indicating relatively strong fidelity to few WC.

Black bear

The one consistent response of black bears to WC was their preference of long WC over time. While black bears did not prefer underpasses to overpasses, they did prefer narrow underpasses to more open underpasses. This might explain the effect of long structures - overpasses are relatively long, and underpasses with low openness may be relatively long also. This pattern conforms to evolved behaviour and life history trait for black bears. The longer, more constricted crossing structures black bears tend to use most for safe passage might be explained by these species' requirements for cover and avoidance of exposed, sparsely wooded habitats (Kansas and Raines 1990, Lyons et al. 2003). We suspect that affinity for cover may be heightened as these species enter inhospitable environments such as the TCH corridor and are faced with the task of traversing it. Interestingly, while we did not find strong evidence for general preference of underpasses in the current analysis, an earlier study based on the first three years of Phase 3A monitoring found that black bears do preferred underpasses to overpasses under certain conditions (Clevenger and Waltho 2005). When given the option of crossing the highway at an exposed wildlife overpass or an adjacent underpass (<300 m away), there was a greater tendency for black bears to select the latter (Clevenger et al., 2009). There are no annual population estimates for black bears in the Bow Valley and their numbers are believed to vary considerably year to year (S Michel, Banff Field Unit, personal communication). Black bear presence in the valley bottom and associated TCH corridor fluctuates annually and is likely influenced by fluctuating food availability (berry crops) and grizzly bear numbers and distribution (see Schwartz et al. 2010). The ICC scores suggested that black bears tended to use few WC initially but as time progressed utilized more structures for safely crossing the TCH.

Wolf

The number of wolf crossings increased over time suggesting that more individuals used the structures; this was confirmed from our classification of WC photos. We often were able to recognize individuals of local packs, as well as transients or individuals from outside packs, and the number of different individuals using the WC appeared to increase over the study period. Wolves did not change their preferences with regards to WC design over time, consistently using large WC, also when our analysis was restricted to just underpasses. The low ICC scores suggested that there was more variance within a given WC than between WC. This can be interpreted as lack of fidelity to specific structures, while maintaining a preference for certain WC types.

The resource selection function covariate did not have much impact on crossing numbers. It is probable that the spatial resolution of the RSF values was not adequate for this purpose. Also, it was interesting that wolves did not appear to be affected by the number of deer, elk or moose at a given WC in the same 3-month period. Yet, the structural preferences for deer, elk, moose and wolves were similar, all preferring more open structures, and deer and wolves increasingly so. Whether they prefer the same structures with more openness would have to be determined. Also both wolves and deer showed an increase in structure fidelity. While this may be coincidental, it hints at some connection. These results confirm our theory that on this time-scale (3 months), species interactions are negligible. However, on a more appropriate time scale (minutes to days), there may likely be a significant effect of predator-prey interactions - be it prey species avoiding an area immediately after use by a predator, or predator species following specific prey species individuals.

Cougar

Cougar crossings were best explained by time, season, WC type, and the percentage of shrub and grass cover around WC. Time was important and not linear. Like black bears, there are no population estimates for cougars in the Bow Valley and their numbers fluctuate considerably over time (S Michel, Banff Field Unit, personal communication). Wolves are the dominant predator in the Bow Valley and can kill or displace cougars and coyotes (Kortello et al. 2007) and previous monitoring of WC in the Bow Valley found spatial and temporal segregation of WC use by both cougar and wolves (Clevenger et al. 2002, 2009). Cougar numbers in the Bow Valley and use of WC will be highly variable as long as wolves are present. Previous research in the study area based on 3-year monitoring periods found a strong preference for constricted WC, particularly small underpasses with low openness values (Clevenger and Waltho 2000, 2005). However our results show an interesting trend where underpasses tended to be used most in the 4YR and 8YR, but then reversed in the 16YR model with greater use of the overpass structures. It is not clear whether the shift is WC use over time was a population-wide phenomenon or the result of a few individuals' preference. The increased use of overpasses may be explained by the dramatic change in habitat on the overpasses the 15 years since completion. Initially open habitat with sparse cover, the vegetation has become dense and matured, providing ample cover. Further, it is interesting to note that despite the limited amount of Phase 3B monitoring, there were only three documented cougar crossings: Two occurred at an overpass (Castle), while the other at open-span underpass with low vertical clearance (Moraine). The variable ICC scores over time suggest there was no apparent trend in how cougars responded to specific WC designs. The highly variable nature of their population suggests that individual behaviours will drive population level responses to WC, thus changing over long time periods beyond the timeframe of one or two generations. Gregory and Beier (2013) discuss a large lag time for using a certain response variable for assessing the effectiveness of landscape corridors. For cougars, with their low numbers and largely fluctuating populations in the Bow Valley, longer monitoring times may be necessary to identify the mechanisms underlying WC use. Additional research on cougar use of WC (with and without wolves) elsewhere will provide valuable comparative information.

Coyote

Coyotes utilized a wide variety of WC types, from overpasses to the smaller underpasses, and even some of the larger drainage culverts (Chapter III.6 and III.8). Also, coyotes can easily pass through small gaps in the wildlife exclusion fence and cross the highway that way (see Chapter II.1. *Effectiveness of Phase 3B mitigation to reduce wildlife-vehicle collisions*). Therefore it was not surprising to find that WC type had little effect on WC use. Coyote use of WC was non-linear in all models up to the 8YR model, and then started to decline and was still declining at year 16. Like most of the large mammals in our analysis, there are no population estimates for coyotes, however, their numbers are likely influenced by the wolves, which are known to kill or displace coyotes (Kortello et al. 2007, Berger and Gese 2007). Coyote use of WC was negatively affected by human use initially (2YR, 4YR models) but had not in the 8YR and 16YR models. Human activity and development was negatively correlated with coyote use of underpasses in southern California (Ng et al 2004). In previous work in our study area, Barrueto et al. (2014)

found similar results suggesting that coyotes tend to avoid WC with high human use in new phases (3A, 3B), but have more crossing events at WC that are heavily used by humans in the older, more established phases (1 and 2). However, at those structures, they adapted their diel patterns, and used the structures often during the night. Noise had a negative effect in the 2YR model, which eventually disappeared over time, further supporting a diminishing effect of human activity on coyote use of WC over time.

Moose

For moose it is apparent that more data needs to be collected to better understand the effects of structural and environmental factors influencing moose crossings. During our 17-year study, moose numbers have been steadily increasing from a few individuals after a liver fluke outbreak decimated the moose population in the 1980s and 1990s (Hurd 1999). Much of the increase in moose use of WC during the last 17 years may be attributed to a general increase in moose numbers in the Bow Valley. Our previous research suggests that early after construction there was a strong tendency for moose to nearly exclusively use overpasses (Clevenger and Waltho 2005, Clevenger et al. 2009). Our data is likely only preliminary, however, because 16 years of monitoring a reduced moose population will not likely provide robust information on moose WC needs. Currently there are conflicting results of moose WC selection from monitoring studies elsewhere. Moose tend to use a wide range of WC types along Highway 175 in Quebec, including underpasses with small openness ratios (Bouffard et al. 2012), while the opposite has been reported for moose response to WC along Highway US93 in Montana (Huijser et al. 2014). The high ICC value, as well as anecdotal data from the WC photographs, suggests that moose had high fidelity to few WC, and that their proximity to favoured habitat may have played an important role in WC selection, but this was not effectively reflected in the habitat covariates we tested.

Effect of elk population size on WC use

We were only able to test the effect of population size on response to WC for one species. Elk are the only species in Banff with sufficient long-term population survey data to use as a covariate in our models. The use of population size, e.g., abundance estimates, as a covariate was examined because previous work suggested there was a modest relationship between elk population size and crossing numbers at WC (Clevenger et al. 2009). If this relationship holds then 1) increases in WC crossing numbers should reflect increases in population size; but 2) may also reflect other factors such as individuals learning to use the WC or changes in habitat and species distributions at or adjacent to WC.

Due to the strong correlation of population size and time, the covariate year appeared to incorporate most of the effects of population size, making the effect of that covariate difficult to interpret. To better understand the pattern of the results, which were a negative effect of population size in the 16 year model, but produced mixed effects in the other three models, we fitted a GAMM to the elk data using gamm(). We used a two-dimensional smoother to allow for an interaction between time and population size. It appeared that elk changed their behaviour. Initially, while elk numbers were decreasing, following management measures to reduce their numbers around Banff townsite (B Fyten, Banff Field Unit, personal communication), WC use continued to increase. However, around year 4, WC use began to drop sharply even as elk numbers started to slowly increase again, apparently contradicting point 1). The reason for this however was probably not behaviour changes, but more likely changes in distribution of elk in the Bow Valley (Duke et al. 2001, Hebblewhite et al. 2002, B Fyten, Banff Field Unit, personal communication). Elk, especially cows, generally prefer areas with low predator presence, which is usually correlated with high and consistent levels of human activity (McKenzie 2001, Hebblewhite and Merrill 2009, Muhley et al. 2011). With the re-establishment of wolf packs centered east of the Phase 3A in the Bow Valley since the mid-1980s, wolf predation on elk has steadily increased, as wolves learned to take advantage of this resource (Hebblewhite et al. 2002, 2005). Consequently, while the Bow Valley elk population has been relatively stable during the last 12 years, after the initial management induced decrease, summer migration patterns have changed considerably, with relatively fewer individuals now residing along Phase 3A (B Fyten, Banff Field Unit, personal communication), leading to fewer crossing numbers at WC. These patterns underscored the difficulty of choosing appropriate population census numbers that take into account local population size, and also highlighted the need for knowledge with regards to local animal population dynamics, especially when they are highly variable and strongly influenced by human activity and disturbance. However, they also showed that in order to explicitly incorporate population size into these models, other methods may be more effective, e.g. adjust the crossing count for population size or include population size as an offset. The elk survey is the only formal long-term population monitoring work conducted in Banff. Yet even with elk survey data to account for fluctuating population levels, trying to measure relative changes in WC use has proven challenging.

Predictive Ability of Phase 3A data

The Phase 3A model was not a good predictor of WC use by deer on Phase 1 and 2. The time effect on WC use was non-linear and could be attributed to changes in deer numbers in the lower Bow Valley during the last decade. Because we combined mule and white-tailed deer in our analysis it is unclear whether the model would have been a suitable predictor of WC use at the species level. On the other hand, the observed Phase 3A crossings in general were good predictors of elk use of the Phase 1 and 2 WC. Despite the predictive ability of Phase 3A models, the predicted winter crossing numbers were lower than observed numbers on Phase 1 and 2. This discrepancy may have arisen because the WC on Phase 1 and 2 are primarily situated on a south-facing slope (hence the high solar radiation values), which is important elk habitat during winter (Woods 1990).

The predicted and observed grizzly bear crossing numbers at Phase 3B were much higher than at Phase 3A in the first few years after construction. In Phase 3B, a large proportion of human use occurred at the new overpasses during the first two years, as landscaping operations took longer than expected, resulting in relatively high levels of human use. Also, the largest wildlife underpass on Phase 3B, a large open span bridge on the Bow River (BOW), is often used by hikers, canoeists and kayakers. This large underpass is a natural movement corridor for many wildlife species and is frequently used by grizzly bears (see Chapter III.1. *Wildlife Crossing Summary Data* above).

The main difference in covariate values for Phase 3A and Phase 3B was a greater number of overpasses in Phase 3B (4 out of 17 crossing structures, compared to 2 out of 9 in Phase 3A). Particularly in the first few years, we found that grizzly bears strongly preferred overpasses to underpasses (see Species Models above). Another factor leading to larger predicted values were generally higher resource selection function values around Phase 3B WC (an average of 8.21 at Phase 3B vs. 7.42 at Phase 3A) suggesting that higher quality habitat in Phase 3B may be explaining earlier use and adaptation by grizzly bears.

The observed data for wolf WC use from Phase 3A fit the prediction interval well on Phase 1 and 2 when both seasons were combined. When we looked at prediction intervals by season, the models underestimated use but only slightly, which may be a statistical effect because random effects were not included in the prediction functions. Phase 3B use was overestimated compared to Phase 1 and 2. The main covariate that contributed to the large predicted values for wolves was openness, with WC in Phase 3B having higher openness values than those in Phase 3A (mean openness of 0.07 vs. -1.06 at Phase 3A). However, it appeared that either wolves did not react to this variable in the same way, or there were fewer wolves using Phase 3B compared to Phase 3A. The same wolf pack uses WC in both phases; therefore, we would not expect a different behavioural response to the Phase 3B WC, because they are familiar with WC on Phase 3A. The fact that the same wolf pack is using WC on both phases indicates that the wolf data are not independent. The more reliable evaluation of the prediction potential therefore would come from our Phase 3A model used to predict wolf WC use on Phase 1 and 2, since different wolf packs are found on each phase. Those models matched well observed wolf use during winter and summer.

Management Implications

We found marked variation in key attributes explaining species use of WC over time. The importance of variables changed substantially for some species, while for others the models only changed slightly. Further, we found mixed results using the long-term data set compared to our previous analysis of Phase 3A WC based on short-term (3 years) data (Clevenger and Waltho 2005). Deer, elk, grizzly bears, black bears and wolves responded similarly to WC openness in short and long-term. Black bears responded similarly to WC proximity to water in short and long term data sets. On the other hand, the effect of human use on crossings differed considerably between short and long term for deer, elk and wolves. Further, the distance to forest cover had high explanatory power for cougars in short term data set, while a strong negative effect was found in the long-term data. The results we present here suggest that monitoring efforts based on short time periods will not adequately explain long-term responses of species to WC.

Because species respond differently to the features of WC, mitigation planning in a multiple-species ecosystem will be a challenging endeavour. However, by examining long-term time-series data from multiple species, we have a much better understanding of what are the key factors that drive the observed patterns and relationships regarding WC use. Further, long-term time-series data has been valuable in supporting evidence that changes in use of WC design types reflects adaptation by some species to a wider range of WC types.

The ability of ungulates to habituate to WC has been documented elsewhere (Reed et al. 1975, Gagnon et al. 2011). Long-term monitoring was essential to describe changes in wildlife underpass use over time (Gagnon et al. 2011). Dodd et al. (2007) came to different conclusions regarding elk response to underpasses after 2.5 years of monitoring than Gagnon et al. (2011) did after 4 years. Monitoring plans will need to provide sufficient time and data to make strong inferences with regard to wildlife crossing performance. In our previous report to Parks Canada (Clevenger et al. 2009) we examined how animals responded or adapted to newly constructed WC because of the direct management implications for the newly constructed Phase 3B. We monitored the responses of multiple species to WC of varying age and design type. Our results agreed, lending evidence that that species are more likely to use crossing structures as time passes, even when controlling for the number of encounters at each WC.

The value of long-term monitoring of the TCH Phase 3B is critical to the maintenance of wildlife populations in Banff and the national park ecological integrity objectives (Banff Bow Valley Study 1996, Golder Associates 2004, Parks Canada 2010). Our analyses and results from time-series models provide stronger inference from past research we have conducted regarding attributes explaining WC use. These results will help inform future monitoring of WC in Banff and LLYK Field Units and highway mitigation projects elsewhere.

In view of the results from our long-term analysis we recommend that monitoring needs to be conducted over longer time periods than the usual 1-3 years as in most studies (Ng et al. 2004, Mata et al. 2005, Grilo et al 2008, Sawyer et al. 2012). Monitoring periods that incorporate adaptation periods for ungulate species should be at least 5 years in length, while for carnivore species a minimum of 7-8 years should adequately integrate species learning and adaptation.

Continued monitoring of WC Phase 3B will be particularly important given the presence of species of high conservation concern, such as wolverine and lynx, and current lack of information with respect to how two of these two species respond to WC (see Chapter IV.3). After 17 years of monitoring WC on Phase 1, 2 and 3A only 10 wolverine crossings were detected. Given the need for this information for both species and their relative low numbers compared to other large mammals in the Bow Valley, we strongly recommend that Phase 3B monitoring be conducted for a minimum of 10 years. The monitoring of WC should be conducted in conjunction with winter roadside surveys to investigate the number of highway crossings not detected at WC, breaches in fence and behaviour from snowtracking in the highway corridor. After a decade of monitoring and roadside surveys, an assessment should be made to determine how these two fragmentation-sensitive species respond to the highway mitigation (WC and fencing) and whether additional monitoring will be required. This approach will allow for an evidence-based assessment of WC performance in meeting the ecological objectives of the Phase 3B twinning project (Golder Associates 2004).

The second part of our WC analysis was to test the generality of our findings from Phase 3A using data from two separate but adjacent mitigated sections of the TCH. Using models developed from phase 3A data, we wanted to know whether these models could predict WC models for four key management species (elk, deer, wolf, grizzly bear) on completely different phases on the TCH. Our investigation shows that some Phase 3A models performed relatively well when explaining and predicting WC use over short and long time series, but in some cases others did not predict well and confidence intervals were extremely large, e.g., grizzly bear use on Phase 1 and 2.

It would be premature at this point to suggest that monitoring a subset of WC can provide results that align with sections with WC that are intensively monitored for wildlife use. As far as we are aware, no one has ever attempted to develop predictive models of WC use for their application to other WC on the same highway or elsewhere. While some of our results validate usage of WC models for predicting species use of WC, they also indicate that incorporating population processes can improve models and their accuracy.

We recommend continued testing of the predictive ability of WC models using independent data from other species and highway mitigation areas. The short-term response model would be the most logical approach to develop models, because there is only one other long-term data set (Gagnon et al. 2011). Candidate highways/species with adequate short-term data include State Route 260 Arizona/elk (Gagnon et al. 2011), Highway 93 South Kootenay National Park, B.C./ white-tailed deer, and US93 Montana/elk, white-tailed deer, mule deer, black bears. This meta-data approach should provide a better understanding of the predictive ability of WC models and would also enable a more robust analysis of species adaptation periods to WC in vastly different landscapes.

4. Wildlife Crossing Structure Location or Type: What is More Important for Grizzly Bears?

Introduction

Undoubtedly one of the unresolved questions regarding animal selection of wildlife crossing structures is whether the observed preferences of crossing structure types are absolute, or relative. Would an animal use a suboptimal or inferior crossing structure if it did not have a preferred structure nearby, or would it refrain from crossing the highway entirely?

In our previous analysis in Chapter III.3., we found that more large mammal species preferred overpasses or very large underpasses to smaller crossing structures. However, these larger structures are more costly to build (Huijser et al. 2007) compared to the smaller structures. Highway mitigation funds for wildlife are always limited on transportation projects. Thus, there is an inevitable decision that needs to be made early in the planning phase regarding how large and how many crossing structures is enough.

An experimental approach would be necessary to fully answer this question: comparing mitigated road stretches of similar length, in similar habitat with the same focal species but different arrangements of crossing structure type and density. To ensure independence, the different road stretches would need to be far enough from each other, in order to rule out presence of the same individuals. Obviously, this experiment is impossible to conduct; therefore we base our recommendations on the observations we are able to make and the most rigorous and well-designed analyses to address this question. Grizzly bears are an ideal species to test these questions because they have demonstrated a strong response pattern to wildlife crossing structure design types in the past and our current analysis (Clevenger and Waltho 2000, 2005; Clevenger et al. 2009; this report).

Healy underpass, the enigma

In Chapter III.3. of our report, we found that grizzly bears preferred overpasses to underpasses, but they did not exhibit any preference for underpass size. We also found that the forecasts for grizzly bear use of Phase 3B crossing structures were accurate, mostly because of the larger number of overpasses (n=4). When examining data from annual crossing frequencies between April 1, 2009 and March 31, 2014, the Healy underpass appeared to have more grizzly bear crossings than any other structure (Chapter III.1, Tables 1a-c).

Healy is situated in Phase 2, was built in 1987, and is considered among the older structures along the TCH (Bunyan 1989). The Phase 3A structures were completed in 1997. By 2009, not all of the structures in Phase 3B were completed (III.3 - Table 3). Thus comparing the pooled numbers for these five years is not objective because of the discrepancy in ages of the crossing structures. Therefore, we analyzed grizzly bear crossing data from 2006 to 2013, but also looked at the older data collected since 1997 to examine how grizzly bears used Healy underpass and other crossing structures.

Healy is a large, open-span crossing structure, situated near the confluence of three important drainages in the Bow Valley - Healy Creek, Brewster Creek and the Bow River. Arguably this crossing structure is situated near important montane, valley bottom habitat for grizzly bears, particularly the reclaimed Healy Pit area with its grass and berry patches, the riparian zones north and south of the highway, and occasional supply of wildlife carcasses deposited by park biologists. Therefore, it has likely become an important travel route for bears.

The next crossing structure, Wolverine overpass (WOP), is located about 2.5 km west of Healy underpass, without any obvious landscape feature nearby important for grizzly bear travel. WOP was built in 1997, sited in this particular location, not because pre-construction data suggested it was a well-defined travel corridor for large carnivores or other wildlife, but rather it was one of two important hot spots for ungulate-vehicle collisions (Anonymous 1995). The fact that WOP is situated primarily on a mesic, north-facing slope that descends abruptly to the south-side approach of the overpass structure led many to believe early on that WOP was not in the ideal location, compared to nearby Healy underpass, and would be underutilized (AP Clevenger, personal observation). However, nearly 20 years later, our long-term monitoring and data analysis of WOP with other WC in Banff strongly suggests that if an optimally designed WC is not in the natural or most suitable location, wildlife are capable of finding the structure, learn to use it, and eventually incorporate the crossing structures into their regular movement patterns in the Bow Valley.

WOP has become a highly frequented crossing structure for most large mammal species; even a wolverine was documented using it in November 2011. Despite its high conservation value as a critical cross-highway corridor, Healy underpass was important for grizzly bears and stood out as the one underpass that grizzly bears frequently used despite an apparent preference for overpasses. Incidentally, wolves also use Healy more than most other crossing structures (Chapter III.1, Tables 1a-c) and we suspect this is for the same reasons as grizzly bears, plus historically having had a wolf den near the Healy Pits. Preference by grizzly bears based on the number of times one underpass is utilized may be viewed as an ability of animals to adapt to suboptimal structures if they were situated in a preferred location.

The Family Group Effect

In our wildlife crossing structure analyses we used animal *sums*, i.e., the sum of all animals passing through a crossing structure within a 3-month interval. Another option would have been to use *counts*. As such, each group of animals passing through a given structure at once would be treated as one count, and then the sums of all counts over a 3-month period would be analyzed. For species that tend to travel in groups, e.g., elk, the difference between sum and count can be considerable. Most large mammal species in the Bow Valley, however, often travel alone or in small or family groups typically composed of a few individuals. The reason we used *sums* in our analysis was that one of the main goals of the highway mitigation was to restore or maintain demographic connectivity - allowing animals to freely and frequently cross the highway, so that territories and home ranges of animals could easily span both sides of the highway. We felt that the number of all individual animals crossing the highway better reflected if the crossing structures achieved this goal, rather than the number of animal groups. We also wanted to use the same metric (sums or counts) for all species, to allow for comparisons.

Grizzly bears in the Bow Valley generally travel alone, the exception being females with young and occasional siblings shortly after family breakup. During mating season, we occasionally observed male-female pairs travelling together at the crossing structures. The difference in using *sums* versus *counts* would therefore reflect mostly use by family groups. Generally, offspring follow their mother and do not make independent choices regarding movements and travel paths. A family group consisting of four bears (mother and three offspring) using one crossing structure preferentially will therefore strongly inflate the importance of this one structure in the analysis if *sums* are used. When the interest is in overall grizzly bear use of crossing structures, the potentially disproportionate impact of family groups could be problematic and using *counts* may be the better option. However, in marginal grizzly bear habitat such as Banff National Park, demographic connectivity may be as much or even more important than genetic connectivity. While genetic connectivity across the Trans-Canada Highway may be achieved with only a few crossings per year, bears need to be able to access critical habitat patches throughout the year in order to successfully reproduce, raise offspring and ensure they are recruited into the population and eventually breed. In this context, specific weight should be given to the behaviour of these family groups.

Sawaya et al. (2013) showed the proportion of all individual grizzly bears that used six different crossing structure types along Phase 1, 2 and 3A, in 2006, 2007 and 2008. Seven individual females and eight males were genotyped across all three years. It is striking that no female grizzly bears used medium sized or large culverts or creek bridge underpasses. While 5 out of 7 females used overpasses and 4 out of 7 used an open span structure (like Healy), only 1 of the 7 females was found to use box culverts. These numbers are conservative insofar as there were only two overpasses among the 22 crossing structures monitored during the study, and one of the females accounted for 18 of 47 (38%) female grizzly bear passages (Sawaya et al, 2013).

To better understand a potential family group effect on crossing structure use, we plotted the annual *sums* and *counts* of grizzly bears at each crossing structure since 2006 (Figure 1). Due to shortage of time, we did not adjust number of counts by camera days. The plots revealed an interesting pattern. As had been expected from anecdotal observations, the most frequently used crossing structures of Healy, WOP and Redearth Overpass (REOP), had in certain years much higher *sums* than *counts*. For Healy, this was the case in 2011, 2012, and 2013; for WOP in 2009, 2011 and 2012; and for REOP in 2006, 2007, 2008 and 2013. From 2006 to 2009, Healy had similar numbers (both *sums* and *counts*) to WOP. From 2006 to 2008, REOP generally had higher numbers than both Healy and WOP. However, this changed in 2009, when REOP numbers dropped drastically through to 2012. The slight difference between *sum* and *count* during these years suggested that no or few family groups used this structure during this period. In 2013, there was another large discrepancy between *sum* and *count* at REOP, this is likely due to five or more passes by adult female F64 and her three offspring.

F64 was known to use the area between 2006 and 2013. She had three cubs of the year in 2006, then only two remained with her in 2007, 2008, 2009. She had three cubs of the year again in 2011, and kept all three with her in 2012 and 2013. A second, unmarked female using the area and frequenting the crossing structures had two cubs in 2006 and was accompanied by the two yearlings in 2007. Another marked female, F130, had two cubs in 2011 and they accompanied her in 2012 (Steve Michel, Banff National Park Field Unit, personal communication). A few other underpasses were used occasionally by one or more of these and potentially other family groups (Figure 1), more so towards the end of the study. However, the three structures Healy, REOP and WOP saw the majority of all grizzly bear crossings. Interestingly, prior to 2006 there was no marked difference between *counts* and *sums* at any of the crossing structures, indicating that there was limited use by family groups at the structures.

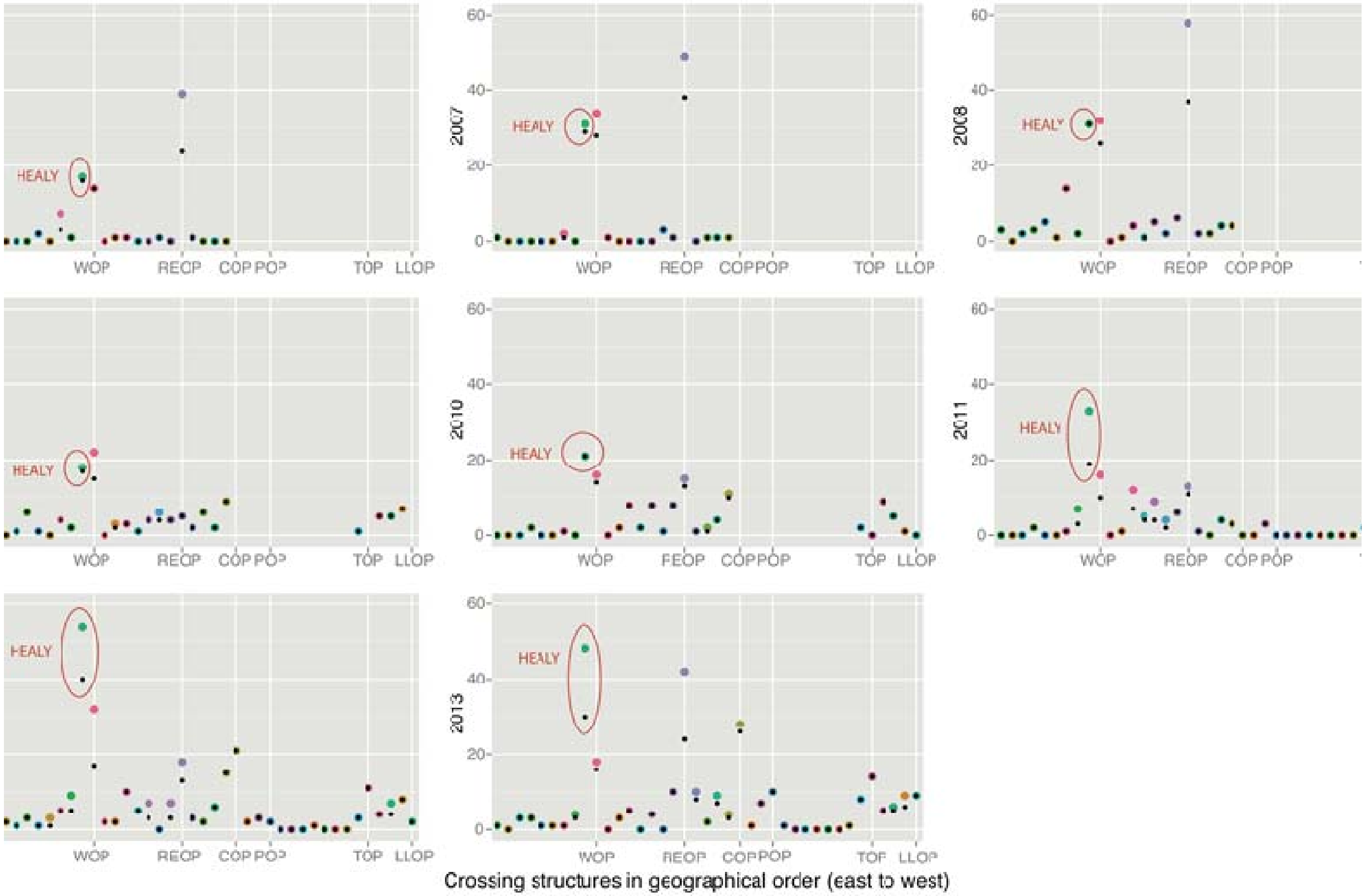

Figure 1. Grizzly bear use of crossing structures, by year, 2006-2013. *Sums* are shown in colour; *counts* are shown in black. Crossing structures are arranged on the X-axis in geographical order from east to west. Healy underpass is marked with a red circle. All overpasses are labelled on X-axis. Crossing structures without data points were not completed in the respective year. Numbers were not adjusted by camera effort.

New Crossing Structures at Phase 3B

In Figure 1, it is also apparent that three underpasses in Phase 3B, Temple underpass (TUP), Bow and Island (numbers 36, 37 and 38 on the plot, between Temple overpass (TOP) and Lake Louise overpass (LLOP)), had relatively high numbers of grizzly bear crossings essentially as soon as they were built. However, it also appears that once TOP and LLOP were built, crossing numbers in the area increased, with Bow and Island still receiving roughly the same numbers of crossings. Interestingly, grizzly bears appeared to shift much of their use from the underpass (TUP) to the nearby overpass (TOP; 1.2 km to the east). Moraine underpass, which is the next crossing structure 600 m east of TOP, received few crossings, except in 2013. Because we were only able to monitor three years after completion of the Phase 3B structures, it was not possible to develop mixed models to analyze patterns of crossing structure use on Phase 3B. However, the yearly numbers in Figure 1 suggest that grizzly bears preferred to use overpasses on Phase 3B (COP, POP, TOP, LLOP), and albeit less markedly, the large open span structures (Bow, Island, Storm (refer to Chapter II.1, Figure 1). Throughout this 3-year period, few if any of the small corrugated steel and concrete box culverts between POP and Moraine (depicted as blue squares; Figure 2) had any grizzly bear crossings, despite being situated in the area between the overpass structures.

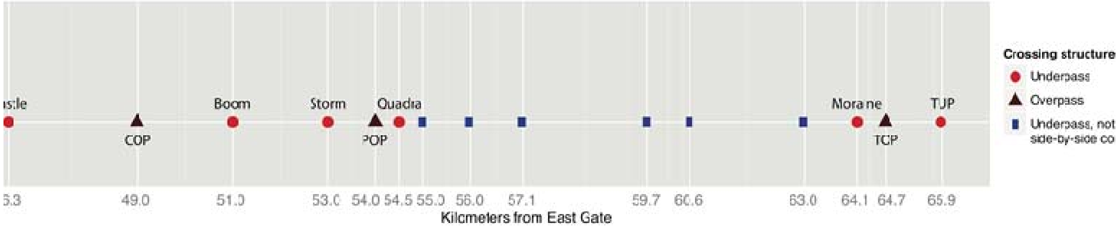

Figure 2. Location chart of crossing structures used in pair-wise comparison of grizzly bear use on Phase 3B of the Trans-Canada Highway. Kilometers on X-axis are measured as distance from the east gate of Banff National Park.

Most of these patterns were not surprising. First, previous multivariate analyses showed a preference of overpasses for grizzly bears (Clevenger and Waltho 2000, 2005). Second, the location of primary crossing structures on Phase 3B was determined by developing landscape resistance models and simulating movements of five species of large mammals (grizzly bears, black bears, wolves, elk, moose) within the Bow River watershed and across the TCH (Clevenger et al. 2002, Chapter 6). The mitigation recommendations by Clevenger et al. (2002) were spatially explicit, based on empirical data, and their movement models were validated with independent data. No mitigation planning projects at that time (2002) and few since then have been able to utilize such rigorous, spatially explicit information for guiding mitigation placement and design.

The placement and design of primary crossing structures consisting of COP, POP, TOP, LLOP and Bow (a very large open span structure) were based on the Clevenger et al. (2002)

recommendations; however, the locations of some primary crossing structures were moved slightly to be better aligned with engineering needs. COP, LLOP and Bow were built at the recommended location; however, POP was placed roughly 1 km east of the proposed site at Taylor Creek, with Quadra actually being closer (500 m) from the "primary" location. At Taylor Creek, a small box culvert was installed primarily for aquatic organisms, while the old Taylor Creek culvert (now dry) has to date seen only one documented crossing by a large mammal (coyote). Similarly, a primary structure was proposed at Moraine Creek; however, it was built 600 m away because the Moraine Creek underpass was designed for passage of harlequin ducks. The TOP was opportunistically built west of Moraine Creek because the terrain was favourable for an overpass, although it was not in the most suitable location (Moraine Creek) according to the landscape resistance models.

Pair-wise Comparison of Overpass vs. Underpass Use on Phase 3B

Previously we have shown that there are some preferences by species when we looked at a "side-by-side" comparison of overpasses on Phase 3A with adjacent underpasses less than 200 m apart (Clevenger et al. 2009). In those pairwise comparisons we found that grizzly bears, along with wolves, moose, and other ungulates prefer overpass structures when there is an underpass nearby.

To add to this body of knowledge and better understand the dynamics of grizzly bear crossings at new overpasses and adjacent underpasses, we conducted pair-wise comparisons of three overpasses on Phase 3B with their adjacent underpasses using data from the first few years after construction. We did not include LLOP, as it lacked any nearby underpasses during our period of study. All underpasses were situated within 0.5 to 2.7 km (Figure 2) of their respective nearest overpass - not a large distance for a grizzly bear to move. One of the overpasses (COP) was built on the recommended location in the Clevenger et al. (2002) report, while the other two overpasses were 600 m (TOP) and 1000 m (POP) off of the recommended location.

The annual frequency of grizzly bear crossings at the three overpasses (green) is shown in Figure 3: Castle overpass (COP), Panorama overpass (POP) and Temple overpass (TOP). The respective closest underpass to the east is shown in red, while the closest underpass to the west is shown in blue. Because camera monitoring or sampling effort was not equal at all crossing structures, we calculated the number of camera-days for each crossing structure. The first year in each comparison had low numbers of camera-days, as construction of some of the structures was just being completed. Monitoring of the new structures began immediately after construction. While Castle underpass, built in 1992, was monitored continuously since 1997, monitoring of COP began on September 13, 2011, and monitoring at Boom began on June 28, 2011. Storm was monitored since June 14, 2011, POP since September 12, 2011, and

Quadra since September 22, 2011. Finally, continuous monitoring of Moraine began before 2010, monitoring of TOP started in late 2009, but no monitoring took place at TOP between May 4, 2010 and November 20, 2010, due to ongoing construction work that summer. Since grizzly bears are active only in summer, this basically means that no grizzly bear crossings could be expected in 2010 for TOP. Temple underpass (TUP) was monitored continuously since 2009. While we adjusted the number of crossings ($X_{crossings}$) for the monitoring effort using the formula

$$X_{adj} = \frac{X_{crossings} * 365}{D_{effort}}$$

with D_{effort} being the number of camera-days, we did not correct for the fact that the probability of grizzly bear crossings is highest in summer, and virtually nil during winter. Figure 3 also displays the number of camera-days (D_{effort}) for each structure and year (coloured dots).

We found there was a remarkable increase in annual numbers of grizzly bear crossings at all overpasses over time (Figure 3). Castle underpass, which had been built in 1992, long before twinning occurred in that part of the highway, had fluctuating numbers of grizzly bear crossings from 2011 to 2013, but once the COP was completed in 2012, it appeared as if grizzly bear use was shunted from the underpass to COP. Boom underpass, a secondary structure and 2 km from the recommended location of a primary structure, had relative low but stable amount of use from 2012 to 2013.

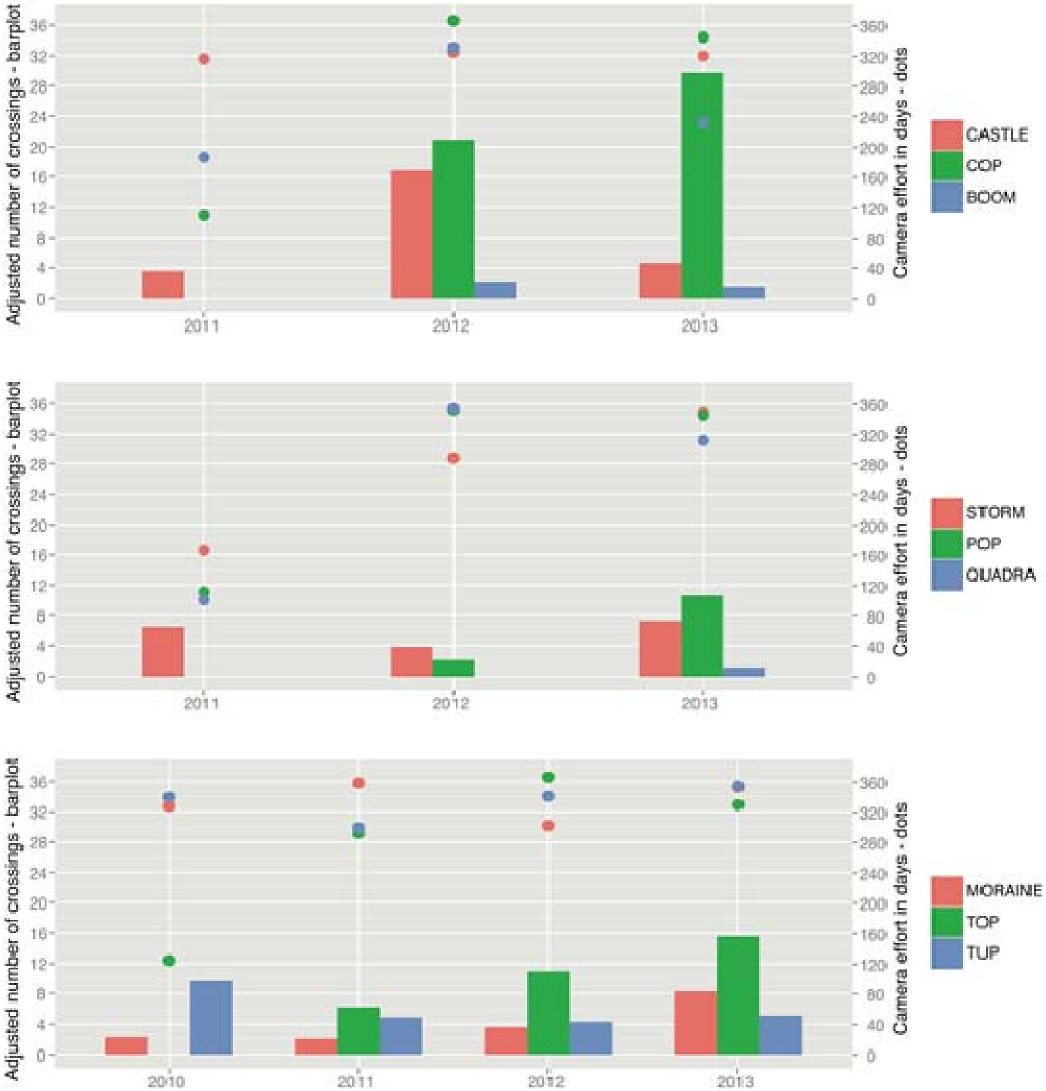

Figure 3. Pair-wise comparisons of annual grizzly bear crossings at newly constructed overpasses and adjacent underpasses on Phase 3B of the Trans-Canada Highway, Banff National Park. The values ($X_{crossings}$) were adjusted by the number of camera-days (D_{effort}), using the formula $X_{crossings}*365/D_{effort}$. Adjusted numbers of crossings are depicted as bars (left Y-axis). The number of camera-days for each year is depicted with dots (right Y-axis). Abbreviations for crossing structure names are found in text.

POP was completed in 2012 and grizzly bear use increased between 2012 and 2013. However, the Storm underpass was completed one year prior to POP and had fluctuating levels of use between 2011 and 2013. In 2012 there were more grizzly bear crossings at Storm compared to the first year of monitoring POP: however, the following year POP had a dramatic increase in use by grizzly bears, outnumbering those at Storm underpass. Quadra underpass, despite being 500 m closer to the primary structure location at Taylor creek than POP, saw only a fraction of those crossings during the first year monitored in 2013.

The same pattern of use was found in the vicinity of TOP, where both Moraine and to a larger extent, TOP, recorded an increasing number of crossings, while the frequency of crossings at TUP remained relatively stable after an initial decrease. It is likely that TUP saw a high frequency of crossings in 2010 because of ongoing construction and landscaping taking place on TOP, rendering it virtually unavailable for grizzly bears. Interestingly, both TUP in 2010, 2011 and 2012, and TOP in 2011 to 2013 saw more crossings than the Moraine Creek underpass, despite Moraine Creek being situated in a high frequency crossing zone (Clevenger et al. 2002).

Conclusions

Our analysis of the importance of crossing location or structure type for grizzly bears is qualitative and was not conducted using an experimental design. Nonetheless, a number of salient points for future transportation management can be highlighted.

At Phase 1, 2 and 3A, the larger crossing structures consisting of Healy, WOP and REOP saw the majority of grizzly bear use across all years (1997 to 2013). Healy underpass is situated in an area of confluence of major drainages in the Bow Valley, it is close to some of the more productive habitat patches in the Bow River watershed, and has the added potential benefit of a large carcass disposal nearby since 2007 (S. Michel, Banff Field Unit, personal communication). Despite these site attributes of the Healy underpass, WOP saw similar numbers in all years but 2012 and 2013, particularly if *counts* are used. From 2006 to 2008, females nearly exclusively used overpasses and open span structures (Sawaya et al. 2013). Furthermore, when we look at a much longer time-series from 1997 to 2013, females with cubs crossed the TCH most often at Healy, WOP and REOP, while rarely using the other structures. On Phase 3B, there was an apparent trend towards a higher proportion of overpass crossings occurring over time, and an overall increase in crossing numbers along with the annual increase in overpass use. We were able to demonstrate this trend at all three Phase 3B overpasses, despite the fact that two of the three overpasses were not placed in the recommended primary location and secondary structures were built in their place.

While grizzly bears in the study area, especially males, appear to have adapted to and eventually used all types of crossing structures, the smallest crossing structures remain virtually underutilized 17 years after construction. There is a clear threshold for what grizzly bears will use and not use. That threshold consists of overpass and large span structures, while structures the size of 4 x 7 m corrugated steel culverts and smaller are underutilized and appear to be of little conservation value.

How much behavioural plasticity grizzly bears are able to display with regards to using small structures if the large, preferred ones are *not* available, remains speculation. However, based on the data we present, we predict that in absence of preferred structure types, there would be sex-biased dispersal across the TCH with primarily male dispersal and no or limited female dispersal across the highway. This pattern of sex-biased dispersal is in essence what has been found elsewhere on highways where mitigation measures do not exist for grizzly bears: Highway 2 in Glacier National Park (Waller and Servheen 2005), Highway 3 in Alberta and British Columbia (Proctor et al. 2012), and the TCH in Banff National Park prior to mitigation (Chruszcz et al. 2003).

Non-lethal effects of highway mitigation have not been addressed in any study we are aware of and they are rarely even considered, but they could be as influential on population persistence as direct effects. Stress can affect physiology, behaviour, and demography of wildlife (Romero 2004). Animals that use crossing structures to access critical habitats and food resources may experience increased health (i.e., survival) and reproductive fitness. We know the Banff crossing structures positively affect bear survival and provide demographic benefits by reducing mortality (Clevenger et al. 2009, Sawaya et al. 2013). However, crossing structures can also increase access to important food resources and cover, and allow escape from predation by other bears. Sawaya et al. (2013) believed that repeated visual observations of bears foraging in the small strip of riparian habitat between the TCH and the Bow River suggested that crossing structures in Banff play an important role in allowing access to seasonal food resources (particularly in spring) that may be especially important to one of the most fragmented, food-stressed, and human-influenced populations of grizzly bears on the planet (Gibeau et al. 2002, Chruszcz et al. 2003). Even though just a few individuals accounted for the majority of female grizzly bear crossings in their study, grizzly bear use of crossings were considered crucial to maintaining population viability, because even slight changes in adult female survival can strongly affect population growth rates for grizzly bears in Banff (Garshelis et al. 2005).

We believe that demographic connectivity of grizzly bears across the TCH is more of a concern than genetic connectivity. The impacts of demographic effects (mortality or reduced reproduction) can be seen in one or two generations' time, while genetic effects take many generations to manifest (Forman et al. 2003, Jackson and Fahrig 2011). This is particularly true in Banff where the effective population size of grizzly bears on both sides of the TCH is large, numbering several hundred individuals on each side of the highway. The results from our analyses of a long-term data set strongly suggest that the recommended mitigation strategy for grizzly bears in protected areas of the Canadian Rockies will be to provide grizzly bears with large crossing structures, preferentially overpasses and only large open span bridge underpasses in areas known to be critical cross-highway dispersal corridors. Failing to do that will likely result in filtered and sex-biased movement of grizzly bears across the TCH; these movements will have harmful demographic effects (primarily on reproduction and survival) and decrease the long-term viability of the Banff grizzly bear population.

5. Anthropogenic Effects on Activity Patterns of Wildlife at Crossing Structures

The results of this research have been published in the journal *Ecosphere* as "Anthropogenic Effects on Activity Patterns of Wildlife at Crossing Structures." The abstract is included here, and the full text is included as Appendix B.

Abstract

Despite the popular perception of protected areas as vestiges of remnant wilderness, the behavior and activity patterns of wildlife in these areas are still subject to many forms of anthropogenic disturbances, such as roads, recreation and resource extraction. In Banff National Park, Alberta, efforts to mitigate the effects of roads on wildlife using wildlife crossing structures (WC) have been successful for a number of large mammal species, when measured as a reduction in mortality from vehicle collisions or the restoration of population connectivity; however, a comprehensive view of mitigation success should also account for the restoration of animal behavior and activity patterns. We evaluated the general hypothesis that existing WC have mitigated the effects of anthropogenic disturbance on wildlife activity, and predicted that the activity patterns of wildlife at WC should be similar to those in areas characterized by little or no human disturbance. We collected data from a long-term monitoring program of activity patterns, in an assemblage of large mammal species, using a network of camera traps throughout Banff National Park. We quantified the inter- and intra-specific overlap of diel activity patterns at 39 engineered wildlife crossings, varying in design (e.g., over and underpasses) and age. We compared activity at WC to baseline conditions at 126 backcountry sites (BC). In general, activity patterns at WC were found to closely match those at BC. Of the eight species we examined, only elk and coyotes showed significantly different peaks in activity. Activity between WC depended on the time of day, the amount of human use and age of the crossing structure; however, the impact of these factors varied among carnivores and ungulates. Our work demonstrates that the impact of people on wildlife activity at WC is highly context dependent and that the restoration of native patterns of activity within protected areas will require management of human activity, even in relatively remote areas.

6. Response Behaviour of Wildlife at New vs. Established Crossing Structures

Authors: Mirjam Barrueto and Anthony P Clevenger

Introduction

The combined effects of a twinned highway with more lanes for traffic on the Trans-Canada Highway (TCH) in Banff National Park, Alberta, threaten to fragment wildlife habitat and populations (Golder Associates 2004). Building environmental mitigation to correct these impacts should enhance ecological connectivity throughout the project area to link habitats for multiple species and ecological processes over time. The desired ecological condition requires improving the permeability of the highway for all organisms, reducing risks of road-related mortality of wildlife (see Chapter II), and providing for the long-term sustainability of populations in the area.

Monitoring is required to further elucidate the interactions of Valued Ecosystem Components with environmental mitigation in order that the impact predictions of the environmental assessment can be validated (Golder Associates 2004). The Golder report indicated that monitoring should include the following:

- Wildlife use of crossing structures (see Chapter II and III)
- Habitat connectivity and genetic interchange for key species (see Chapter IV)

The Golder report further emphasizes the importance of rigorous, evidence-based monitoring and research of the environmental mitigation over a 5-year period. We are unable to report on the recommended 5-year monitoring because mitigation construction was delayed and by the time our 5-year research project was completed most of the 21 crossing structures had been in place for only 2-3 years and four of those structures were only completed in November 2013.

In this report, we assessed the use and effectiveness of wildlife crossing structures and culverts during the 5-year project. The response of wildlife to different crossing structure design types were measured in two ways: (1) multivariate analysis of attributes of crossing structures that facilitate movement by large mammals, and (2) measuring behavioural responses of large mammals to crossing structures from remote camera monitoring at their entrances. Using short-term data available from the “new” Phase 3B crossing structures we compared rates of passage/avoidance with “old” established crossing structures.

Similar work with the same objectives was performed on previous TCH mitigation phases, not using cameras but conducted through snowtracking at the entrances to crossing structures during three winters (see Clevenger et al. 2009, Ford and Clevenger 2010). Unlike the multivariate analysis in Chapter 3 of this report, the response behaviour of wildlife approaching crossing structures is assessed from camera placed outside the crossing structures. This will provide supplemental information on how different large mammal species respond and perhaps eventually adapt and start to use crossing structures.

Methodology

Study Area

Banff National Park is situated approximately 150 km west of Calgary, Alberta, in the Bow River Valley along the Trans-Canada Highway (TCH). The TCH is the major transportation corridor through Banff National Park, covering roughly 80 km between the park's eastern and western boundaries. In the 1970s, safety issues compelled planners to upgrade the TCH within Banff from two to four lanes, beginning from the eastern boundary and working west (Ford et al. 2010). Large animals were excluded from the road with a 2.4-m-high fence erected on both sides of the highway, and underpasses were built to allow wildlife safe passage across the road. The first 27 km of highway twinning (Phases 1 and 2) included 10 wildlife underpasses and was completed in 1988. Fencing and wildlife crossing structures on the next 18 km section (Phase 3A) was completed in late 1997 with 11 additional wildlife underpasses and two 50-m wide wildlife overpasses. The final 30 km of four-lane highway to the western park boundary (Phase 3B) includes 21 crossing structures, including four, 60-m wide wildlife overpasses and was completed in late 2013.

Methods

Since 2005, motion-sensitive digital cameras (Reconyx Inc., Holmen, Wisconsin) were used to supplement track pads to monitor species use of the crossing structures (Ford et al. 2009). Cameras were located within or adjacent to (ca. 15 m away) from wildlife underpasses and on top of and at the center of wildlife overpasses. All cameras used in this study provided metadata on date, time and ambient temperature during each crossing/passage event (Barrueto et al. 2014). Once set up, all cameras were running 24 hrs/day, year round, but with occasional periods of camera malfunctioning and/or premature battery failure. Cameras were checked for operation (battery life) and CF/SD cards were switched out every 2-3 weeks year-round. Camera data collected at crossing structures were stored in Microsoft™ Access and Excel databases on the Parks Canada server in Banff National Park, Alberta (Barrueto et al. in press).

Data collection for this analysis consisted of "outside-structure" camera monitoring to obtain avoidance rates at crossing structures. Crossing structure design types on Phase 3B consisted of: 60-m wide overpass, 18-m wide open-span underpass, Bow River Bridge underpass, 8 x 3 m underpass, 4 x 7 m elliptical underpass, and 2.8 x 2.6 m concrete box culvert. Cameras were placed at crossing structure types that afforded replicates and comparisons with old vs. new structures. Remote cameras were placed at both entrances at each crossing structure and situated ca. 15 m away and in plain view of the entrances. To control for the effect of crossing structure design in the analysis we focused exclusively on elliptical underpasses with dimensions approximately 4m x 7m on the "new" Phase 3B (n=4; Temple, Babel, Quadra, Boom) and "established" Phase 3A (n=4; Wolverine, Massive, Copper, Castle). Data for this analysis was derived from cameras only. We used data collected from 2009-2014 at the new Phase 3B structures and from 2007-2014 at the established Phase 3A structures.

We attempted to identify photographs to species level. There are numerous wildlife species in our study area; however, for this exercise there were few species with sample sizes that merited attention. Mule deer *Odocoileus hemionus*, white-tailed deer *O. virginianus*, elk *Cervus elaphus*, wolves *Canis lupus* and coyotes *C. latrans* were selected based on sample size. Because of their similarity in habitat use and life-history, and occasional difficulties in distinguishing the two deer species from some of the low-quality nighttime photos, we pooled the two *Odocoileus* spp. (hereafter referred to as "deer spp."). The analysis was conducted at a species level, pooling data from both sexes and all age classes. Counts were used rather than the number of animals because individuals in groups are usually not independent, particularly family groups.

For each attempted crossing event behaviours were classified as:

- A = outside structure avoidance (ignores structure, does not approach).
- NH = No passage, after hesitation.
- T = No passage, turned around.
- No = No passage.
- H = Hesitates, then confirmed passage
- Y = No hesitation, confirmed passage
- Yes = Yes passage (these entries were yes/no entries, but without information about hesitation)

We opted to use proportion tests rather than t-tests in this analysis because of the limitations due to the small sample size for most species (Zar 1999).

Results and Discussion

Deer

We ran a proportion test between the proportions of the number of times deer passed (H, Y), when approaching, and did not pass (NH, T). We did not include the Yes and No entries, because we were not confident that the No entries may have also included "outside structure avoidance" events, and not just hesitant/turned around attempts.

The new structures had a slightly higher avoidance rate (26.6%) compared to the established structures (23.7%). The proportion test was not significant (X-squared = 0.3923, df = 1, p-value = 0.5311). The proportions of deer passing and not passing when having approached did not differ between the new and established crossing structures.

We then ran tests just between the proportions of the different behavioural responses between new and established structures, for the passages and the non-passages (Table 1). To calculate the *total* numbers (to be able to get proportions), we did not include the entries "Yes" and "No", as they did not have any behaviour assigned to them. We found that the passage proportions (Y-H and Y-Y) were similar to the proportion test between the passage behaviours and was not significant (X-squared = 0.3752, df = 1, p-value = 0.5402). However, it appeared there was more avoidance by turning around (N-T) at the new structures. To test this, we conducted proportion tests and found it was highly significant (X-squared = 21.70, df = 1, p-value = 3.178e-06), i.e., the proportion of animals that actually entered the structure but then turned back (rather than just approached, hesitated and left again) was higher at established structures.

Table 1. Proportion deer behaviours of total behaviours classified. Behaviours consist of: N-H = No passage, after hesitation; N-T = No passage, turned around; Y-H = Hesitates, then confirmed passage; Y-Y = Yes passage.

	N-H	N-T	Y-H	Y-Y
Established	0.096	0.140	0.104	0.659
New	0.216	0.033	0.116	0.583

Elk

There were few data on non-passages from the new Phase 3B section as we found only one *entered-turned back* event, thus making any testing difficult. Nonetheless, we calculated the proportions of No and Yes passages at new and established structures and found the proportion of non-passages was lower at the new structures. The fact that there were only 16 elk events collected here suggests there is little statistical strength in these results.

When we looked at through-passage by elk, there was an issue with the small sample size; only 12 records at the new structures. Sample size aside, we found there was slight differences in proportional avoidance between new and established structures.

Wolf

Similar to elk, there were few data for wolves, primarily lacking data at the new structures. There were only 16 records, all but one were passage by wolves with no hesitation at the crossing structures. When we looked at the proportions of passage to no-passage there were only slight differences between new vs. established structures.

Coyote

Similar to elk and wolves, there were few data from the new section to test for differences between new and established structures. Looking at the numbers themselves, there were proportionally more no-passages by coyotes at established structures than new structures.

Conclusions

Our conclusions are based on an analysis that suffered from insufficient data from the newly established Phase 3B crossing structures compared to Phase 3A. For only one species was there sufficient data to evaluate differences between response behaviour at new vs. established crossing structures. Although we found there were only slight differences in deer behaviour between new and established, we caution that the tests are conservative (not all entries were included – see Methods). There was only a slightly higher avoidance (turnaround) rate by deer at the new structures compared to the established. The apparent lack of deer avoidance of new structures may be explained by their tendency to adapt more easily to crossing structures and more quickly than other large mammals in our study area (see Chapter III.3.).

These recent results contrast with results obtained from snowtracking deer during three winters between 1997-2000 at new (Phase 3A) structures compared to established structures on Phase 1 and 2 (Clevenger et al. 2009). We were unable to standardize for structure type as in our current analysis; however, we grouped crossing structure types by similar design and dimension. We detected substantially higher avoidance rates within a 100-m radius at new Phase 3A crossing structures compared to established structures; 15% vs 30% at creek bridge underpasses and 13% vs. 43% at small culverts. Sample sizes were also small but the pattern of higher avoidance at new compared to old held for nearly all species and crossing structure type comparisons.

The differences between our previous study and the results we present here may be attributed to differences in data collection. Snowtracking animal movements within a 100-m radius of a crossing structure entrance will likely provide more information and more reliable data on how species respond to a fenced highway with crossing structures compared to camera monitoring within a 15-m focal distance of a structure. Camera monitoring is a simpler, more cost-effective and time-efficient method compared to snowtracking, but may be more biased by detecting individuals that have approached within 15 m of crossing structures and have largely committed to passing through. Because snow tracking gathers data from a larger and wider area around the crossings, it will most likely result in larger sample sizes and behavioural information from individuals beyond the 15 m around crossing structures.

7. Bighorn sheep, Mountain Goats, and Wildlife Crossings in Banff National Park, Alberta

Authors: Anthony P Clevenger, Alan Dibb, and Mirjam Barrueto

Introduction

During the last 17 years our research has focused on collecting data on large mammal use of the Banff National Park crossing structures. A large part of that work has focused on carnivores and their main prey species, elk and deer, and to a lesser extent moose. Rocky Mountain bighorn sheep and mountain goats have not been at the forefront of data analyses or summaries despite residing in Banff and local populations found in close proximity to the Trans-Canada Highway (TCH).

On a regular basis sheep and goat biologists inquire about information on how to design wildlife crossings for these two species. Little information has been published to date on the type of crossing structure requirements for bighorn sheep or mountain goats (Singer 1978, Singer and Doherty 1985, Pedevillano and Wright 1987). A quick search of *Web of Science* and *Google Scholar* comes up with the abovementioned mountain goat publications and no publications regarding Rocky Mountain bighorn sheep and highway crossings.

The impetus for this summary came from Alan Dibb (wildlife biologist, Lake Louise Yoho Kootenay Field Unit) in 2011 for a co-authored presentation with Tony Clevenger at the 2012 Northern Wild Goat and Sheep Council meeting in Kamloops, British Columbia. The purpose of the summary was to present information on bighorn sheep and mountain goat use of the Banff wildlife crossings, which at that time was based on a 14-year monitoring period. For this summary we have added subsequent years of data to the summary (2012, 2013).

None of the Banff crossing structures were designed to be species-specific mitigation measures. However, until now, bighorn sheep and mountain goats have not played an important part of the mitigation planning process (Anonymous 1995). Nonetheless, both species are present in the Bow Valley year-round and intuitively they need to travel at local and regional/metapopulation scales to meet their biological requisites seasonally and annually. Some of these movements will require crossing the TCH. As the TCH twinning has moved west to the Continental Divide and will extend into Yoho National Park, both species, particularly mountain goats, will need to be given a higher profile in planning and design of mitigation measures. An evaluation of potential crossing structures for mountain goats in Yoho National Park was prepared recently for the Lake Louise Yoho Kootenay Field Unit (Poole 2012). The Poole report is comprehensive, consisting of a review of literature and data on mountain goat ecology, behaviour, crossing structures and population genetics as they relate to eastern Yoho National Park.

Bighorn sheep habitat modeling and ranges

The following range maps were derived from Parks Canada's random observations, formal surveys, and (in the case of mountain goats) the Bow Valley Naturalists' High Elevation Localized Species (HELS) database (January 2012). Points used in the mapping go back to the early 1980s. The range polygons were estimated in a subjective way, drawing polygons by hand around outermost points, encompassing 90% of points (Alan Dibb, personal communication). There is considerable observer bias in this method, but gives an approximation of bighorn sheep summer range.

Bighorn sheep winter and summer range

Although bighorn sheep are in the general area year-round, the sheep's winter range along the TCH is centered in the Healy to Edith Pass area and mainly east of the Sunshine interchange (Figure 1). Summer range is typically in the high elevations but found on both sides of the TCH and in relatively close proximity to the transportation corridor (Figure 2).

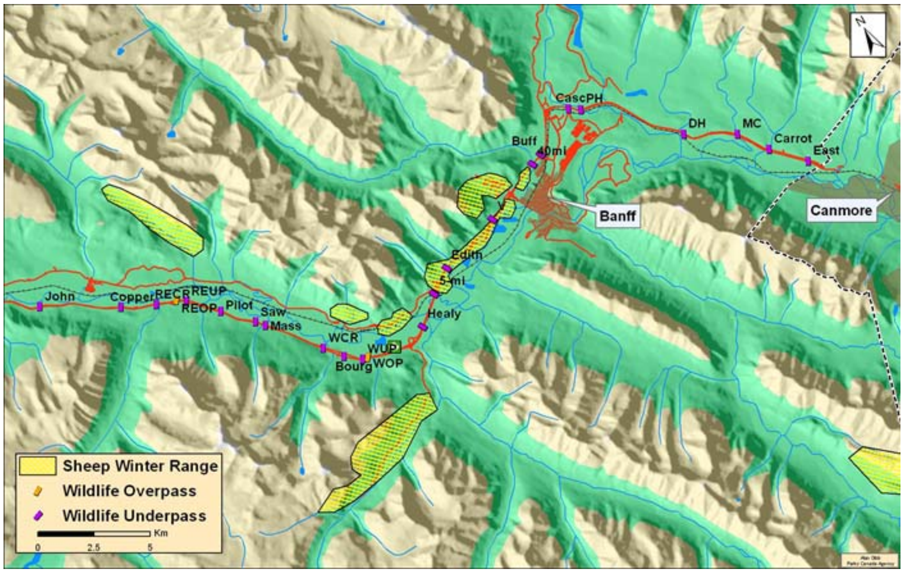

Figure 1. Winter range of bighorn sheep based on mapping observation data. Names and locations of crossing structures are shown. Map prepared by Alan Dibb, Parks Canada.

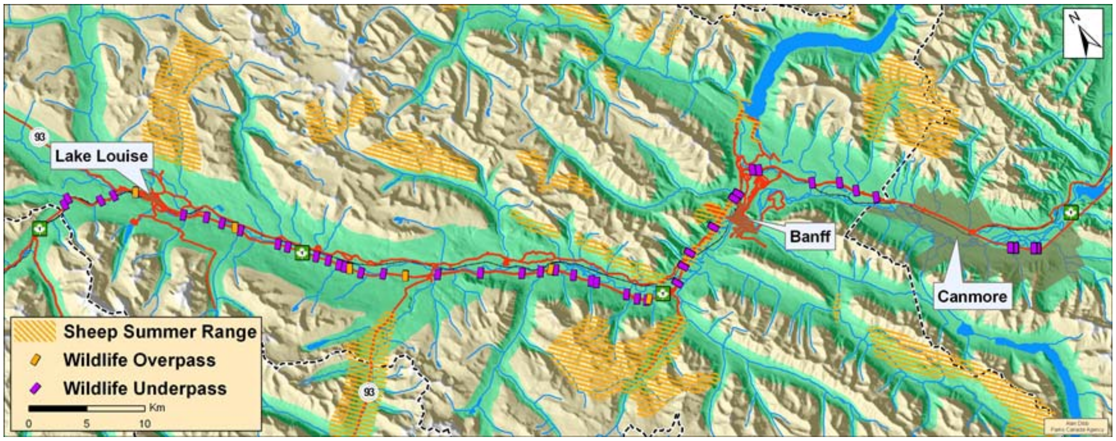

Figure 2. Summer range of bighorn sheep based on mapping observation data. Crossing structures types (underpass, overpass) are shown. Map and observation data prepared by Alan Dibb, Parks Canada.

Bighorn sheep: Confirmed crossings at Banff crossing structures

Data were obtained from camera traps at the Phase 1, 2, and 3A crossing structures from 2007-2013. We have monitored wildlife use of the crossings year-round since 1996 and the majority of those years we relied almost exclusively on track pad monitoring. We have over 4000 crossings by bighorn sheep in our database, but we question the accuracy of those ‘presumed’ sheep crossings based solely on tracks. Therefore, we only present the confirmed crossings as detected by camera trapping.

Although these data are from 2007 to 2013, camera-based monitoring was limited spatially as not all crossing structures had camera traps deployed until late 2010 (Figure 3). During the seven years of camera monitoring, we have not photo-detected bighorn sheep using any of the overpasses. While the Vermilion underpass, and to a lesser extent the Edith underpass, had relatively large numbers of bighorn sheep crossings, typically sheep only descend to the highway to lick salt and then return to their escape terrain. Thus we do not believe many (if any) of the documented uses of these two wildlife underpasses resulted in actual cross-valley movements. Documented crossing events that potentially were movements across the highway occurred at Redearth Creek underpass (n=4) and Duthil underpass (n=1). In addition to these detections obtained from our routine monitoring, one subadult male bighorn sheep was detected using the Healy underpass in 2005. This observation was captured on video as part of the pilot project testing hair-snagging methods at underpasses (Clevenger and Sawaya 2009).

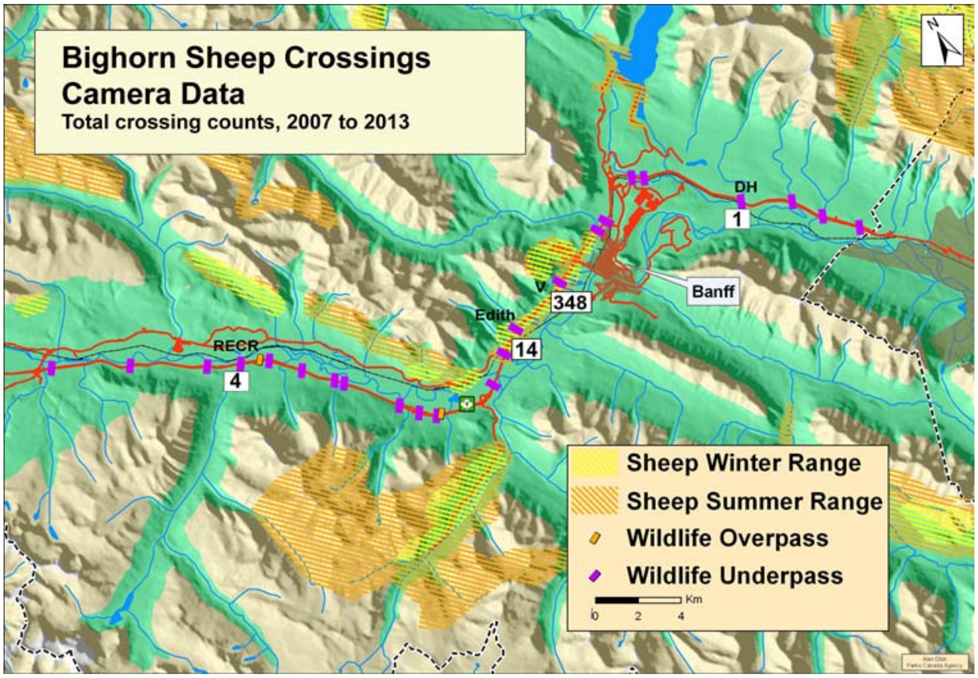

Figure 3. Summary of bighorn sheep use detected by cameras at wildlife crossing structures in Banff National Park, 2007-2013. Map prepared by Alan Dibb (Parks Canada) and Mirjam Barrueto.

Mountain goat habitat modeling and ranges

We used logistic regression to develop a mountain goat habitat model (Alan Dibb, Lake Louise Yoho Kootenay Field Unit, unpublished data), based on terrain variables (elevation, slope, distance to escape terrain) and using the national park database of mountain goat observations (random observations in addition to formal survey data).

The map highlights that in the Bow Valley between Castle Junction and the Yoho border there are wide gaps between suitable habitat patches on either side of the valley (Figure. 4). The valley floor at this location is 5-6 km wide and consists of gentle, forested, low elevation slopes far from escape terrain. Near Banff townsite, the valley floor is narrower (~2 km) but still may be difficult for mountain goats to cross. In Yoho National Park to the west, there are several locations along the TCH where mountain goat habitat comes close to the TCH on both sides and may represent potential crossing opportunities.

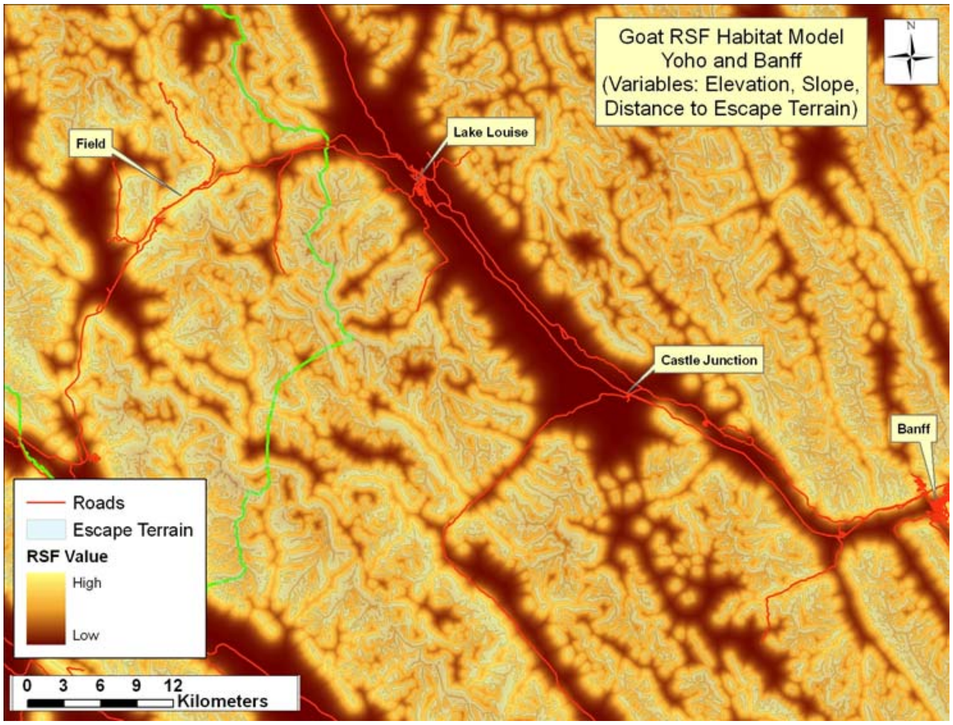

Figure 4. Mountain goat habitat resource selection function model based on observations. Model developed and map prepared by Alan Dibb, Parks Canada.

Mountain goats are in the general area year-round. However, similar to bighorn sheep, they rarely come to the valley floor anywhere in the Bow Valley. As mentioned above, Tom Hurd and Jon Jorgenson both indicated they had no knowledge of goats occurring in or near valley floor near Banff or Canmore-Exshaw.

Mountain goats: Confirmed crossings at Banff crossing structures

To date there have been no photo-detected crossings of mountain goats at the crossing structures. There was one unique observation of a mountain goat on the north side of the TCH, just above the Lake Louise wildlife overpass while it was still in the early stage of construction.

There are extremely few mountain goat observations in or near the Bow Valley floor in Banff and adjacent provincial lands. The Bow Valley appears to be a potential barrier to mountain goat movement and not an artifact of sampling or proper survey data. This could be verified through additional monitoring, more thorough goat surveys, and population genetics-based work (Epps et al. 2005, Poole et al. 2011).

The conservation value of wildlife crossing structures for bighorn sheep and mountain goats

At this moment there is little information on what types of crossing structures are preferred in Banff or whether location and proximity to escape terrain is the most important predictor variable.

There are roughly a dozen years of camera trap data from two wildlife underpasses near Canmore. These two underpasses were frequently used by bighorn sheep, largely to lick salt and return to escape terrain/habitat; it is unlikely they were used for cross-valley movements. Long-term monitoring at the Canmore underpasses and the Banff crossing structures will provide information about crossing structure use by high elevation localized species such as mountain goats. By continuing to monitor use of the Banff crossings, and particularly the newly-constructed Phase 3B crossings, this is an excellent opportunity to learn how mountain goats and bighorn sheep respond to highways and crossing structures designed to allow their safe passage.

Note: This information was gathered and presented at the 2012 Wild Northern Sheep and Goat Council bi-annual meeting in Kamloops, British Columbia. Alan Dibb (Parks Canada) co-authored the presentation with Tony Clevenger. Alan was responsible for preparing the mountain goat and bighorn sheep maps based on observation data and RSF modeling.

8. Factors Affecting Passage by Small and Medium-sized Mammals at Culverts

Authors: Mirjam Barrueto and Anthony P Clevenger

Introduction

A review of the ecological effect of roads reported that barrier effects might emerge as the greatest ecological impact of roads with vehicles (Forman and Alexander 1998). In an increasing number of landscapes, the regular movements of animals involve road crossings. Efforts to increase road permeability and mitigate potential barrier effects might offset the risk of isolating or reducing populations (Opdam et al. 1993; Canters 1997, Riley et al. 2006). Specifically, wildlife underpasses and overpasses have been designed to facilitate movement of wildlife across roads (Forman et al. 2003 Gagnon et al. 2011). Although not designed for animal passage, drainage culverts are ubiquitous features in road and rail corridors.

Little attention has been given to investigating the effectiveness of culverts as a means of increasing road permeability and habitat connectivity for small- and medium-sized mammals. Relatively few studies have evaluated mammal use of drainage culverts and fewer have focused on culverts specifically designed for mammal passage (Yanes et al. 1995, Grilo et al. 2008, Mateus et al. 2011). This is surprising given that culverts are commonly found in surface transportation infrastructure, relatively low-cost, and have the potential to serve as an important habitat linkage by connecting habitats and populations of mammals (Clevenger et al. 2001, Ascensao and Mira 2007, Grilo et al. 2008).

The Trans-Canada Highway (TCH) is a major transportation corridor through Banff and Yoho National Parks in the Canadian Rocky Mountains (McGuire and Morrall 2000). This multilane highway and other roads bisect critical montane and subalpine habitats in Banff's Bow River Valley on which many mammals depend for year-round habitat (Banff-Bow Valley Study 1996). Over 70% of montane habitat in Banff is within the transportation corridor. The first 47 km of TCH was successively twinned from two to four lanes (Phases 1, 2, 3A) between 1982 and 1997. The remaining 30 km (Phase 3B) was recently twinned between 2008 and 2013. The combined effects of a twinned highway with increased traffic on the TCH threatened to fragment wildlife habitat and populations (Golder Associates 2004). As part of environmental mitigation to correct the impacts over 70 culverts of varying sizes were installed to improve ecological connectivity and link habitats for multiple species over time.

Over a decade ago, research investigated drainage culvert use by small- and medium-sized mammals along roads in Banff National Park, Alberta (hereafter referred to as Banff). An array of culvert types was sampled varying in dimensions, habitat, and road features during the winters of 1999 and 2000 (Clevenger et al. 2001). The research demonstrated that drainage culverts can mitigate the potentially harmful effects of busy transport corridors by providing a vital habitat linkage for many small- and medium-sized mammals. Reproducibility is an important aspect of scientific process. Research should be designed so that it can be replicated elsewhere by other investigators using the same methodology (Kelly 2006). Further, repeat studies in the same study area can help confirm changes in species response to human disturbance, landscape alterations, or other environmental perturbations over time.

The newly constructed culverts on Phase 3B provide an opportunity to repeat our previous research in the same study area (Clevenger et al. 2001), monitor species response to newly-constructed culverts, and assess whether species use patterns are consistent with past findings (Clevenger et al. 2009, Gagnon et al. 2011).

Our specific objectives were to:

1. Determine what species used culverts to cross the TCH;
2. Evaluate whether culverts served all species equally or whether some culverts limited habitat connectivity across roads in taxon- or species-specific ways;
3. Model species' response to structural, landscape, and road-related attributes and identify which were most important in explaining species passage;
4. Determine if species responded differently to old vs. new structures, with regards to passage frequency and covariate importance; and
5. Provide recommendations for incorporating small- and medium-size mammal requirements into culvert design and transportation corridor planning.

Methods

Study Area

The study area was located in Banff National Park, situated approximately 150 km west of Calgary, Alberta, in the Bow River Valley. The Bow River Valley is situated within the front and main ranges of the Canadian Rocky Mountains. Topography is regarded as mountainous with elevations from 1300 m to over 3400 m, and valley floor width from 2-5 km. The climate is continental and characterized by relatively long winters and short summers (Holland and Coen 1983). Mean annual snowfall at the town of Banff is 250 cm. The Trans-Canada Highway (TCH) transportation corridor traverses the montane ecoregion. Vegetation in the park encompasses montane, subalpine and alpine ecoregions. Montane habitats are found in low elevation valley bottoms and characterized by Douglas fir *Pseudotsuga menziesii*, white spruce *Picea glauca*, lodgepole pine *Pinus contorta*, aspen *Populus tremuloides* and natural grasslands. Subalpine and alpine ecoregions primarily consist of Engelmann spruce *Picea engelmanii* and subalpine fir *Abies lasiocarpa* forests interspersed with riparian shrub communities, subalpine grasslands, and avalanche terrain, giving way to open shrub-forb meadows in the alpine ecoregion (Achuff and Corns 1983).

The TCH is the major transportation corridor through Banff, covering roughly 80 km between the park's eastern and western boundaries. Traffic volume along the TCH is relatively high for the region, with an average of 17,970 vehicles per day in 2008 and increasing at a rate of 2.5 percent per year (Highway Service Centre, Parks Canada, Banff, Alberta). Upgrading the TCH from 2 to 4 lanes has progressed in phases. Along each phase highway mitigation measures consisting of wildlife exclusion fencing and crossing structures were installed (McGuire and Morrall 2000; Clevenger and Waltho 2000, 2005). Phase 1, 2 and 3A mitigations are found on 44 km of TCH, while Phase 3B encompasses 39 km. Currently there are 44 wildlife crossing structures (6 overpasses, 38 underpasses) along the entire length of TCH between the park east gate and the border between British Columbia and Alberta.

Historically drainage culverts were installed at irregular intervals along the TCH as a standard measure to remove storm water runoff. As the TCH was twinned, new drainage culverts were installed to extend existing culverts. The average distance between culverts on Phase 1, 2, and 3A is approximately 400 m (Clevenger et al. 2001). Previous research in the study area showed the importance of drainage culverts as habitat linkages for small and medium-sized mammals (Clevenger et al. 2001). As a result of their findings and recommendations on Phase 3B, additional culverts were installed and spaced at shorter intervals, ca. 250 m (Golder Associates 2004). On this section, some new culverts were located next to old drainage culverts in side-by-side fashion. Our study was carried out along all 4-lane sections of the TCH including Phase 1, 2, 3A and newly-twinned Phase 3B.

Culverts

A total of 28 culverts were identified for sampling during December 2011 (Figures 1a and 1b). Culvert selection was stratified by habitat type and culvert size. We characterized each culvert with continuous (*n* = 20) and categorical (*n* = 5) variables encompassing structural, landscape and road-related attributes (Table 1).

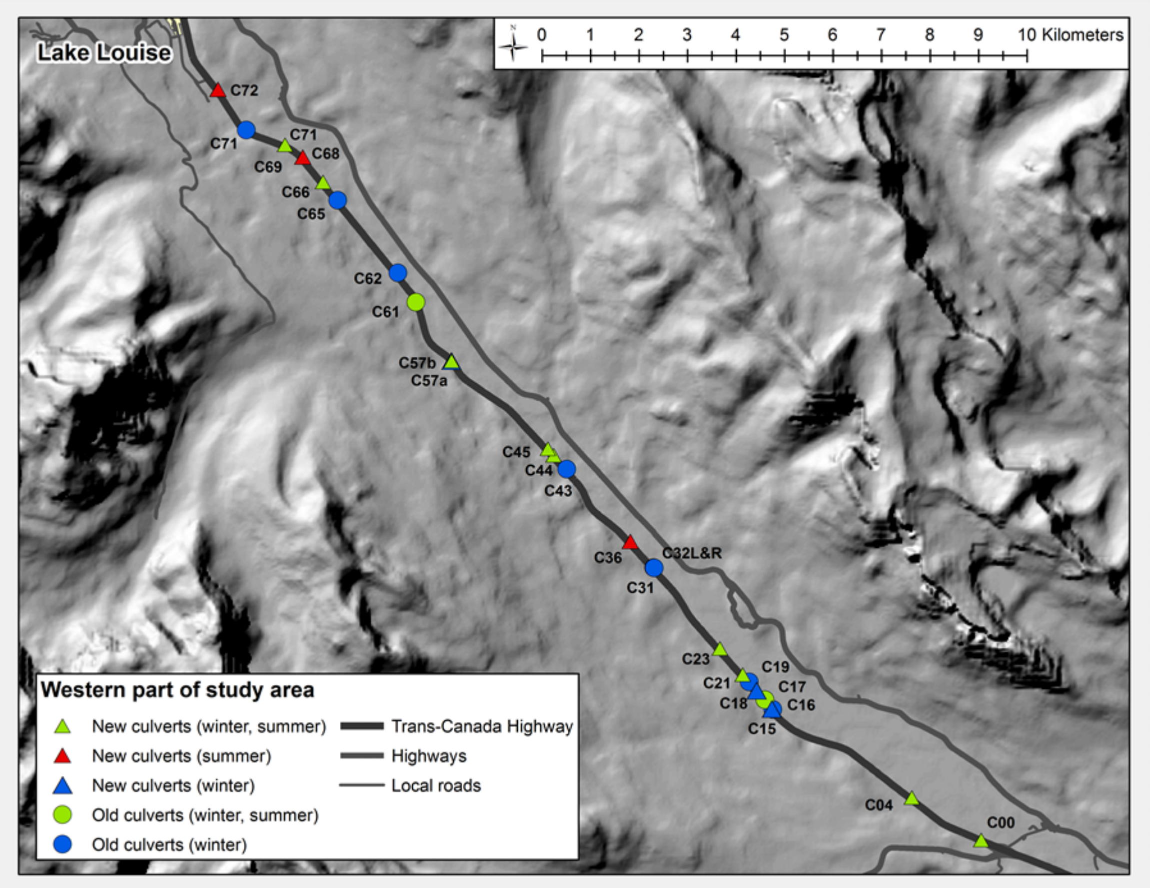

Figure 1a. Map of western part of culvert monitoring study area along Trans-Canada Highway in Banff National Park, Alberta. Displayed are locations of culverts monitored during winter and summer and whether they were “new” culverts (newly installed for twinning project) or “old” culverts (same culvert location prior to highway twinning but extended).

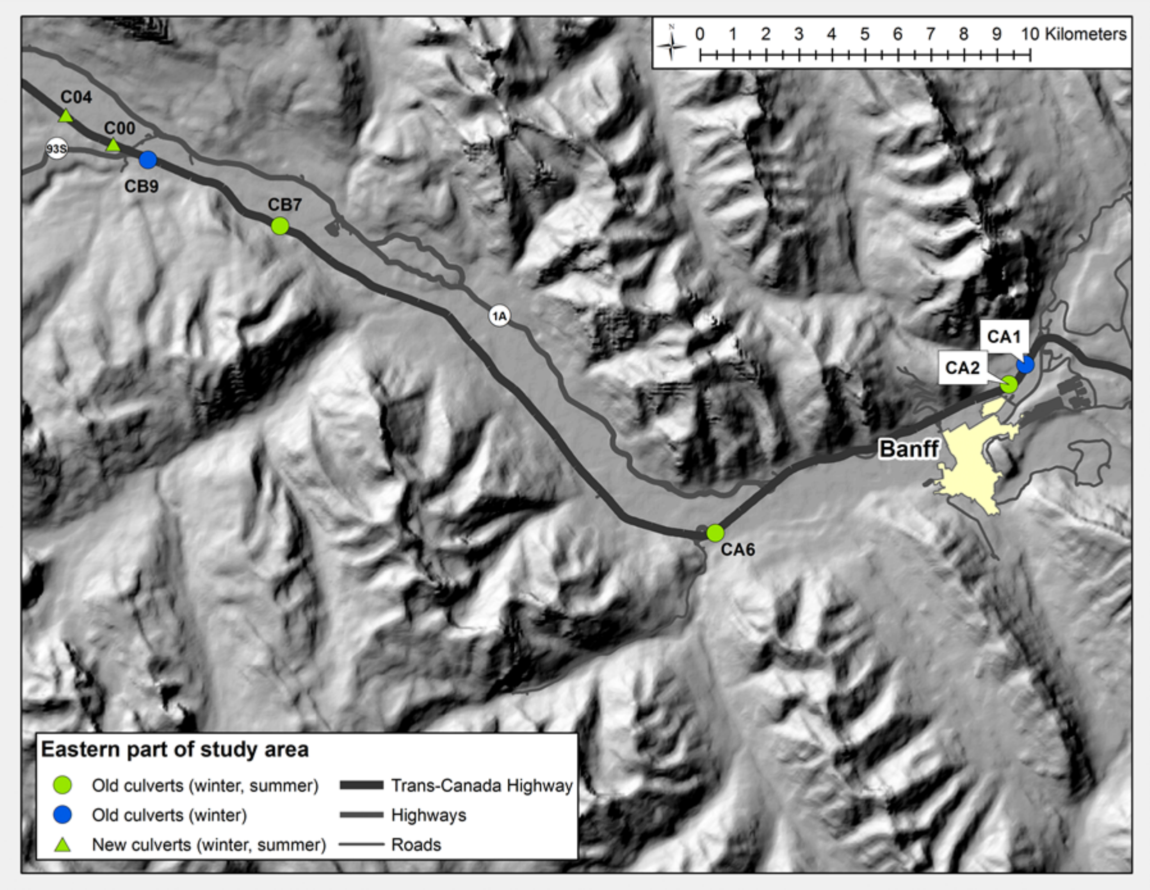

Figure 1b. Map of eastern part of culvert monitoring study area along Trans-Canada Highway in Banff National Park, Alberta. Displayed are locations of culverts monitored during winter and summer and whether they were "new" culverts (newly installed for twinning project) or "old" culverts (same culvert location prior to highway twinning but extended).

Table 1. Names and definitions of variables used in a multivariate analysis of factors influencing mammal passage at 28 drainage culverts in Banff National Park, Alberta (2011-2012).

Attribute group Attribute	Code	Definition
Structural		
Width[a]	width	Culvert width (m)
Height [a]	height	Culvert height (m)
Diameter[a]	D	Diameter (cm) - used as height and width for the round culverts.
Length	L	Culvert length (m)
Openness	OP	Culvert openness (= width x length/height) [b]
Landscape		
Habitat type[a]	HAB	1=forest-open mix, 2=closed forest
Percent forest cover[a]	FOR	Measured as % forest cover along 2, 100-m transects[c]
Percent shrub cover[a]	SHRUB	% shrub cover measured along 2, 100-m transects[c]
Percent open	OPEN	% open habitat measured along 2, 100-m transects[c]
Distance to cover	D_COV	Distance to cover in metres (trees or shrubs >1.5 m high)
Elevation[d]	ELEV	Elevation (m)
Creek drain	Crkdrain	1: Yes, 0: No
Road-related		
Open median	OP_MD	1: Yes, 0: No
Road width	RD_W	Width between outer edges of road pavement (m)
Verge width[a]	VER_W	Width from pavement edge to ecotone created by road (m)
Road clearance[a]	RD_CL	Distance of road width + verge width (m)
Noise level	NOISE	Mean of decibel value readings obtained from sound meters place outside culvert (5 m in front) at 5-min intervals over 24-hr period. Battery failure resulted in some culverts being sampled < 24 hrs.
Traffic volume	T_VOL	Mean annual average daily traffic volume.
Age of culvert	OLD	1: Yes, 0: No
Season	Season	W=winter; S=Summer
Species occurrence		
Marten	maam	Proportion sites sampled with marten presence
Red squirrel	tahu	Proportion sites sampled with red squirrel presence
Chipmunk	tami	Proportion sites sampled with chipmunk presence
Mice and voles	large	Proportion sites sampled with mice/vole presence

Shrew spp	sorex	Proportion sites sampled with shrew spp. presence

[a] Removed from multivariate analysis due to collinearity.

[b] Reed and Ward 1985.

[c] Transect1, on the culvert axis extended 100-m from the opening. Transect2, in front of the opening and 50-m out on both sides.

[d] Only used for one weasel model, as elevation was collinear with many variables and was not generally included. This particular model was best model in 2001 for weasels.

We conducted preliminary sampling at all culverts to confirm the most suitable tracking methods and make any methodological adjustments prior to collecting field data. Such sampling exercises included placing remote cameras inside culverts to test their ability to photograph mammal passage and correctly identify track patterns and species identification.

From late December 2011 to May 2012, we monitored culverts for small and medium-sized mammal use. Culverts were located on all four phases of the TCH (1, 2, 3A and 3B) with 81% located on Phase 3B.

During summer 2012, we re-initiated culvert monitoring from June through September. We monitored a subset (n=17) of the winter culverts during the summer due to frequent rain and water flow at many of the culverts, and added three culverts that had not been monitored during winter (C36, C68, C72).

Observed Passage

We monitored the passage of animals at each culvert using sooted track-plates (100 x 35 cm; Zielinski and Kucera 1995, Clevenger et al. 2001) and cameras at select culverts. Track-plates were sooted with a kerosene flame and white contact paper was taped to the centre section covering one-third of the track-plate length. Multiple plates were used to cover the bottom of culverts wider than one track-plate. No baits were used. We checked track-plates at 7-10 day intervals and recorded each species' presence, estimated the number of species crossings and the direction of travel. We noted the presence of species' tracks in the snow within a 5-m radius of culvert openings. If tracks indicated the culvert was used but there was no recording on the track-plate(s) we counted this as passage.

Mammal species we expected to find using culverts included coyote *Canis latrans*, American marten *Martes americana*, weasel spp. *Mustela erminea*, *M. frenata*, snowshoe hare *Lepus americanus*, red squirrel *Tamiasciurus hudsonicus*, chipmunks *Tamias spp.*, bushy-tailed wood rat *Neotoma cinerea*, deer mice *Peromyscus maniculatus*, red-backed vole *Myodes gapperi*, meadow voles *Microtus pennsylvanicus*, and shrews *Sorex* sp. There were many difficulties identifying tracks of small mammals to species level. Therefore, we attempted to identify tracks using reference track prints obtained by having live-trapped deer mice, meadow vole and red-backed vole walk across track plates in a controlled environment. Mammal track guides were also used to supplement track identification (Murie 1954, Elbrock 2003). Weasels are notoriously difficult to distinguish by track size alone. We therefore classified all weasel tracks as *Mustela* spp. and did not attempt classification to species level. We had similar difficulties of species identification of small mammal and chipmunk species, therefore we pooled all tracks into single taxa categories of *mice and voles* and *chipmunks*, respectively.

Expected Passage

Snowtrack transects were set up in January 2012 for all culverts to collect data on species expected occurrence using the same methodology previously applied (Clevenger et al. 2001). However, due to staffing limitations we were unable to run the transects. Therefore, we decided to collect expected occurrence data using remote cameras on transects for select species, red squirrel-sized and larger. For each culvert, we located a camera trap site on a transect perpendicular to the culvert entrance at a distance of 100-125 m from culvert entrance. At each site a small piece of bait (e.g., chicken leg size) consisting of either beaver or elk meat, was nailed to a tree, commercial trapping lure applied nearby, and camera was positioned approximately 5-7 m opposite the baited tree. Camera trap sessions ran for at least 10 days, presence or absence of species was tallied, and detection probabilities (expected occurrence) calculated in daily increments for the 10-day period, e.g., presence of snowshoe hares on 4 days = 0.4 probability of detection). Detection probabilities for the two transects at each culvert were averaged.

Expected passage frequencies during summer were obtained from measures of relative abundance of each species in the vicinity of each culvert. Enclosed track-plate boxes were used for medium-sized mammals (Long et al. 2008). Track-plates were sooted with a kerosene flame and white contact paper was taped to the centre section covering one-third of the track-plate length. Plates were placed in enclosed triangular-shaped boxes made of black coroplast measuring 32 cm at the base, 34 cm at the apex. No baits were used, however a drop of anise oil was used on lateral edge of each track-plate to act as a lure for all species.

Our sampling design was based on a 100 m grid centered at the culvert entrance (Figure 2). A sampling site consisted of a track-plate and track tube paired on each end of a culvert. The highway frontage site was located along the habitat edge (forest/open) and behind the wildlife exclusion fence. The rear site was located 100 m behind the habitat edge. When the rear site encountered a major river or disturbed habitat we located the site at less than 100 m. Track tubes were used for detecting small mammals (Nams and Gillis 2003). Out of four possible locations on a given side of highway (A1, A2, B1, B2) we randomized placement of enclosed track plates on each side of the culverts. We randomly chose one near-highway (A1 or A2) and distant-highway (B 1or B2) site. There were never more than two sites sampled on a given side of highway and always opposing each other, e.g. A1 and B2 or A2 and B1 (Figure 2). When culverts were located within 100 m of each other, we used one sampling site for both culverts.

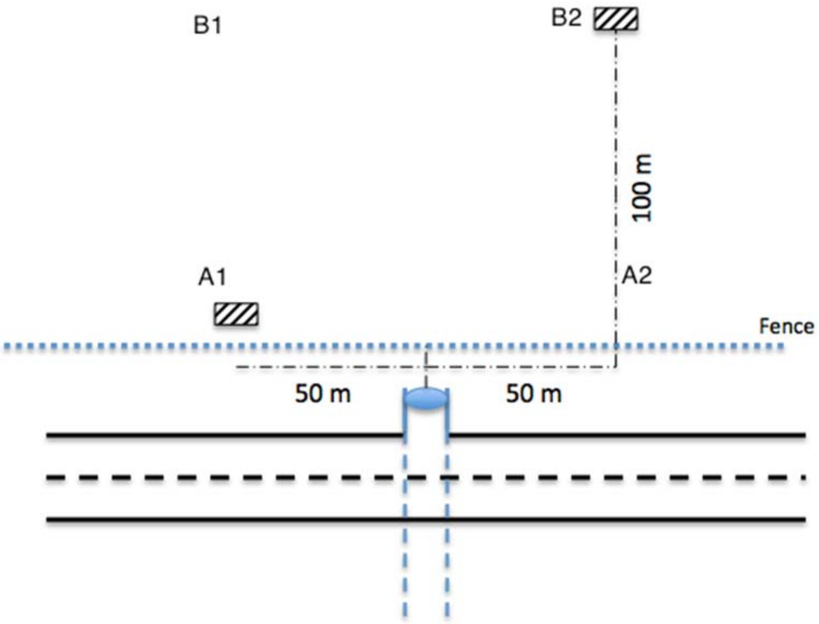

Figure 2. Track-plate box and track tube sampling design was based on a 100 m grid centered at each culvert entrance. The arrangement of two sampling sites (A1 + B2 or A2 + B1) were randomly selected and set on each side of highway. The layout below shows a typical sampling design with track plate and track tube at A1 + B2.

We collected data on species expected occurrence during 2, 14-day sampling sessions. We tallied the presence or absence of species, and detection probabilities (expected occurrence) calculated for the two 14-day sessions. Expected occurrence was calculated as the proportion of sampling sites at a given culvert that had detected presence of the focal species.

We tested for the effects of season (winter, summer) on species passage by including season as a factor in our models. Expected occurrence data was included in models as a covariate describing species expected occurrence in the vicinity of culverts.

Data Analysis

To determine which factors affected through passage of culverts by small- and medium-sized mammal species, we used generalized linear mixed models (GLMM), an extension to the generalized linear models (GLMs) that had been used in the 2001 study (Zuur et al. 2009). GLMMs are more suitable to our nested data where multiple measurements were taken at individual culverts. We took into account sampling effort (measured in days) by using an offset in all models. *Culverts* were treated as random effect by design. We used the Poisson distribution with log-link function for all models.

$$D_j \sim Poisson(\mu_j)$$
$$E(D_j) = \mathrm{var}(D_j) = \mu_j$$

and

$$\log(\mu_j) = \mathrm{cov}\,ariate1_j + \mathrm{cov}\,ariate2_j + ... + \log(effort_j) + a_j$$
$$a_j \sim N(0, \sigma^2_{CS})$$

We conducted all analysis in R (R Core Development Team 2008), and specifically used the package lme4 (Bates et al. 2011) for all modeling. Data exploration yielded no outliers for either response or explanatory variables, with the exception of the mice and vole data, where two large counts were identified as potentially problematic; however, we decided to retain these data points for the analysis. One variable that had potentially nonlinear effects on crossing numbers was *noise* in the case of shrew numbers. We tested covariates for collinearity by calculating variance inflation factors for each covariate (Zuur et al. 2009). We only included covariates in the models that did not exceed a threshold of VIF=2 (Table 1). Model selection was conducted using an information-theoretic approach (Burnham and Anderson 2002). We formulated 14 to 16 candidate models for each species, based on the results of previous culvert studies. We then compared AIC and BIC values of the candidate models. Kass and Raftery (1995) proposed a cutoff of ΔBIC=2 to decide on the relative goodness of fit of candidate models compared to the relative best model. AIC and BIC values of GLMM need to be used with some caution (Zuur et al. 2010). Therefore we decided to use a less stringent, but essentially equally arbitrary cutoff of ΔAIC or ΔBIC<6, to choose the model(s) we would treat as having non-negligible probability of being the "best" model. Also, AIC and BIC ranks of models can vary, therefore some contradicting results were expected.

Results

A total of 2338 culvert-sampling days were spent monitoring small- and medium-sized mammal use of culverts during winter and summer in our study area (Table 2). Sampling effort was unequal across culverts and seasons. The average number of winter sampling days was 56.0 (±0.4) at 28 culverts compared to 45.2 (±20.3) days at 17 culverts during summer. We detected 704 passages by small and medium-sized mammals at the culverts during winter (Table 3). Mice and voles (n=338 times) were detected using the culverts most frequently, followed by red squirrels (n=164), weasels (n=66), shrews (n=64) and martens (n=51). We did not find snowshoe hare use of the culverts during either season. In one culvert we found evidence of snowshoe hares crossing the TCH using a culvert during our preliminary monitoring. Prior to installing the track plates, we obtained photographs of a number of snowshoe hare passages, however, no tracks were found on the track plates in the culvert. A total of 12 coyote passages were detected using the culverts in addition to detecting bushy-tailed woodrats three times and wolves twice.

Table 2. Sampling effort (in days) in monitoring mammal use of culverts on the Trans-Canada Highway, 2011-1012. This includes sessions where the track plates were covered by mud, water or dirt, as tracks were occasionally still visible.

Culvert	Winter	Summer	Total
C00	56	60	116
C04	56	46	102
C15	57	-	57
C16	57	-	57
C17	55	60	115
C18	55	-	55
C19	56	-	56
C21	56	60	116
C23	56	14	70
C31	56	-	56
C32L	56	-	56
C32R	56	-	56
C36	-	60	60
C43	56	-	56
C44	56	21	77
C45	56	14	70
C57A	56	-	56
C57B	56	14	70
C61	56	14	70
C62	56	-	56
C65	56	-	56
C66	56	60	116
C68	-	53	53
C69	56	60	116
C71	56	-	56
C72	-	53	53
CA1	56	-	56
CA2	56	60	116
CA6	56	60	116
CB7	56	60	116
CB9	57	-	57
Mean (SD)	56.0 (0.4)	45.23 (20.2)	
Total	1569	769	2338

Table 3 Summary of total frequency of small- and medium-sized mammal passage at culverts on the Trans-Canada Highway, 2011-1012

	Marten	Red squirrel	Chipmunk	Weasel spp.	Mice and voles	Shrews	Grouse	Coyote	Wolf	Woodrat	**Total**
Winter	51	168	0	66	338	64	0	12	2	3	**704**
Summer	63	126	75	9	956	11	1	0	0	0	**1241**

A total of 1241 mammal passages were recorded during summer. Mice and voles (n=956) were most commonly detected followed by red squirrels (n=126), chipmunks (n=75) and martens (n=63). A total of 11 shrew spp. passages were detected using the culverts in addition to a grouse crossing the TCH using a culvert one time. There were no discernible trends in species use of the culverts between winter and summer. Mice and voles were most numerous followed by red squirrels, weasels, chipmunks and martens. There was a noticeable decline in use of culverts by weasels and shrews during summer compared to counts from winter.

Passage counts at culverts during winter ranged from a low of no passages detected (C04, C18) to slightly more than 140 counts (CA1, CA6; Table 4). Eleven of the 28 culverts received less than 10 passages during winter. Passage counts at culverts during summer ranged from a low of no passages detected (C61) to 276 counts (CA6; Table 5). Four of the 17 culverts monitored in summer received 10 or less passages by small- and medium-sized mammals. Three culverts monitored during winter and summer had consistently low counts (<10; C44, C45, C61). Of the culverts receiving low use during summer, all but C57B had low passage counts during winter. Four low use culverts during winter had a reasonably high level of use during summer (C04, C21, C62, CA2). Culvert C57B was not monitored during winter but had low use during summer. Sampling small- and medium-sized mammal use of the culverts during both seasons proved challenging due to abruptly changing weather patterns causing track plates to be covered in water, ice, and mud. Two culverts during winter were inoperative during nearly half the sampling days (28 of 56 days) due to ice covering the track plates, while one culvert (C61) during summer was either covered with silt or under water much of the sampling period.

Table 4 Summary of total frequency of small- and medium-sized mammal passage by culverts during winter on the Trans-Canada Highway, 2011-1012

CULVERT	Marten	Red squirrel	Weasel spp.	Mice and voles	Shrews	Coyote	Wolf	Woodrat	**Total**
C00	10	36	1	2	0	0	0	0	**49**
C04	0	0	0	0	0	0	0	0	**0**
C15	0	1	0	13	2	0	0	0	**16**
C16	6	1	0	12	3	0	2	0	**24**
C17	4	1	0	5	0	0	0	0	**10**
C18	0	0	0	0	0	0	0	0	**0**
C19	3	0	2	8	2	0	0	0	**15**
C21	2	0	0	6	0	0	0	0	**8**
C23	0	0	0	10	0	0	0	0	**10**
C31	1	0	0	5	19	0	0	0	**25**
C32L	0	0	13	0	0	0	0	0	**13**
C32R	0	0	0	6	1	0	0	0	**7**
C43	5	0	1	0	0	0	0	0	**6**
C44	0	0	0	4	0	0	0	0	**4**
C45	0	0	1	0	0	0	0	0	**1**
C57A	0	0	0	5	0	0	0	0	**5**
C57B	0	0	1	12	0	0	0	0	**13**
C61	0	0	2	2	1	0	0	0	**5**
C62	0	0	5	3	1	0	0	0	**9**
C65	2	0	0	11	9	0	0	0	**22**
C66	3	0	3	42	0	0	0	2	**50**
C69	8	1	15	15	2	0	0	1	**42**
C71	1	0	10	1	3	0	0	0	**15**
CA1	0	88	1	29	9	15	0	0	**142**
CA2	0	1	0	6	0	0	0	0	**7**
CA6	2	37	3	95	6	0	0	0	**143**
CB7	0	0	1	37	4	0	0	0	**42**
CB9	4	2	7	9	2	0	0	0	**24**
Total	**51**	**168**	**66**	**338**	**64**	**15**	**2**	**3**	

Table 5 Summary of total frequency of small- and medium-sized mammal passage by culverts during summer on the Trans-Canada Highway, 2011-1012

CULVERT	Marten	Red squirrel	Chipmunk	Weasel spp.	Mice and voles	Shrews	Grouse	**Total**
C00	4	33	34	0	67	1	0	**139**
C04	0	0	3	0	45	0	1	**49**
C17	7	1	1	3	39	0	0	**51**
C21	0	0	0	2	54	0	0	**56**
C23	0	0	0	0	40	0	0	**40**
C36	1	0	8	0	6	0	0	**15**
C44	1	0	0	0	0	0	0	**1**
C45	0	0	0	0	2	0	0	**2**
C57B	7	0	0	0	3	0	0	**10**
C61	0	0	0	0	0	0	0	**0**
C66	0	4	15	0	108	2	0	**129**
C68	5	0	0	0	73	0	0	**78**
C69	29	0	0	1	47	0	0	**77**
C72	3	0	5	0	42	0	0	**50**
CA2	0	49	0	2	38	3	0	**92**
CA6	6	39	8	1	217	5	0	**276**
CB7	0	0	1	0	175	0	0	**176**
Total	**63**	**126**	**75**	**9**	**956**	**11**	**1**	

Species/taxa-specific models

We formulated 14 to 16 candidate models for each species, based on the results of our 2001 study (Clevenger et al. 2001) and other culvert studies found in the published literature (Tables 6 and 7). The rationale for each model was based on expecting repeat results from previous research in the study area (best 2001 model) and hypotheses regarding the influence of environmental and structural variables explaining culvert use, or adaptation to culverts (new vs. established). We also included minimal and full models as candidate models. We describe our results below for each species divided into model exploration and best model results.

Table 6 American marten, red squirrel and weasel models. All models also included an offset (sampling effort in days), and one random effect (culvert). Mo was used for weasels only.

Model	Fixed covariates	Rationale
M1	rwidth + noise + dcov	Best model 2001 (factor)
M2	rwidth + noise + elev	Best model 2001 (group)
M3	rwidth + noise + dcov + season	Best model 2001 variation I
M4	rwidth + noise + elev + old	Best model 2001 variation II
M5	rwidth + noise + elev + old + maam	Best model 2001 variation II
M6	open + crkdrain + dcov	Environmental variables
M7	median + openness + length	Structural variables I
M8	openness + length + season	Structural variables II
M9	Length + season	Structural variables III
M10	old * noise + season	Adaptation I
M11	old * openness + season	Adaptation II
M12	old * rwidth + season	Adaptation III
M13	open + rwidth + median + crkdrain + dcov + noise + openness + length + old + season + maam	Full model
M14	season	Minimal model I
M15	maam	Minimal model II
M16	Intercept only	Minimal model III
M0	openness + dcov + forest + noise	Best model 2001

Table 7 Mice and vole, and shrew models. All models also included an offset (sampling effort in days), and one random effect (culvert).

Model	Covatiates	Rationale
M1	Dcov + rwidth	Cover I
M2	Dcov + rwidth + large/sorex	Cover II
M3	Dcov + rwidth + large/sorex + season	Cover III
M4	Dcov + season	Cover IV
M5	Old * dcov + season	Cover adaptation
M6	Old * rwidth + season	Road adaptation
M7	Open + crkdrain + dcov	Environmental variables
M8	Median + openness+ length	Structural variables I
M9	Median * season + openness + length	Structural variables II
M10	Noise + season	Traffic variables I
M11	Old * noise + season	Traffic variables II
M12	Large/sorex + season	Occurrence I
M13	Large + season * median	Occurrence II
M14	Median * season	Snow cover of culverts
M15	Intercept only	Minimal model
M16	Open + rwidth + median + crkdrain + dcov + noise + openness + length + old + season + large/sorex	Full model

American Marten

Models

AIC values of GLMMs have to be used cautiously (Zuur et al. 2009). Using a stringent cutoff of ΔAIC=2 and ΔBIC=2, model M8 had the lowest AIC and BIC scores (see Appendix C – Table 1). ΔAIC for the second model was 6.9, meaning that there was strong evidence against model M9. ΔBIC of the second best model (M9) was 3.9, which is considered “positive” evidence against model M9 (Kass and Raftery 1995). The BIC includes a potentially stronger penalty term against additional parameters than AIC, and thus tends to prefer fitted models that are more parsimonious than those chosen by AIC. M8 had one more term (*openness*) than M9. A likelihood ratio test between M8 and M9 was highly significant (Chi-square = 8.87, df=1, p=0.003), suggesting additional support for the more complex model M8. Because of this additional support, the nested nature of M8 and M9, and the large ΔAIC of M9, we only present the results of model M8. The Akaike weight of M8 was 0.94, indicating that robust inferences can be made using this model.

Model M8 was slightly overdispersed (phi = 1.722). There were no problematic residual patterns when plotting residuals against fitted values, and against all covariates, also those not in the model. There was no residual spatial correlation. However, there was a relatively large number of zeros (111 zeros vs. 39 non-zeros). The main effect of minor overdispersion is underestimation of standard errors (Zuur et al. 2010). Since the effects in M8 were strong, we concluded that the biological effects described by model M8 were not merely an artifact arising from use of an unsuitable model on overdispersed data. We therefore decided to retain M8 and to not proceed with other options, e.g., the use of negative binomial models instead of Poisson models, or zero-inflation models (Zuur et al 2009).

Predictors

There were more crossings at culverts by martens in summer than in winter. Marten use of culverts increased with openness and length of the culvert (Table 8). Openness was not strongly correlated with length (r=-0.306) and they were not collinear. The regression coefficient estimate for openness was large compared to the other estimates, mainly because openness values were small (range from 0.003 to 0.066).

Table 8 American marten best model (M8). Number of observations = 150, number of groups (culverts) = 31. logLik= -113.1; deviance = 226.1.

Covariate	Effect	Estimate	Std. error	*z* value	*p* value	Variance	Std.Dev
Intercept	Fixed	-8.944	1.294	-6.913	<0.001		
Openness	Fixed	40.782	12.494	3.264	0.001		
SeasonW	Fixed	-0.927	0.231	-4.008	<0.001		
Length	Fixed	0.086	0.018	4.683	<0.001		
Culvert	Random					0.463	0.681

Red Squirrel

Models

In the 2001 study, red squirrels were found to be in the same species group as martens based on performance indices using principal component analysis (Clevenger et al. 2001). For red squirrels, we therefore used the same selection of models as martens. Model M6 had the lowest BIC value and the second lowest AIC value (see Appendix C - Table 2). M13 (full model) had the lowest AIC value, but only the 10th lowest BIC, with a ΔBIC of 18.4. ΔAIC for M6 was 5.6. No other model had a ΔBIC or ΔAIC smaller than 6.0. Due to the large complexity of M13 compared to M6, and the strong evidence against M13 based one the BIC, we only present the results of M6. As always with model selection based on information=theoretic criteria, the chosen model represents the best model from among the chosen subset of models, not necessarily an absolute best model. However, by presenting the model with most support from both criteria, we were choosing a medium between best predictive and best descriptive properties of a model.

Overdispersion of M6 was similar to the best model of the marten analysis, with phi=1.715. However, as the effects of M6 were not strongly significant, we added an observation level random effect to model the overdispersion. There were no obvious residual patterns with any of the covariates, nor was there residual spatial correlation. Plotting fitted versus observed values yielded a fairly spread out pattern for model M6, and a straight line in model M6.obs, as is expected in the case of models that include observation level random intercepts.

Predictors

Model M6 suggested that red squirrel use of culverts increased with higher percentage of open land around crossing structures, and especially with less distance to cover. Culverts that were also creek drainages, received less use by red squirrels (Table 9). In the resulting model M6.obs, the effect of proximity to creek drainages was not significant at the 5% threshold; the standard errors of the other effects, however, did not change dramatically. This suggests that openness and distance to cover were important biological variables, but the effect of culverts also being creek drainages was not supported by the data.

Chipmunks

Models

We classified all chipmunk tracks as *Tamias* spp., being either least chipmunk (*Tamias minimus*) or yellow pine chipmunk (*Tamias amoenus*). Chipmunks hibernate and consequently no tracks were found in winter. We analyzed the summer data using the same set of models as red squirrels, however without the factor *season*. Three models had ΔAICs or ΔBICs smaller than 2.0, and six models smaller than 6.0 (see Appendix C). Also, there was no clear pattern in the covariates of these models.

Predictors

The four best-supported models (ΔAIC and ΔBIC both <6.0) all had completely different covariates (*chipmunk presence around culverts; intercept only; old*openness; length*). These results most likely indicated insufficient data, or suggested that we had only measured non-relevant covariates. We therefore do not present these models in detail, but suggest that further research is necessary to determine factors influencing *Tamias* spp. use of culverts.

Weasels

Models

We used the same set of models for weasels as for marten and red squirrels, and a model comprising the significant coefficients of a multivariate regression performed in the 2001 study (Clevenger et al. 2001). Three models had ΔAIC or ΔBIC <2.0, and 11 models with <6.0 (see Appendix C). The four models that had both ΔAIC and ΔBIC lower than 6.0 showed some patterning (Table 10).

Table 9. Red squirrels, best model (M6) and best model with observation level random intercept (M6.obs). For M6: Number of observations = 150, number of groups (culverts) = 31. logLik= - 131; deviance = 262. For M6.obs: logLik = -77.17, deviance=154.3, AIC= 166.3, BIC= 184.4. Generalized linear mixed models fit by the Laplace approximation.

Model	Covariate	Effect	Estimate	Std. error	*z* value	*p* value	Variance	Std.Dev
M6	Intercept	Fixed	-10.376	4.776	-2.172	0.030		
M6	% Open	Fixed	0.190	0.079	2.401	0.016		
M6	crkdrainY	Fixed	-2.648	1.188	-2.229	0.026		
M6	dcov	Fixed	-0.614	1.152	-4.050	<0.001		
M6	Culvert	Random					2.575	1.605
M6.obs	Intercept	Fixed	-11.787	4.969	-2.372	0.018		
M6.obs	% Open	Fixed	0.207	0.083	2.485	0.013		
M6.obs	crkdrainY	Fixed	-2.405	1.247	-1.930	0.054		
M6.obs	dcov	Fixed	-0.648	0.163	-3.968	<0.001		
M6.obs	Culvert	Random					1.550	1.245
M6.obs	Obs. level	Random					2.339	1.529

Table 10. Weasel *Mustela* spp. best models (both ΔAIC and ΔBIC <6). M14: logLik = -94.36; deviance = 188.7. M9: logLik = -93.34; deviance =186.7. M15: logLik = -95.69; deviance = 191.4. M3: logLik = -93.78; deviance = 187.6.

Model	Covariate	Effect	Estimate	Std. error	*z* value	*p* value	Variance	Std.Dev
M14	Intercept	Fixed	-5.082	0.477	-10.655	<0.001		
M14	SeasonW	Fixed	1.097	0.409	2.682	0.007		
M14	Culvert	Random					2.048	1.431
M9	Intercept	Fixed	-7.190	1.602	-4.487	<0.001		
M9	SeasonW	Fixed	1.085	0.407	2.664	0.008		
M9	Length	Fixed	0.035	0.025	1.414	0.157		
M9	Culvert	Random					1.874	1.369
M15	Intercept	Fixed	-5.144	0.555	-9.275	-0.001		
M15	Old-YES	Fixed	1.601	0.684	2.340	0.019		
M15	Culvert	Random					1.867	1.367
M3	Intercept	Fixed	-3.444	1.685	-2.044	0.041		
M3	SeasonW	Fixed	1.077	0.410	2.629	0.009		
M3	R_width	Fixed	-0.038	0.039	-0.986	0.324		
M3	Culvert	Random					1.972	1.404

Predictors

Winter had more crossing numbers than summer, and the estimate was comparable across all models. Old or established culverts appeared to have more crossings than new ones. Road width and culvert length appeared in one of these four models each, but without significant effect, and with opposite effect estimates. Due to the weakness of these results we do not present further model results and validation for weasels.

Mice and voles

Models

The models for mice and voles were the same as those used for shrews. Two models (M14 and M13) stood out as having most support from both AIC and BIC values (see Appendix C). A model M9 had third rank with both criteria, but much higher ΔAIC and ΔBIC values. An interaction between culvert opening at the median and season was significant.

We tested M13 for overdispersion and residual patterns. The overdispersion ratio phi was 6.2, indicating serious overdispersion. There were no worrisome residual patterns and no residual spatial correlation, thus there was no indication of missing covariates or non-linear patterns. The number of zeros was relatively high, but lower than in any other species we analysed. However, the largest observed counts were high (87 and 92) and could be considered outliers. A negative binomial model would potentially have been more appropriate for this dataset. However, at the time of writing, negative binomial models were not developed yet for the R-package we were using to do all modelling (lme4). We therefore fitted an observation level random effect to model the overdispersion, and compare the coefficient estimates to model M13. The resulting model M13.obs had an overdispersion ratio of 0.256, meaning the observation-level random effect more than accounted for all overdispersion. While the estimate of the covariate *large* did not change much and became slightly more significant in model M13.obs, the interaction between season and median disappeared. Only the factor *season* itself stayed important (Table 11).

Table 11. Best models for mice and voles. M13: logLik = -462.9; deviance = 925.9. M14: logLik = -464.8; deviance = 929.6. M9: logLik = -464.3; deviance = 928.5. M13.obs: logLik=-219.4; deviance = 438.8; AIC=452.8; BIC=473.9.

Model	Covariate	Effect	Estimate	Std.error	*z* value	*p* value	Variance	Std.Dev
M13	Intercept	Fixed	-1.504	0.459	-3.278	0.001		
M13	Large	Fixed	1.315	0.649	2.027	0.043		
M13	seasonW	Fixed	-1.011	0.078	-12.911	<0.001		
M13	MedianOpen	Fixed	0.502	0.683	0.735	0.462		
M13	SeasonW:medianOpen	Fixed	-2.023	0.619	-3.267	0.001		
M13	Culvert	Random					1.141	1.068
M14	Intercept	Fixed	-0.735	0.252	-2.916	0.004		
M14	MedianOpen	Fixed	0.772	0.756	1.020	0.308		
M14	seasonW	Fixed	-1.014	0.078	-12.943	<0.001		
M14	SeasonW:medianOpen	Fixed	-2.447	0.712	-3.437	0.001		
M14	Culvert	Random					1.425	1.194
M9	Intercept	Fixed	0.176	1.298	0.136	0.892		
M9	MedianOpen	Fixed	0.591	0.763	0.774	0.439		
M9	seasonW	Fixed	-1.012	0.078	-12.922	<0.001		
M9	Length	Fixed	-0.010	0.019	-0.522	0.601		
M9	openness	Fixed	-18.060	17.721	-1.019	0.308		
M9	Season:medianOpen	Fixed	-2.378	0.697	-3.413	0.001		
M9	Culvert	Random					1.345	1.160
M13.obs	(Intercept)	Fixed	-1.183	0.466	-2.537	0.011		
M13.obs	large	Fixed	1.236	0.573	2.156	0.031		
M13.obs	seasonW	Fixed	-1.855	0.252	-7.352	<0.001		
M13.obs	MedianOpen	Fixed	-0.808	0.720	-1.123	0.261		
M13.obs	seasonW:medianOpen	Fixed	-0.017	0.889	-0.019	0.985		
M13.obs	Culvert	Random					1.053	1.026
M13.obs	Obs. level	Random					0.460	0.678

Predictors

There were fewer crossings in winter than summer, and culverts that opened at the highway median had fewer crossings in winter than those that were closed. However, the factor *open median* across both seasons did not have any significant effect. High expected occurrence of mice and voles around the culverts had a positive impact on crossing numbers. Culvert length and openness appeared in model M9, but had no significant impact on crossing numbers.

Shrews

Models

We used the same model set for shrews as for mice and voles. Two models (M5 and M4) had a ΔAIC or ΔBIC <2.0. Five models (M4, M5, M11, M1, M7) had a ΔAIC or ΔBIC <6.0 (see Appendix C). We discuss models M4 and M5, as well as M7, as they had the most support from the ICs. In model M4, distance to cover negatively impacted crossing numbers by shrews. The estimate was the same in M5 and M7. However, in M5 the standard error for distance to cover was large. In both M4 and M5, there were more shrew tracks in winter than in summer, but only in M4 was the effect significant at the 5% threshold. All other covariates present in models M5 and M7 (*old, old*dcov, %open, creek drainage*) did not have significant effects (Table 12).

When testing M4 and M5, we only found little overdispersion (phi=1.15 for M4; phi=1.21 for M5). However, because the effect of *season* was not strong in either model, we fitted M4 with an observation level random intercept. The resulting model M4.obs showed a now non-significant effect of season. Of note was that with an observation level random effect, the culvert effect all but disappeared, suggesting low correlation between sampling intervals within culverts.

Predictors

Overall, the results suggested that the main covariate explaining shrew crossings at culverts was distance to cover (Table 12). However, the number of zero counts as well as the patterns in residual vs. culvert plots indicated that the data was rather sparse; a good number of culverts appeared to have less shrew counts than expected by the model.

Table 12. Shrew spp. best models. M4: logLik= -77.35; deviance = 154.7. M5: logLik=-74.05; deviance = 148.1. M7: logLik=-77.75; deviance = 155.5.

Model	Covariate	Effect	Estimate	Std.error	*z* value	*p* value	Variance	Std.Dev
M4	Intercept	Fixed	-2.735	0.658	-4.154	<0.001		
M4	Dcov	Fixed	-0.185	0.054	-3.412	0.001		
M4	seasonW	Fixed	0.860	0.426	2.019	0.044		
M4	Culvert	Random					1.099	1.048
M5	(Intercept)	Fixed	-3.701	1.244	-2.975	0.003		
M5	old1	Fixed	0.987	1.337	0.738	0.461		
M5	dcov	Fixed	-0.186	0.116	-1.608	0.108		
M5	seasonW	Fixed	0.778	0.428	1.817	0.069		
M5	old1:dcov	Fixed	0.063	0.131	0.482	0.630		
M5	Culvert	Random					0.726	0.852
M7	(Intercept)	Fixed	-4.920	1.746	-2.817	0.005		
M7	open	Fixed	0.043	0.028	1.570	0.116		
M7	crkdrainY	Fixed	0.589	0.567	1.038	0.299		
M7	dcov	Fixed	-0.189	0.057	-3.295	0.001		
M7	Culvert	Random					1.047	1.023
M4.obs	Intercept	Fixed	-4.089	0.771	-5.304	0.000		
M4.obs	Dcov	Fixed	-0.190	0.068	-2.798	0.005		
M4.obs	seasonW	Fixed	1.385	0.742	1.866	0.062		
M4.obs	Culvert	Random					0.162	0.403
M4.obs	Obs.level	Random					3.456	1.859

Discussion

Our results suggest that culvert attributes influence species use in different ways. Depending on the species different attributes weighed more heavily than others in ultimately determining the use of a culvert. For example, martens preferred long culverts with high openness values, while red squirrels tended to use culverts close to vegetative cover and mice/voles generally avoided using culverts that opened in the central median. Much like large mammal responses to wildlife crossing structures (see Chapter III.3. Long-term data…), small- and medium-sized mammals reacted differently to structural, landscape and road-related attributes of culverts. Therefore mitigation planning, for crossing structures or culverts, will require a multi-species strategy that meets their varied ecological and behavioural needs.

In our 2001 analysis, we found that traffic volume, and to a lesser degree noise levels and road width, ranked high as a significant factor affecting how species used culverts (Clevenger et al. 2001). These three variables were not important factors explaining passage in our study. This can be attributed to the lack of variation of these road-related variables in our study area, thus the reason we decided not include traffic volume in our analysis. The 2001 study was conducted over a wide range of road types (2-lane Bow Valley Parkway, 2-lane TCH, 4-lane TCH) with equally diverse traffic volumes, associated noise levels and road widths, while culverts we sampled for this study were exclusively on a 4-lane section of the TCH with slightly varying traffic volumes.

The dimensions of culverts are considered to be the most important variable in the design of effective passages including culverts (Cain et al. 2003, Ng et al. 2004, Mata et al. 2005, Grilo et al. 2008, Mateus et al. 2011). One common theme that agreed with our 2001 analysis was that structural attributes largely explained culvert use by small- and medium-sized mammals. Martens, weasels, and mice/voles responded most to the structural attributes of culverts. Martens had a tendency to use culverts that were long with high openness values. Openness and length were negatively correlated and openness values for the culverts we monitored were relatively small, suggesting that despite being statistically significant, length may have been the most important factor explaining marten use of culverts. Longer culverts tend to provide more cover, less light and have low through-culvert visibility, all of which are important habitat elements for martens (Buskirk and Powell 1994, Cheveau et al. 2013, Fisher et al. 2013).

Age of the culvert was a significant attribute influencing weasels, preferring to use "old" culverts, that existed before the Phase 3B twinning (and were extended as part of TCH reconstruction) or new culverts that replaced old ones. It is unclear in the case of weasels whether culvert age being a factor is related to slow adaptation time and their possible aversion to using new culverts in new locations or the importance of this attribute may be more an artifact of local habitat conditions than of direct significance on their passage. Age of culvert did not explain passage for any other species and should not be important for small mammals (red squirrel-sized and smaller), being short-lived species with short generation times.

Landscape variables may also be important in explaining habitat elements that facilitate the use of culverts by small- and medium-sized mammals. The presence or amount of cover (shrubs or trees) at passage entrances has been considered an essential component for designing effective tunnels (Hunt et al. 1987, Rodriguez et al. 1996, 1997; McDonald and Cassady St Clair 2004, Grilo et al. 2008). It is believed that increased cover provides greater protection and security for animals approaching the passages. Our results indicated that distance to cover was a significant factor determining passage for red squirrels and shrews (all negative correlations).

We found that passage frequencies were highest for small mammal species. This result concurs with those from other culvert-based studies (Yanes et al. 1995, Rodriguez et al. 1996 1997; Mata et al. 2005, Ascensao and Mira 2007) that found that small mammals constituted the majority of crossings at culverts. The number of small mammals (shrews, mice and voles) we detected using the culverts were most likely underestimations. Especially in summer when the culvert substrate was not level, shrews could possibly pass underneath the track plates at most culverts. Further, when we had cameras in the culverts we observed that all three small mammal species occasionally tried to avoid the track plates by walking on the edges.
Perhaps one of the most noteworthy results was the lack of passage at culverts by snowshoe hares. In our previous study hares were detected using culverts, but substantially less than most species (Clevenger et al. 2001). This may partly be explained by sampling design, effort and proximity to snowshoe hare habitat. In 2001 we sampled culverts over a wide area compared to our current study that was focused nearly exclusively on Phase 3B. Despite not being found using the culverts by our tracking methods, however, hares were commonly found outside the culverts from anecdotal observations and expected occurrence surveys. Hares are often seen in the larger wildlife crossing structures, which suggests they may avoid small structures and require larger structures with high through-culvert visibility (Clevenger et al. 2001).

Season was a significant factor explaining use by all small- and medium-sized mammals except for red squirrels. Serronha et al. (2013) also found that culvert use was highly seasonal and positively associated with species activity throughout the year.
We found that that results from our current study generally agreed with the 2001 study results.

We did find, however, that there were fewer important variables explaining species passage. This may likely have to do with differences in analysis, e.g., in 2001 grouping by culverts was not taken into account, which likely inflated significance of covariates. The key variables explaining species passage models in 2001 were marginalized in our study because we focused on one phase of TCH rather than all three phases along with the entire length of the Bow

Valley Parkway. Further, key landscape correlates of culvert use deemed significant in 2001 continued to be important in our study.

In our previous study we found the predominance of martens and weasels at the culverts contrasted sharply with the scarcity of prey species such as snowshoe hares and red squirrels, despite these prey species being some of most abundant on transects outside the culverts (Clevenger et al. 2001). We were unable to assess whether this pattern of interspecific segregation occurred because we did not use the same snowtrack transect method as in 2001. The constraining effect of culverts on animal movement may make prey species distribution more predictable and lead to higher rates of predation. The prey trap hypothesis states that wildlife passages are used by predators to facilitate prey detection and capture.
Although there is little evidence in the current literature for the existence of prey traps, few studies have specifically addressed this issue at all (Little et al. 2002, Ford and Clevenger 2010). These studies notwithstanding, questions continue to persist about the degree of prey species vulnerability at culverts and crossing structures among the public and professionals from both transportation and wildlife agencies.

Management Implications

Like the results from previous research (Clevenger et al. 2001), our results suggest that for many small- and medium-sized mammals culverts can mitigate harmful effects of the TCH. All species but snowshoe hares were found using the culverts during out study. For forest-associated species like most of the species we studied, culverts appear to provide a safe means of crossing open habitat created by the TCH corridor (some places up to 120 m wide) and a vital habitat linkage.

The lack of consistent evidence indicating snowshoe hare use of the culverts is noteworthy and should be of management concern. Despite hares being present and relatively abundant outside the culverts, the lack of passage detections may be due to habitat or comparatively small culverts we monitored (mean diameter: 80.5 cm, SD: 32.8) compared to the 2001 study. More monitoring of culverts with special attention to hares and their habitat would be required to gain a better understanding of their response to culverts. In addition, monitoring of large mammal crossing structures may provide ancillary information on the structural attributes that facilitate snowshoe hare passage.

In our previous study area the mean distance between all mitigation passages (large wildlife crossing structure or full-length culvert) along the TCH and Bow Valley Parkway was 465m (SD=411m). In our report to Parks Canada (Clevenger et al. 2002), we urged that to improve the permeability of roads for small- and medium-sized mammals that culverts be placed at more frequent intervals (150 – 300 m) to provide sufficient opportunities for animals of all body sizes to avoid crossing busy roads. The Highway Service Centre followed this recommendation when designing the reconstruction of Phase 3B as most culverts are spaced approximately 250 m apart. This spacing interval should be a standard guideline for culvert placement for small- and medium-sized mammals on the TCH (and other highways) until new research appears that would justify a change. In a previous study we found that snowshoe hare road-kills occurred where culverts and crossing structures were located farther away than expected by chance (Clevenger et al. 2003). This suggests that when passages are relatively far apart there may be a greater tendency for animals to cross above the road, whereas when in close proximity they are more likely to use these structures for safe passage.

If a highway does not have large wildlife crossing structures in place, we recommend a mixed size class of culverts to accommodate the greatest variety of species possible. The size of the culverts will depend on the body size of wildlife most likely to be using the passages to connect habitats and populations. Large culverts (1·0 –1·5 m diameter) will facilitate passage for medium- sized mammals (e.g. coyote), while small culverts (0·5 – 1·0 m diameter) will best serve small mammals (marten and smaller). Snowshoe hares would require large culverts as a minimum to function as a habitat linkage.

Lastly, we advise that vegetative cover be present near culvert entrances to enhance passage by carnivores and small mammals. There is general consensus among all culvert studies underscoring the importance of cover near culvert entrances to ensure use and connectivity. It is believed that increased cover provides greater protection and security for animals approaching roads. The lack of cover and low connectivity may inhibit animal movement across roads particularly forest interior species (Bennett et al. 1994, McDonald and Cassady St Clair 2004), ultimately leading to reduced demographic connectivity.

IV. RESTORE POPULATION-LEVEL MOVEMENTS ACROSS THE TRANS-CANADA HIGHWAY AND IMPROVE HABITAT CONNECTIVITY AND GENETIC INTERCHANGE FOR KEY SPECIES

1. Effects of Transportation Infrastructure on Fine-Scale Genetic Structure of Wolverines in Banff and Yoho National Parks

Authors: Michael A. Sawaya and Anthony P. Clevenger

Introduction

Wolverines are a rare-occurring species that move over vast areas and without recognizing political boundaries. They inhabit some of the most extreme alpine and subalpine environments and their populations have experienced considerable range reduction over the last 50 years (Brodie and Post 2010). Loss of habitat and barriers to movement, along with continuing warming climate, are recognized as threats that further diminish and fragment the critical landscapes they need for dispersal within their metapopulation (Inman et al. 2013).

Federally, the wolverine is listed as a species of *Special Concern*, while in Alberta it is listed as Data Deficient (Alberta Fish and Wildlife 2008). In the United States, the wolverine is a candidate species for federally listing as threatened (US Fish and Wildlife Service 2013). In the Canadian Rocky Mountains, little is known about wolverines (Fisher et al. 2009). Despite ongoing trapping and development, land managers in British Columbia and Alberta have expressed concern about the species current management and conservation. In both provinces, wolverines are under intense pressure from recreational activities, transportation, and oil and gas development (Lofroth and Ott 2007, Fisher et al. 2009).

Presently little is known about the status of wolverines in the national parks of the Canadian Rocky Mountains (Suitor 2005). Recent research in central Alberta suggests that national parks may be a source population for unprotected areas in British Columbia and Alberta (Fisher et al. 2009). Thus, monitoring populations of wide-ranging species, such as wolverine, has been identified as a critical management objective in Banff and Yoho National Parks (Parks Canada 1997, 2007).

The current expansion (2 to 4 lanes) of the Trans-Canada Highway (TCH) in Banff National Park presents a unique opportunity to address one of the most important threats to wolverine conservation at a trans-boundary metapopulation scale. As the TCH expansion moves up Banff's Bow Valley towards the Continental Divide, the highway enters subalpine habitats of prime importance for wolverines. Our research will be particularly important for evaluating the impact of this major highway on the regional population of wolverines in one of the core protected areas of the species range.

Our research is the first to systematically collect information on wolverine occurrence in the Canadian Rocky Mountains and examine whether transportation corridors affect movements and gene flow. Specifically we are interested in examining how the TCH affects genetic structure in wolverines and evaluating whether wildlife fencing and crossing structures may be effective solutions for restoring connectivity to wolverine populations.

Methods

Study Area

Our study area is located in the Canadian Rocky Mountains, encompasses approximately 9000 km^2 and includes parts of Banff, Yoho and Kootenay National Parks, Mt. Assiniboine Provincial Park, the Columbia Valley in British Columbia, and adjacent provincial lands in BC (hereafter referred to as the park complex). The Bow River Valley of Banff National Park (BNP) is situated within the front and main ranges of the Canadian Rocky Mountains. The topography is steep and mountainous with elevations from 1300-3400 m, and a valley floor width from 2-5 km. The climate is continental and characterized by relatively long winters and short summers (Holland and Coen 1983). Vegetation in the park encompasses montane, subalpine and alpine ecoregions. Montane habitats are found in low elevation valley bottoms.

The lower Bow Valley is a human-dominated landscape with the TCH, the Banff Townsite (10,000 residents), a golf course, 3 ski areas, Canadian Pacific Railway (CPR), and a secondary highway. Neighbouring Yoho National Park (YNP) is situated on the west side of the Continental Divide and is characterized by steep rugged terrain with narrow valleys and continental climate consisting of short, cool summers and long winters with high snowfall. The Kicking Horse River is the main east-west aligned watershed in YNP, which parallels the TCH and CPR mainline. Differing from the Bow Valley, the Kicking Horse Valley is sparsely populated, as Field (300 residents) is the only townsite within the national park.

DNA Collection and Genetic Analysis

For sampling purposes our survey area was delineated by creating a 30-km buffer around the TCH from Castle Junction (BNP) to the west boundary of YNP. We surveyed wolverine occurrence using a systematic sampling design consistent with past wolverine research (Fisher et al. 2013), enabling eventual data pooling and large, landscape-scale analyses. The survey area was divided into 12-km x 12-km grid cells. Hair traps and motion-detection cameras were used to sample wolverine occurrence (Fisher et al. 2013).

One sampling location was located in each grid cell. However, to increase probability of detection and movements within the TCH corridor an additional sampling site was placed in select grid cells that overlaid the TCH. Hair traps and cameras were checked during 3, 30-day sessions between January and April. Hair samples were stored at room temperature on silica desiccant and later analyzed at the USDA Forest Service Conservation Genetics Lab (Missoula, Montana). The lab uses protocols for DNA extraction and microsatellite analysis of samples (Schwartz et al. 2009).

Transportation Effects on Population Structure

We assigned each wolverine to the north or south side of the TCH based on where they were detected in relation to the highway and then examined genetic structure using population-based and individual-based analyses. We first calculated the population-based metric for genetic differentiation, Fst, using Genalex (Peakall and Smouse 2006). We used program Genetix (Belkhir 1999) to perform a factorial correspondence analysis (FCA) to visually examine our data for patterns of clustering related to the TCH. We used three independent methods to identify individual wolverines that crossed the TCH. We define migrants as any wolverine detected moving across the fracture zone using any one of 3 criteria (Proctor et al. 2012): 1) wolverines detected on both sides of the highway using non-invasive genetic sampling (NGS) methods, hair traps or opportunistic faecal sample collections, 2) wolverines cross-assigned to population of origin using frequency-based assignment tests (Paetkau et al 1995), and 3) wolverines cross-assigned to population of origin using Bayesian clustering in program STRUCTURE (Pritchard et al. 2000).

We examined isolation by distance patterns in wolverines using Mantel tests to calculate the individual pair-wise genetic distance, which is useful for examining isolation by distance in individuals (Smouse et al. 1986, Rousset et al. 1997). We determined wolverine locations from sampling points using GPS and recorded geographic locations in the UTM coordinate system. Some wolverines in the study were located more than once and their locations were averaged to obtain a detection centre.

We performed Mantel tests using Genalex (Peakall and Smouse 2006), and examined our data for a correlation between genetic and geographic distance. To evaluate whether the highway has an effect on gene flow and resulted in genetically isolating populations north and south of the highway (fine-scale genetic structuring) we used individual clustering methods to examine current population genetic structure and identify recent migrants (Pritchard et al 2000). This method uses allele sharing to cluster individuals using no a priori assumptions about population origin.

Results

DNA Collection and Genetic Analysis

Between February 2010 and May 2013, we collected 2563 hair samples, 20 scat samples, 1 urine sample, and 1 vomit sample (Table 1). To operate within our budget constraints, we sub-selected the best samples. We analyzed 793 of the 2586 samples collected (31%) and 314 of those 793 samples (40%) produced multi-locus genotypes (i.e. individual IDs). Across all methods and years, we detected a total of 64 unique individuals (25 females, 39 males). By far, the majority of samples were collected from hair traps in years 1 and 3, the years of intensive sampling effort. Out of 75 hair trap locations sampled, 60 of them (80%) produced at least one individual ID (Figure 1). More than one individual wolverine was detected at 39 of 75 sites (52%), with Lower Baker Creek hair trap yielding the most individual IDs (3 females, 3 males) per sampling site (Figure 2).

Table 1: DNA sample collection and genotyping success for wolverine hair and scat* samples collected in parks complex with barbed wire hair traps and snow tracking.

Sampling Period	# samples collected	# samples attempted	# genotypes	# individuals	# females	# males
Pilot Year	43	27	11	4	2	2
Wtr 2010-2011	849	256	88	22	8	14
Wtr 2011-2012	295	54	22	13	7	6
Wtr 2012-2013	1176	365	132	33	12	21
Peripherals	114	21	13	5	1	4
Incidentals	94	70	48	23	6	17
Hawk Cr Killsite	15	0	0	0	0	0
TOTALS	**2586**	**793**	**314**	**64**	**25**	**39**

*1 tissue sample, 1 urine sample, and 1 vomit sample were also analyzed.

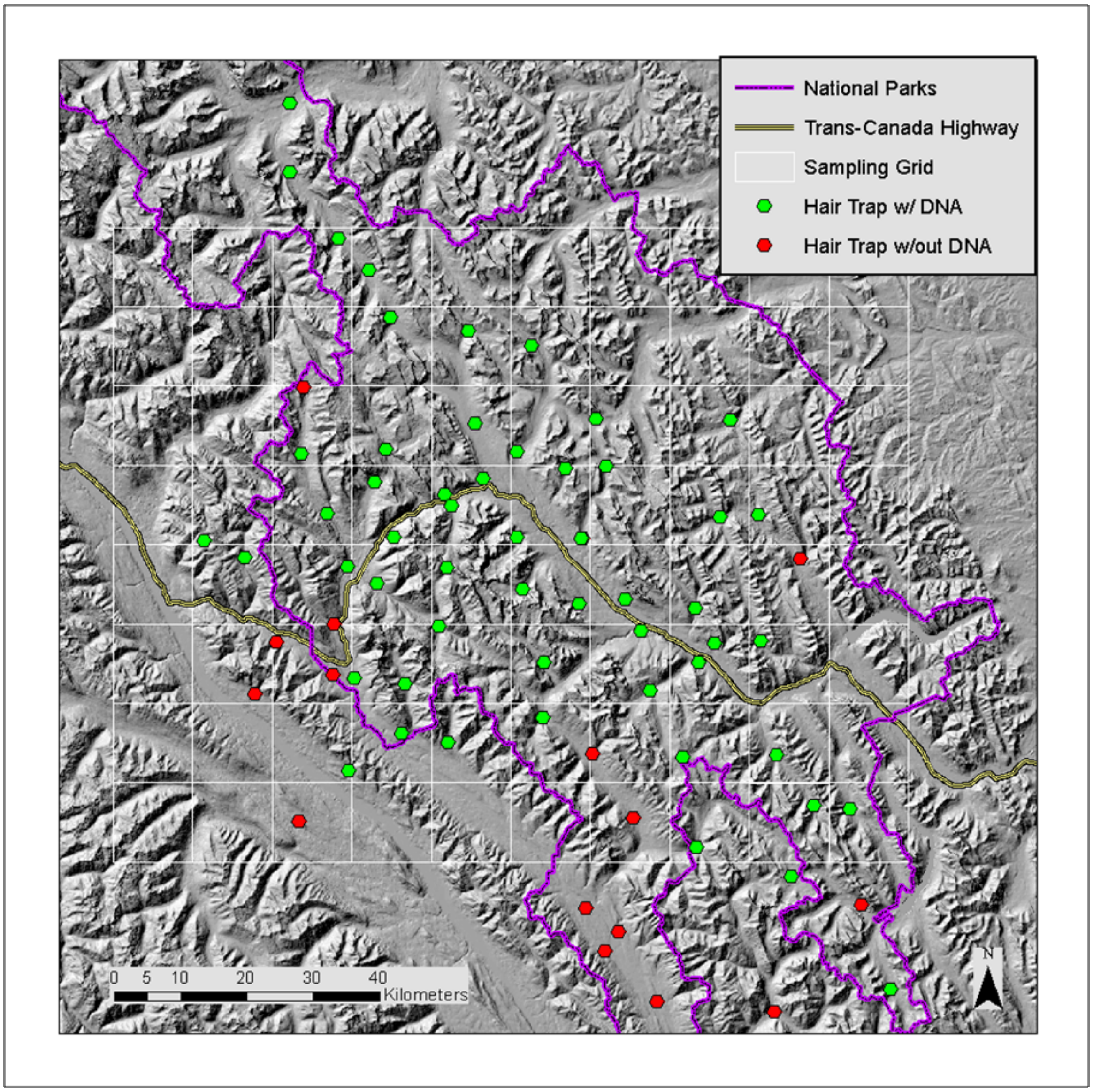

Figure 1: Wolverine hair trap success in parks complex between 2011 and 2013.

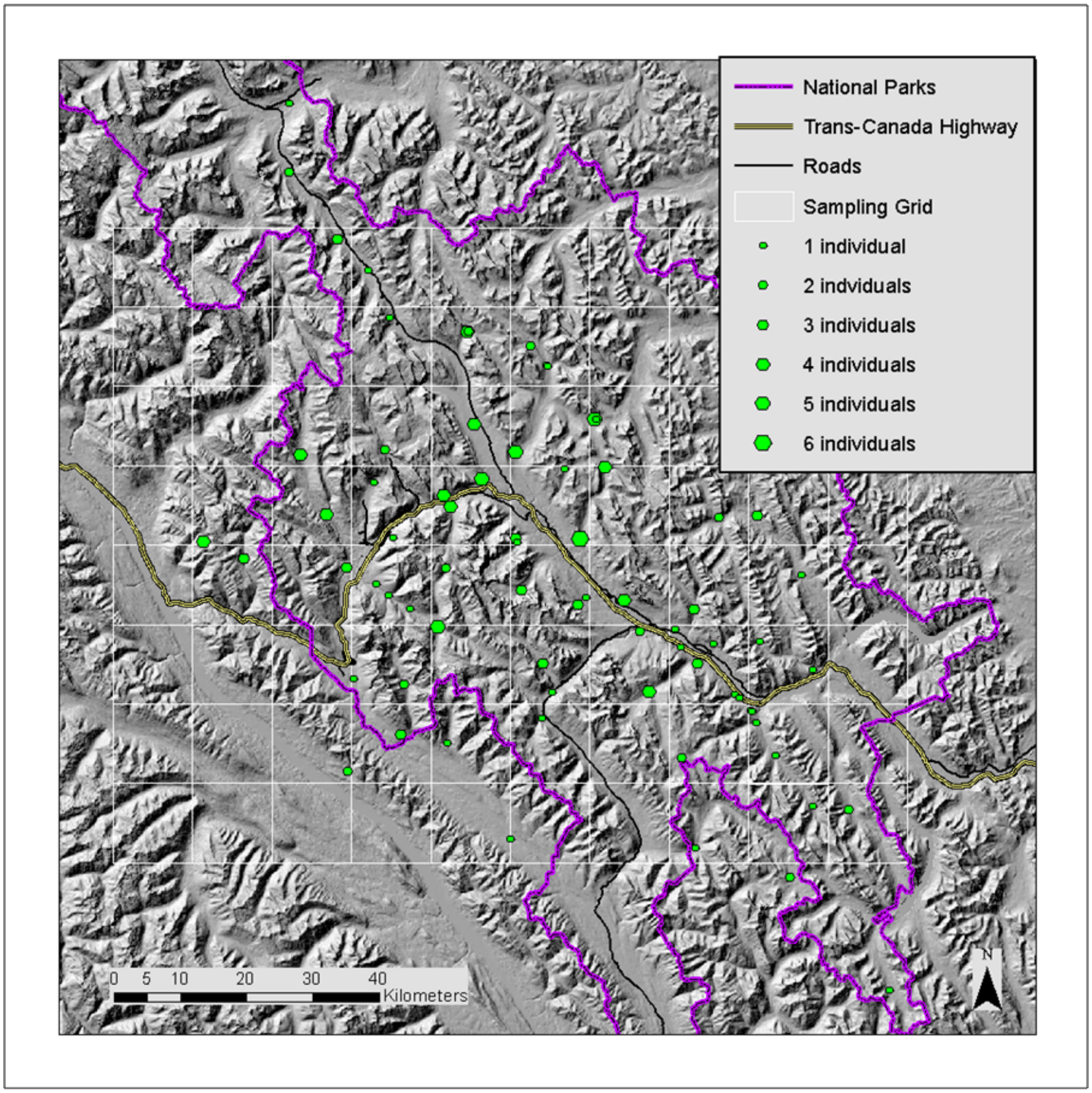

Figure 2: Number of unique wolverines detected at each sampling site in parks complex between 2011 and 2013.

Transportation Effects on Population Structure

We examined wolverine population structure and fine-scale movements using 229 unique locations (74 female, 155 male) in space and time (Figure 3). We detected males more frequently than females, averaging 3.97 locations per male and 2.96 locations per female. Male wolverines were detected throughout the sampling area (Figure 4), whereas female detections were more concentrated towards the center of the mountain park complex (Figure 5). Of the 64 wolverines, 32 were detected on the north side of the highway (13 females, 19 males) and 32 were detected on the south side of the highway (12 females, 20 males).

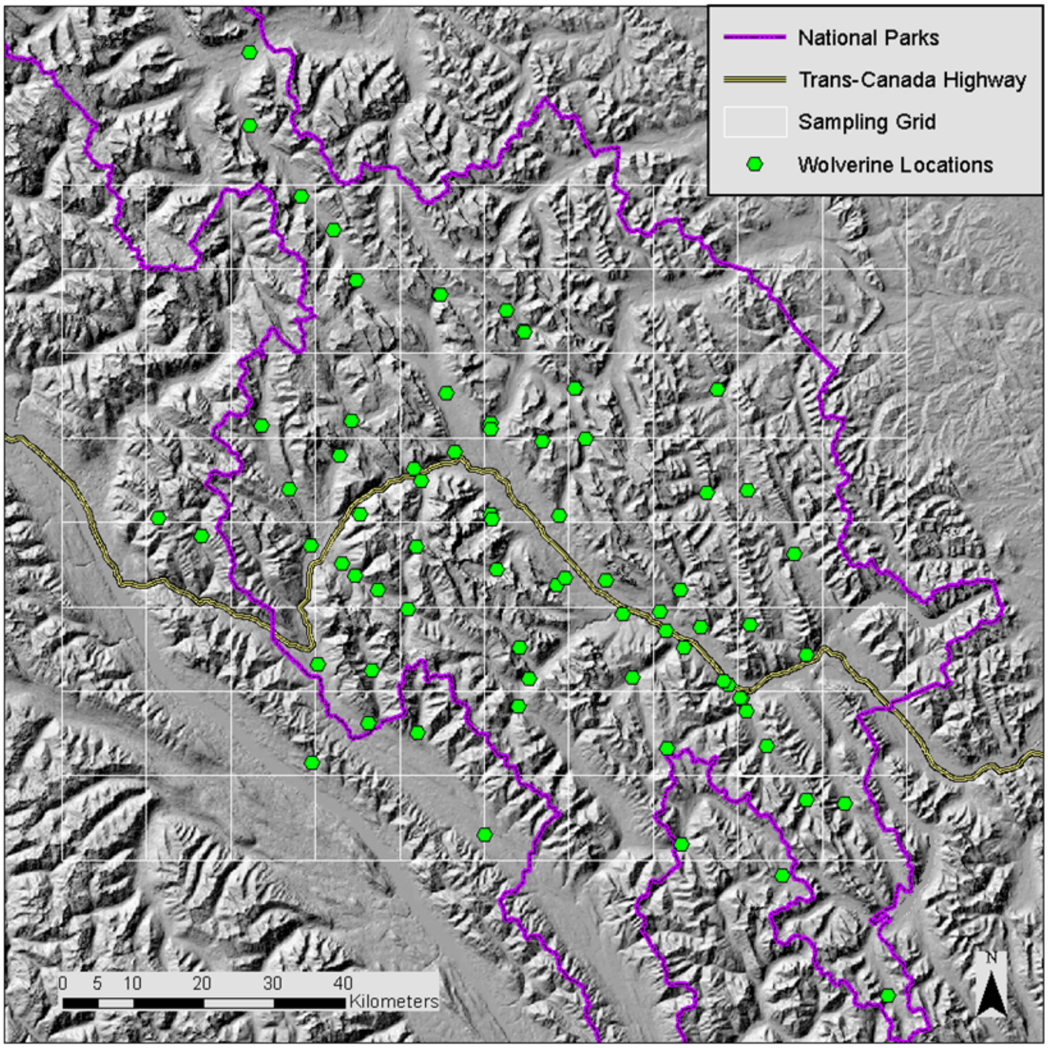

Figure 3: Locations of 229 wolverine detections in parks complex between 2011 and 2013.

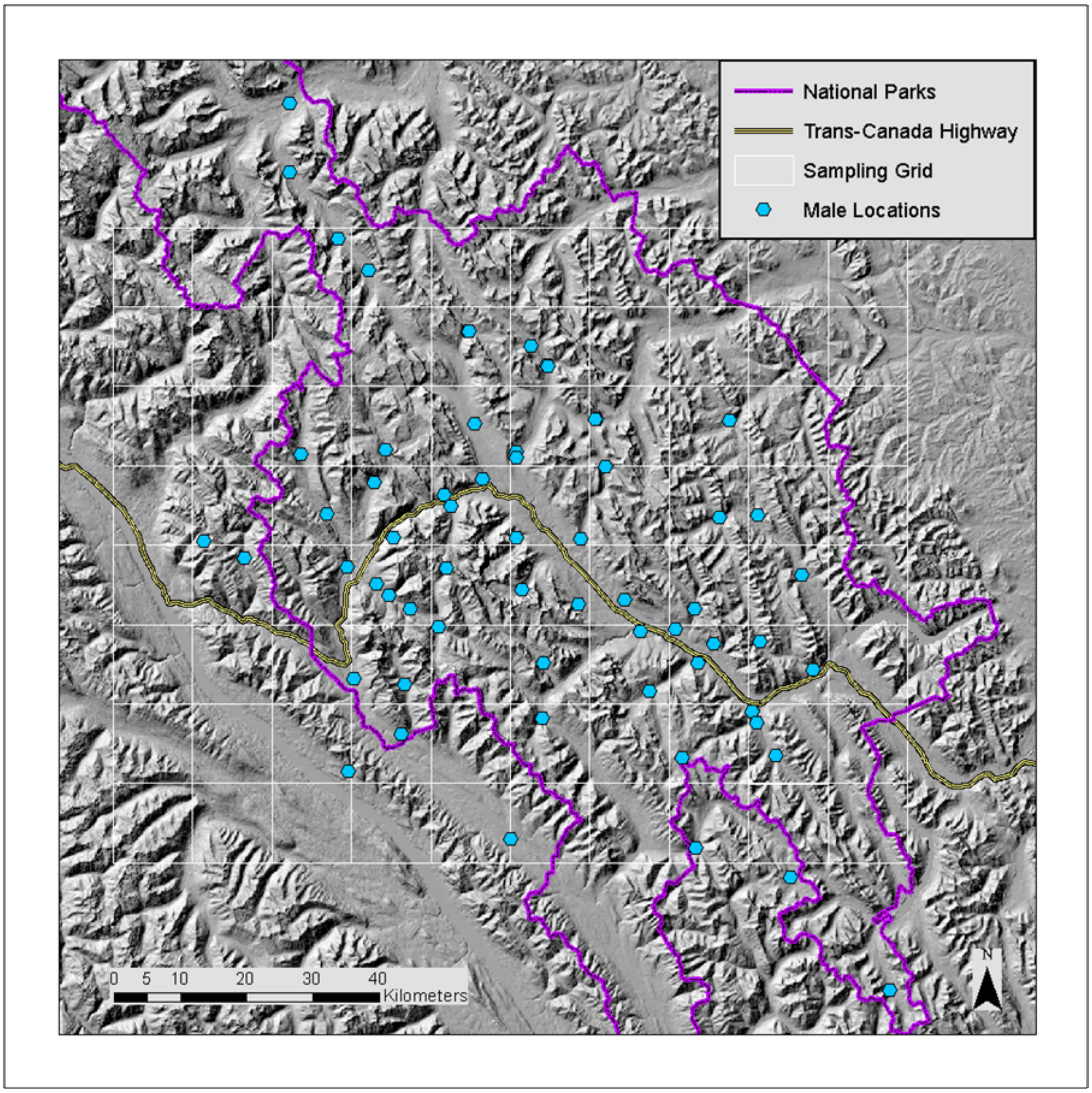

Figure 4: Locations of 155 male wolverine detections in parks complex between 2011 and 2013.

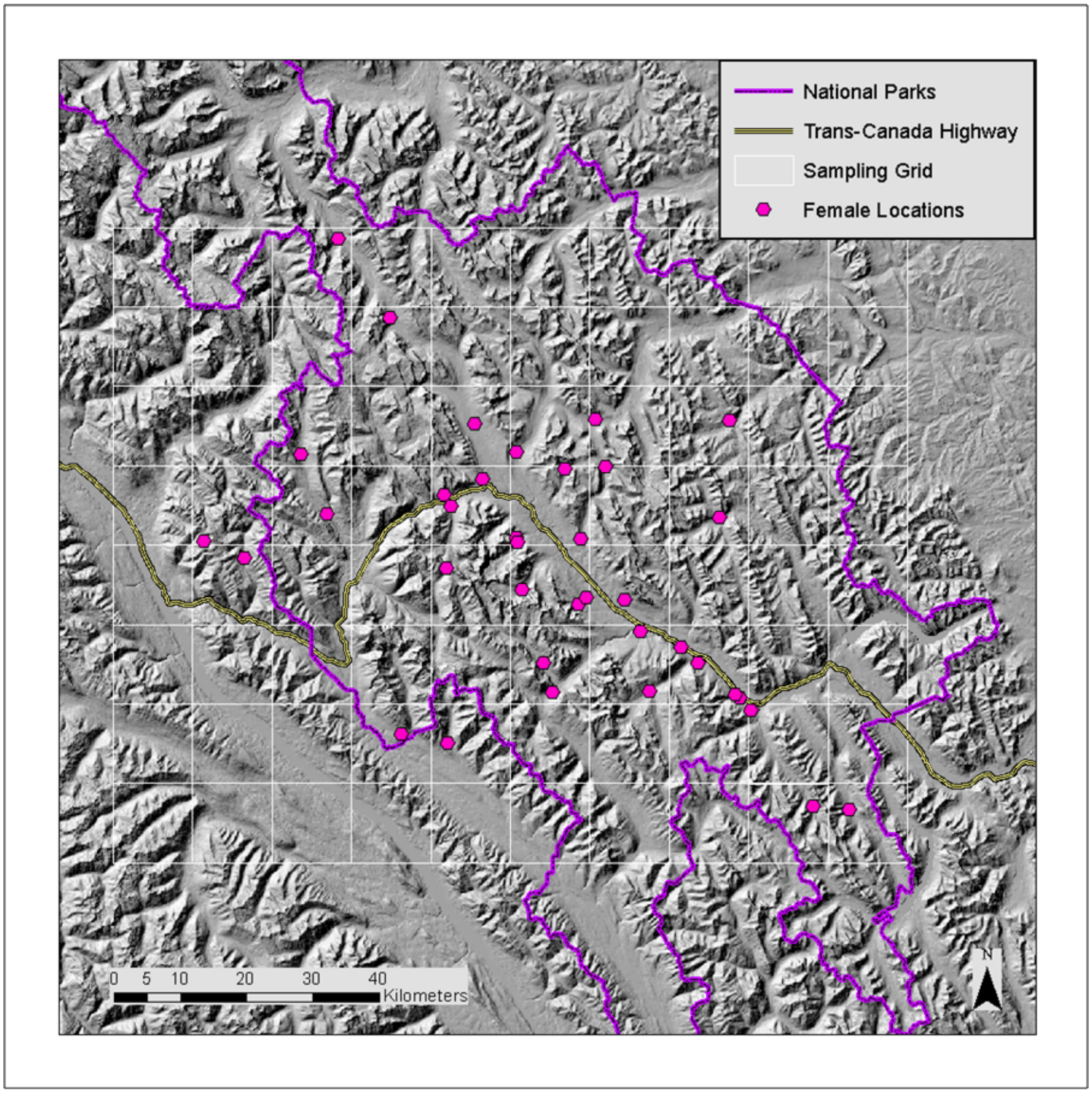

Figure 5: Locations of 74 female wolverine detections in parks complex between 2011 and 2013.

The results of our Mantel tests (R^2=0.12) indicated a weak correlation between geographic distance and genetic distance in our dataset. We calculated Fst for the total population of 64 individuals (Fst=0.32) and for each sex separately (female Fst=0.70, male Fst=0.25). Our FCA plot with all 64 individuals showed some genetic clustering, but not in relation to the highway (Figure 6); however, FCA plots broken out by sex revealed structuring of females (Figure 7), but not males in relation to the highway (Figure 8). Interestingly, plots of the total population and males-only revealed that M036 had an unusual genotype within the dataset (Figure 6 and 8).

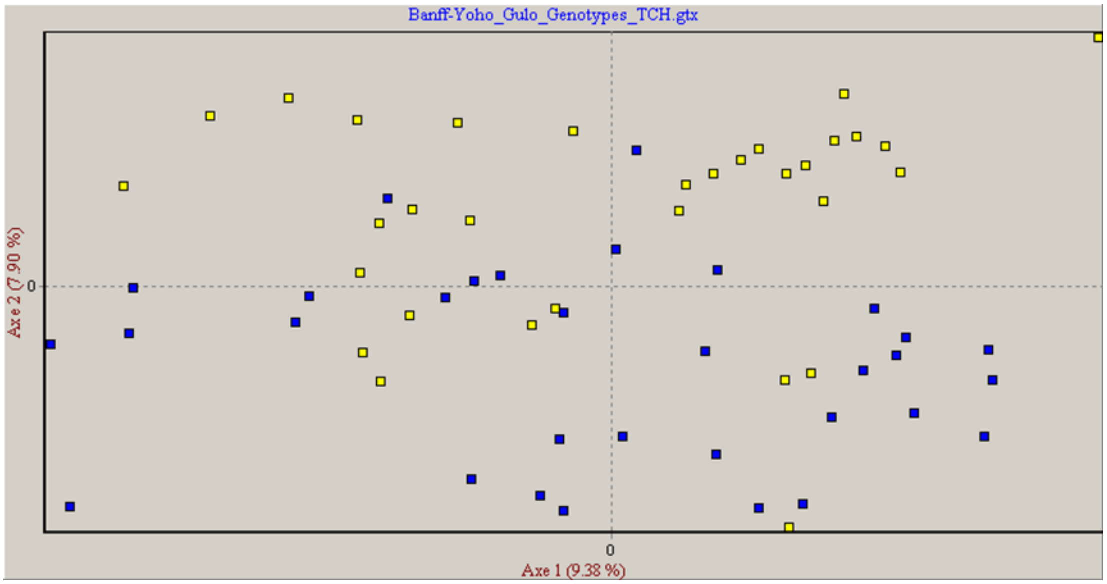

Figure 6: Factorial Correspondence Analysis plot showing 64 wolverines detected to the north (yellow) or south (blue) of the Trans-Canada Highway in the parks complex between 2011 and 2013. M036 is located in far lower left portion of graph.

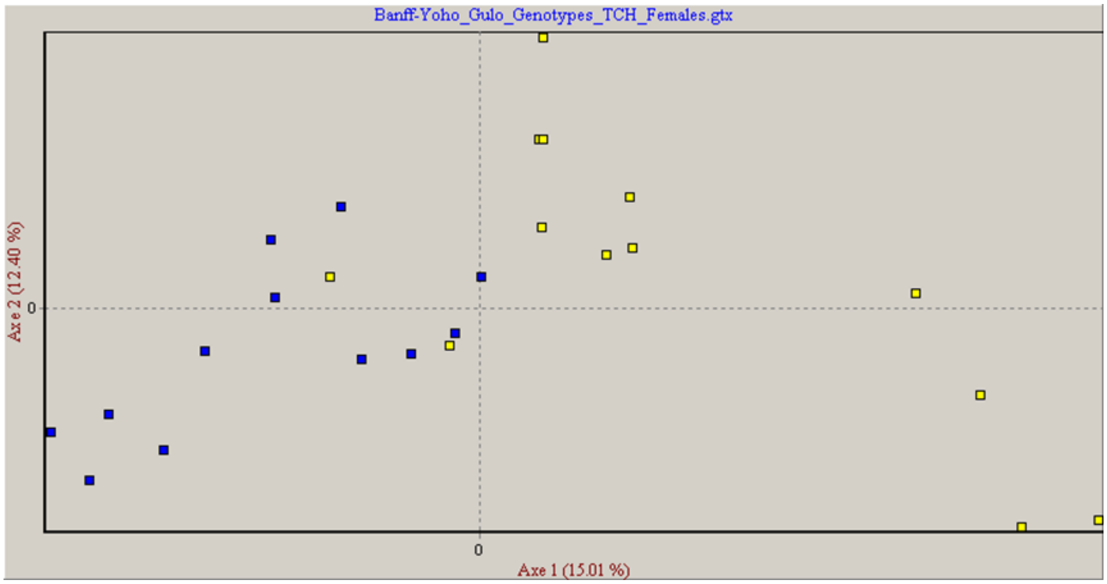

Figure 7: Factorial Correspondence Analysis plot showing 25 female wolverines detected to the north (yellow) or south (blue) of the Trans-Canada Highway in the parks complex between 2011 and 2013.

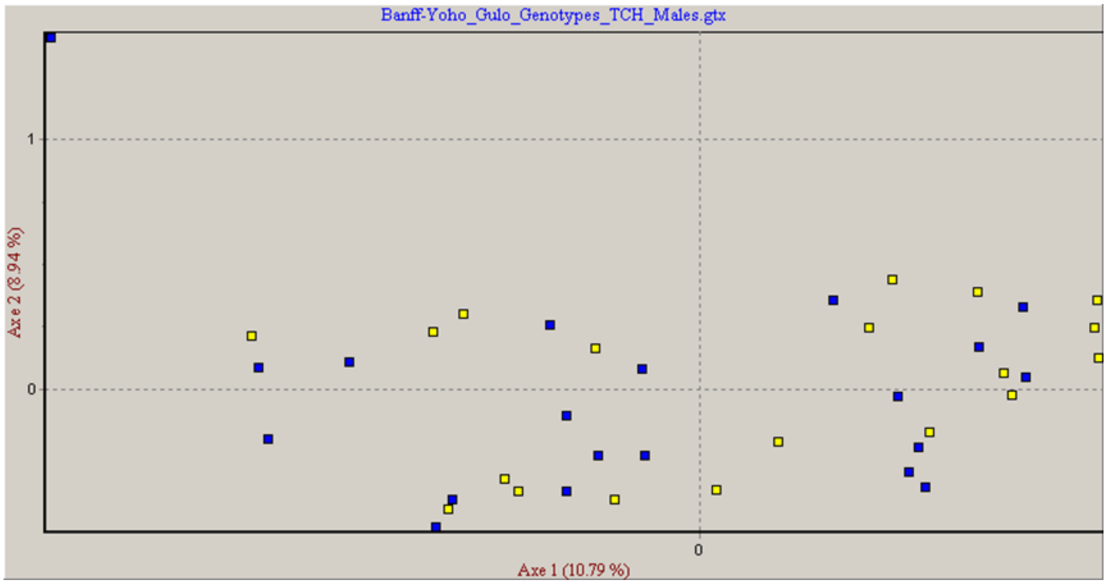

Figure 8: Factorial Correspondence Analysis plot showing 39 male wolverines detected to the north (yellow) or south (blue) of the Trans-Canada Highway in the parks complex between 2011 and 2013. M036 is located in far upper left portion of graph.

We detected 7 wolverines that crossed the TCH, including two females and five males with DNA detections that spanned the roadway (Appendix D, Figures A.1-A.7). Self-assignment probabilities (females=0.92, males=0.62) and population assignment graphs (Figure 9, Figure 10) from sex-specific frequency-based assignment tests indicated clustering of females, in particular. Two females and fifteen males were identified as cross-population migrants from frequency-based assignments tests. Results from program STRUCTURE indicated that there were three populations of wolverines (Appendix D, Figures B.1-B.2), with more structuring in males than females. Surprisingly, a spatial examination of the population clusters from STRUCTURE did not suggest an effect of the TCH on genetic isolation. When the individual spatial locations of population clusters are examined, clustering appears related to the TCH for females (Figure 11), but unrelated to the TCH for males (Figure 12).

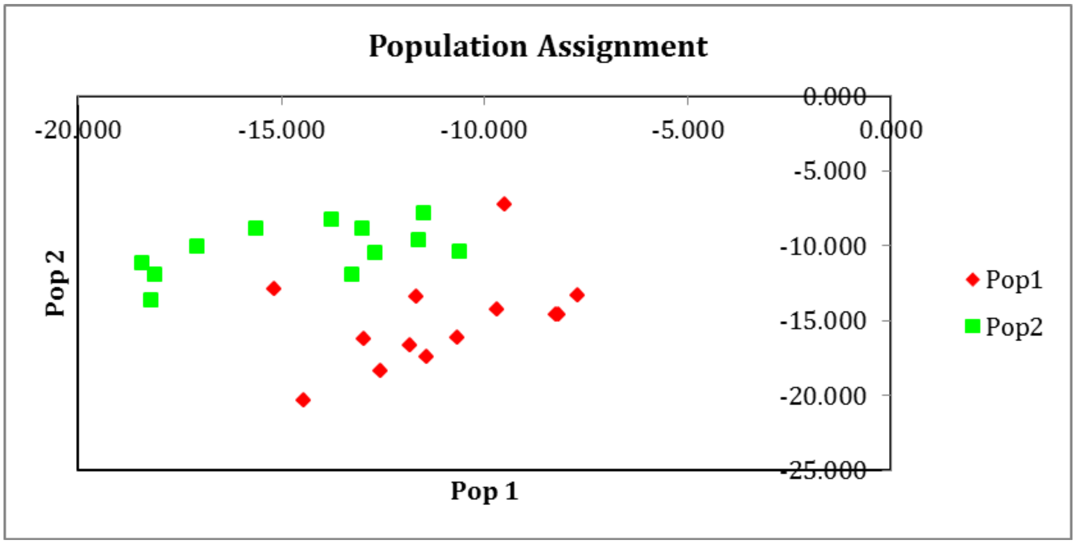

Figure 9 Population assignment graph showing 25 female wolverines detected to the north (red) or south (green) of the Trans-Canada Highway in the parks complex between 2011 and 2013.

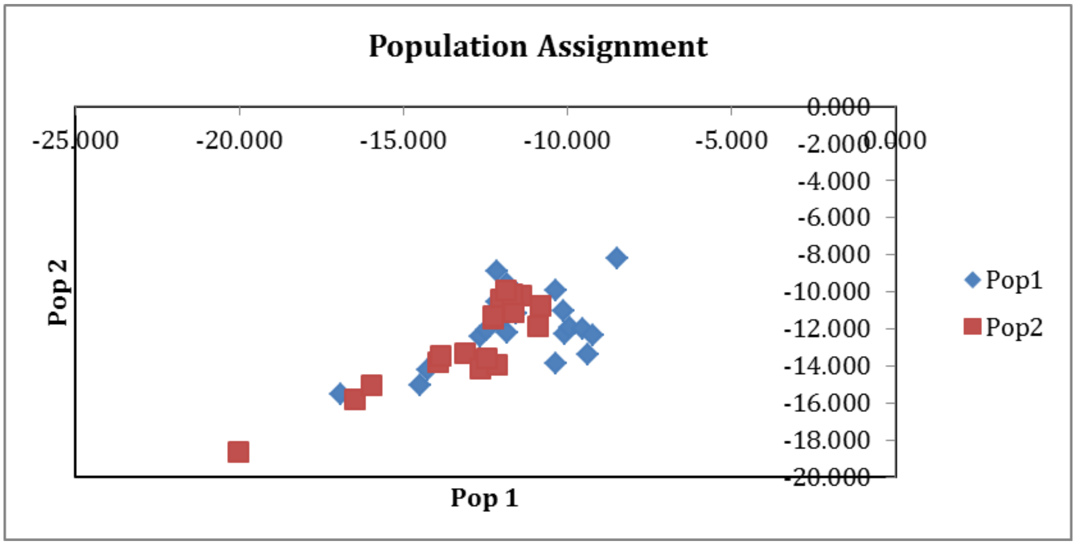

Figure 10: Population assignment graph showing 39 male wolverines detected to the north (blue) or south (red) of the Trans-Canada Highway in the parks complex between 2011 and 2013.

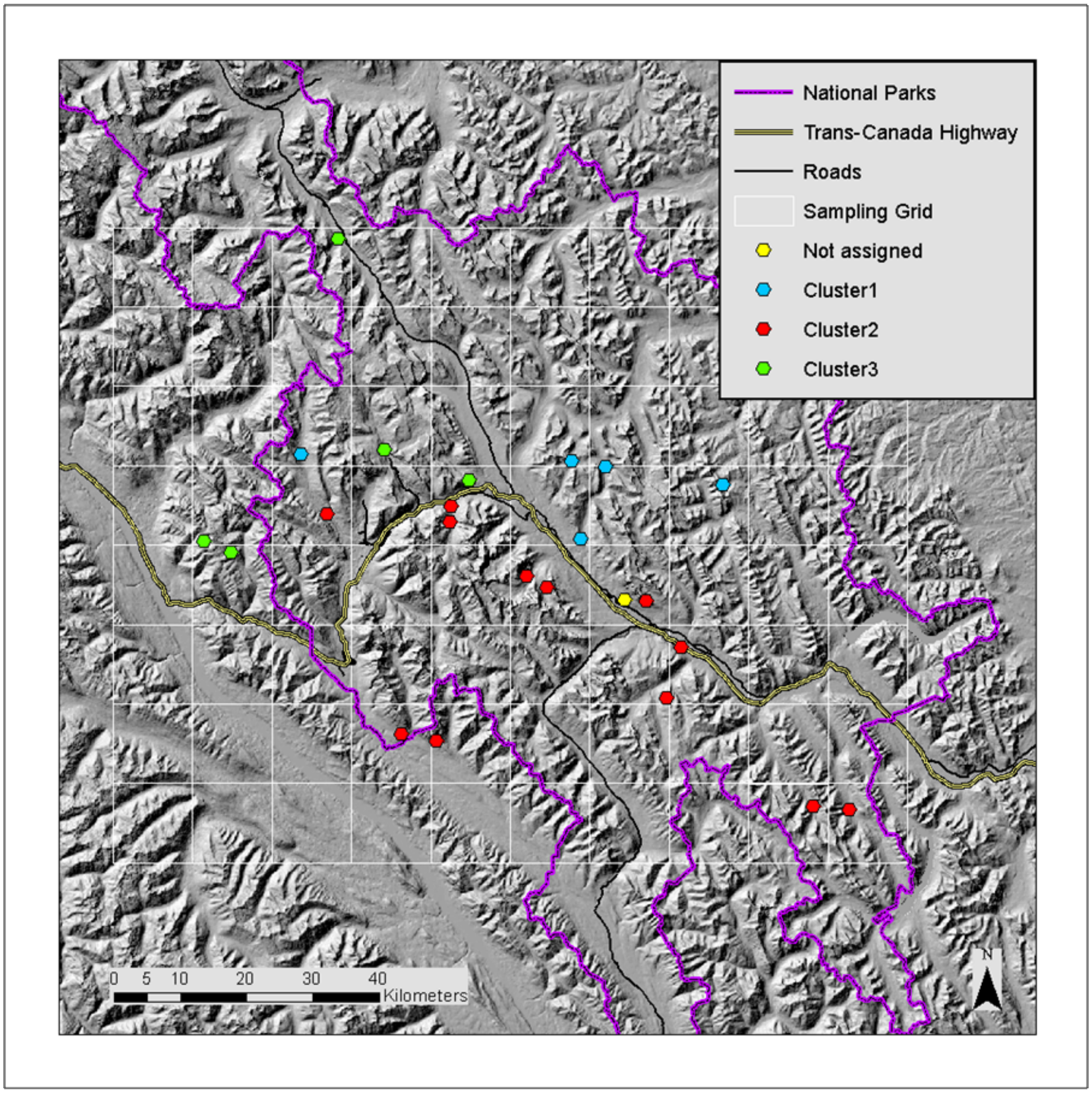

Figure 11: Individual detection centers of 25 female wolverines color-coded by their assignment to one of three population clusters identified in program STRUCTURE to examine the effect of the Trans-Canada Highway on fine-scale genetic differentiation in the parks complex between 2011 and 2013. Individuals with q-value<0.7, was not assigned to population cluster for this analysis.

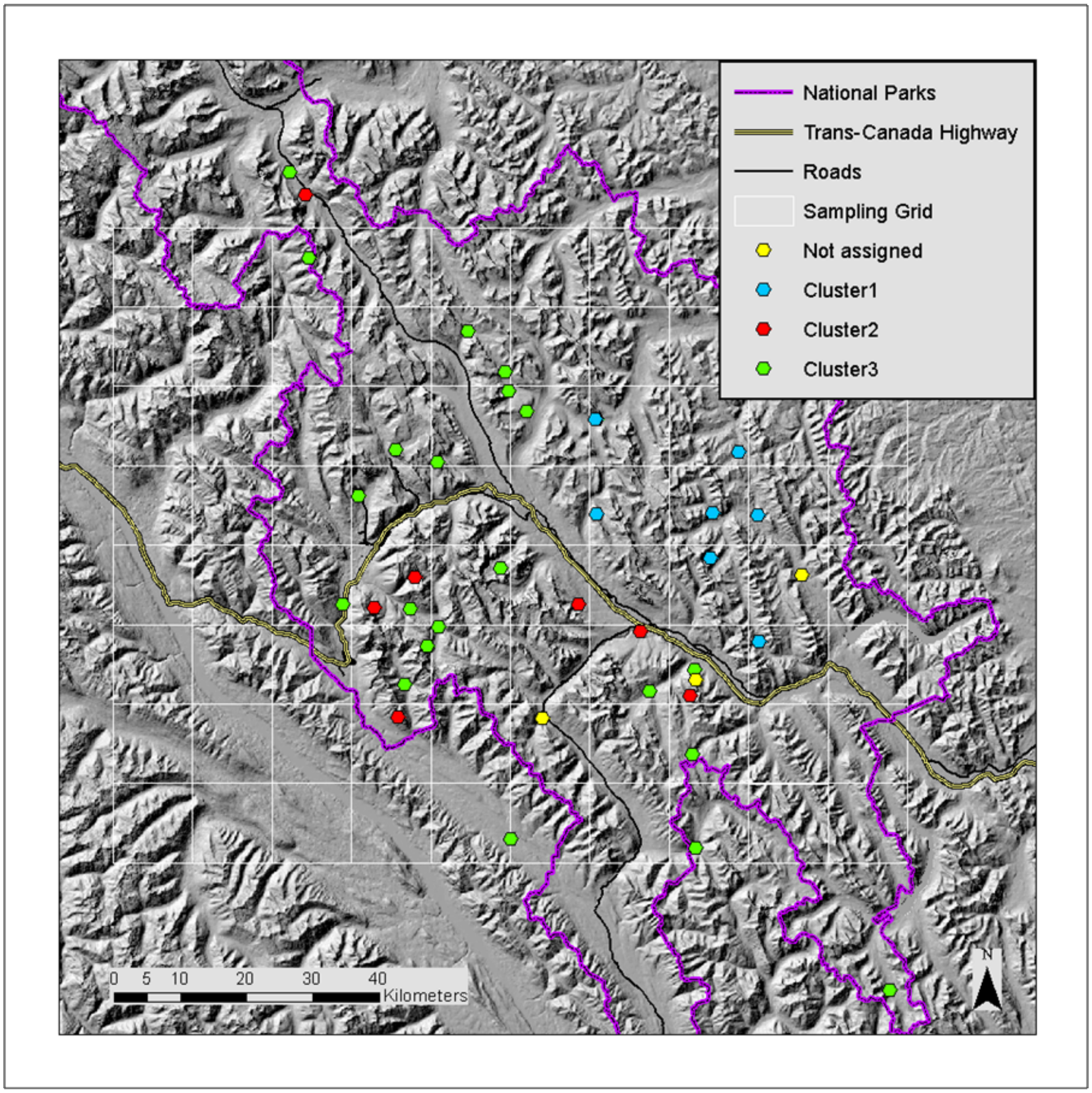

Figure12: Individual detection centers of 39 male wolverines color-coded by their assignment to one of three population clusters identified in program STRUCTURE to examine the effect of the Trans-Canada Highway on fine-scale genetic differentiation in the parks complex between 2011 and 2013. Individuals with q-value<0.7, were not assigned to population cluster for this analysis.

Mitochondrial DNA sequencing identified four different haplotypes within the population of 64 wolverines (Figure 13). All of these mitochondrial haplotypes had been documented in past studies of populations to the north, south or west of our study area. Three of the four haplotypes (Cegelski L, Wilson A, Wilson H) are common in both males and females and were previously identified within Alberta; however, one haplotype (Wilson I) was only identified in three different males and had never been documented in the Canadian Rocky Mountains before. An examination of the individual spatial locations of haplotypes did not indicate an effect of the TCH on mitochondrial DNA haplotype diversity.

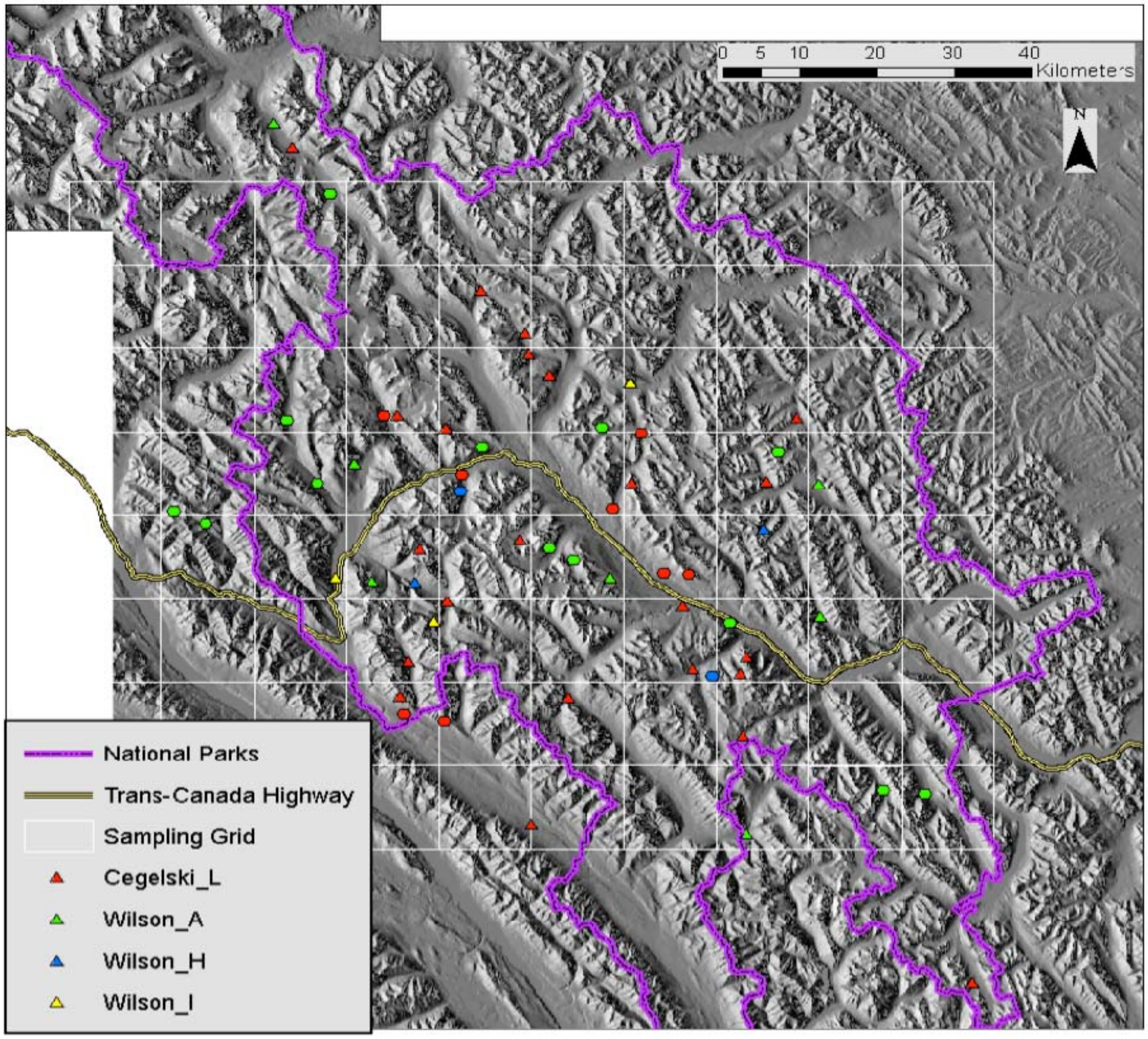

Figure 13: Individual detection centers of 64 wolverines with M036 color-coded blue to highlight his location in relation to other wolverines detected with noninvasive genetic sampling to examine the effect of the Trans-Canada Highway on fine-scale genetic differentiation in the parks complex between 2011 and 2013.

Discussion and Management Implications

Wolverines are quickly becoming recognized as an important indicator of healthy northern montane ecosystems. In the face of climate change, it's increasingly important to understand what landscape features influence population structure of snow-dependent species so that mitigation strategies can be optimized to ensure their survival (McKelvey et al. 2011). With little empirical evidence, the Mountain Parks are already considered havens for wolverine populations in the Central Canadian Rocky Mountains (Fisher et al 2013) and now we have provided the first evidence-based insight into their abundance, relative density, and population structure in this ecologically important area. Here, we present the first fine-scale examination of wolverine genetic structure and provide results that suggest transportation systems have limited female movements leading to sex-biased dispersal and gene flow.

DNA Collection and Genetic Analysis

We were successfully able to detect a large number of wolverines using our noninvasive genetic sampling methods. Fortunately, we had reasonable sampling coverage on both sides of the TCH so we were able to get relatively equal samples sizes of males and females to the north and south of the highway. Our high success at hair trap sites allowed us to obtain genetic information from an adequate sample size of wolverines to examine genetic structure. Interestingly, female detections were more concentrated towards the center of the mountain parks (Figure 5), whereas male detections were more dispersed (Figure 4). However, the greater number of detections and more widespread distribution were not surprising considering the well-documented mobility of the male wolverine.

Transportation Effects on Population Structure

Our results show that many female and male wolverines call the parks complex home, but the two sexes are affected differently by transportation infrastructure. We detected ample male movement across the TCH and lack of genetic differentiation to infer that the highway has not genetically isolated male wolverines. Conversely, we found that females were structured by the TCH, although we also found direct evidence that at least two females made it safely across the highway, possibly at one of the wildlife crossing structures. Restricted female movements and sex-biased population structure has been documented in other carnivore species (Proctor et al 2005) and this demographic fragmentation can reduce meta-population viability; however, wildlife crossing structures can help to restore demographic and genetic connectivity (Sawaya et al 2013, 2014). Fortunately, evidence suggests that females may be starting to use wildlife crossings. For example, a female wolverine, F015, may have been the wolverine detected crossing northward at Castle Underpass on February 16, 2011 (Clevenger

2013) as she was detected just two days prior at a nearby hair trap south of the underpass (Figure 14).

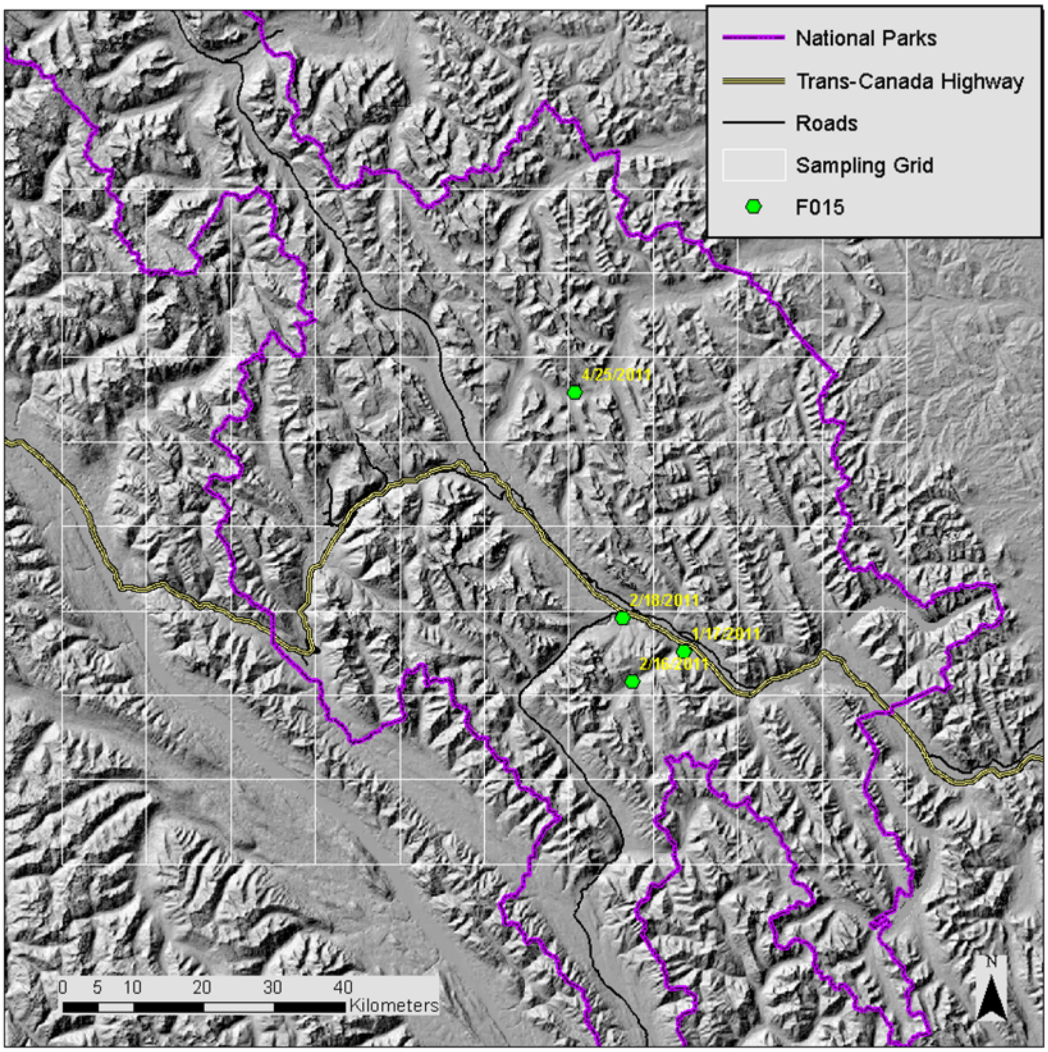

Figure 14: Pooled DNA-based detection locations with dates of sample collection for wolverine F015 that span the Trans-Canada Highway in the parks complex between 2011 and 2013.

The results of the Mantel tests to look for isolation-by-distance patterns indicated a weak correlation between geographic distance and genetic distance in our dataset, suggesting that distance alone did not account for a high percentage of the genetic variation observed. Results of examining genetic structure were congruent across population-based (i.e. Fst) and individual-based analyses (FCA, assignment tests) which allows for more powerful inference that there was a difference in how the TCH effects males and females. Surprisingly, a spatial examination of the population clusters from STRUCTURE did not suggest a strong effect of the TCH on genetic isolation, but it's been well-documented that STRUCTURE has difficulty assigning population clusters when levels of genetic differentiation are low such as with our study. The weight of evidence suggests that there is an effect of the highway and that it's greater for females than for males, but individual-based methods are extremely sensitive, so the relative magnitude of the transportation effect if unknown.

Using population-based and individual-based measures of genetic structure, we detected relatively strong genetic differentiation in female compared to male wolverines across the TCH. We had good sampling coverage and representation of individuals both north and south of the highway, though our samples sizes and methods may not have had adequate power to detect structure at such a fine spatial scale in a species with home ranges that can exceed the size of national parks. Future analyses that involve a larger geographic extent and include more individuals from nearby regions (i.e. Kananaskis Country, Mount Revelstoke and Glacier National Parks) would allow much more powerful inference about the effects of transportation systems and other anthropogenic activities on wolverine population structure and gene flow.

To gain a better understanding of how to effectively mitigate the fragmentation effects of the TCH on female wolverines, Parks Canada should continue monitoring of wildlife crossing structures on the TCH, particularly the newly constructed crossings west of Castle Junction (BNP). This will be important given the current lack of information with respect to how wolverines respond to crossing structures (see Chapter IV.3). After 17 years of monitoring roughly two dozen crossing structures only 10 wolverine crossings were detected (Clevenger 2013). Crossing structure monitoring should be conducted in conjunction with winter roadside surveys to inform regarding the number of highway crossings by wolverines not detected at crossing structures, breaches in fence and behaviour from snowtracking in the highway corridor. Last, Parks Canada should consider following tracks in snow to collect hair from wolverines that use wildlife crossing structures to traverse the TCH so that sexes can be determined to help separately evaluate the effectiveness of different crossing structure types to determine the best designs for increasing female movement. In short, we detected healthy numbers of wolverines in the mountain parks, but we also found an effect of the highway on female genetic interchange, which may be a possible threat to the viability of wolverine populations, highlighting the urgent need to maintain demographic and genetic connectivity in the Rocky Mountains.

2. Distribution Models for Wolverines in Central Canadian Rocky Mountains: An Analysis of 2010-11 and 2012-2013 Camera Trap Data

Authors: Jason T Fisher, Nicole Heim, and Anthony P Clevenger

Introduction

Wolverines are a rare-occurring species that move over vast areas without recognizing political boundaries. They inhabit some of the most extreme alpine and subalpine environments and their populations have experienced considerable range reduction over the last 50 years (COSEWIC 2003, Laliberte and Ripple 2004, Brodie and Post 2010). Loss of habitat and barriers to movement, along with continuing warming climate, are recognized as threats that further diminish and fragment the critical landscapes they need for dispersal within their metapopulation (Krebs et al. 2004, Schwartz et al. 2009, Copeland et al. 2010, Inman et al. 2013).

Federally, the wolverine is listed as a species of *Special Concern*, while in Alberta it is listed as Data Deficient (Alberta Fish and Wildlife 2008). Presently little is known about the status of wolverines in the national parks of the Canadian Rocky Mountains (Suitor 2005). Recent research in central Alberta suggests that national parks may be a source population for unprotected areas in British Columbia and Alberta (Fisher et al. 2009, 2013). Thus, monitoring populations of wide-ranging species, such as wolverine, has been identified as a critical management objective in Banff and Yoho National Parks (Parks Canada 1997, 2007).

Until now wolverine distributions and habitat have been studied primarily in multi-use landscapes (Copeland 1996, Edelmann and Copeland 1999, Rowland et al. 2003, Aubry et al. 2007, Krebs et al. 2007, Fisher et al. 2013). These studies have shown that wolverines' distribution at regional scales is driven by multiple natural and anthropogenic landscape features. Natural landscape ruggedness, as well as linear features (seismic lines) resulting from petroleum extraction development, have been shown to predict wolverine occurrence in west-central Alberta (Fisher et al. 2013). Elsewhere, human use, including winter recreation and the presence of roads, has been shown to reduce habitat value for wolverines (Copeland 1996, Krebs et al. 2007, K. Heinmeyer, unpublished data).

The three contiguous national parks of the Canadian Rocky Mountains (Banff, Yoho, Kootenay) make up a vast protected area complex encompassing roughly 10,000 Km2 one of the most ecologically intact areas remaining in North America (Weaver 1996, 2013). Intuitively the park complex should be an important core area for wolverines at a metapopulation scale. The park complex lacks the resource extraction industries and associated road densities common in multi-use landscapes. Therefore the underlying mechanisms explaining wolverine distribution and habitat associations should differ from what has been reported from multi-use landscapes.

Within a protected area such as the national parks complex, human impacts are less spatially extensive, but instead are clustered in space and may be more intensive over smaller areas. More than 4 million tourists visit Banff National Park (BNP) annually, however, Kootenay and Yoho National Parks receive only a fraction of that amount. Similarly, BNP's Bow Valley is a highly developed landscape with a major east-west transportation corridor and three ski areas, while Yoho and Kootenay National Parks have significantly less transportation infrastructure and no ski areas. These disparities in landscape disturbance within a protected area complex may affect wolverine occurrence at a park-wide scale. Further, at the ecosystem scale, the absence of many of the main effects explaining wolverine occurrence in working landscapes presents a unique opportunity to model wolverine habitat under a different landscape-human disturbance regime. This analysis would increase our understanding of functional habitat relationships of species increasingly impacted by landscape disturbance and fragmentation and changing climate (McKelvey et al. 2012).

We asked whether wolverine occurrence within national park complex was affected by natural and anthropogenic features, and whether these differed from the features known to affect occurrence outside of protected areas. We used two different approaches to answer this question: hierarchical occupancy models and generalized linear models.

Methods

Study Area

Our study area is located in the Canadian Rocky Mountains, encompasses approximately 9000 km^2 and includes parts of Banff, Yoho and Kootenay National Parks, Mt. Assiniboine Provincial Park, the Columbia Valley in British Columbia, and adjacent provincial lands in BC (hereafter referred to as the park complex). The Bow River Valley of Banff National Park (BNP) is situated within the front and main ranges of the Canadian Rocky Mountains. Topography is regarded as mountainous with elevations from 1300 m to over 3400 m, and a valley floor width from 2 to 5 km. The climate is continental and characterized by relatively long winters and short summers (Holland and Coen 1983). Vegetation in the park encompasses montane, subalpine and alpine ecoregions. Montane habitats are found in lower- elevation valley bottoms. The lower Bow Valley is a human-dominated landscape with the Trans-Canada Highway TCH, the Banff Townsite (10,000 residents), a golf course, three ski areas, Canadian Pacific Railway (CPR), and a secondary highway. Neighbouring Yoho National Park (YNP) is situated on the west side of the Continental Divide and is characterized by steep rugged terrain with narrow valleys and continental climate consisting of short, cool summers and long winters with high snowfall. The Kicking Horse River is the main east-west aligned watershed in YNP, which parallels the TCH and CPR mainline. Differing from the Bow Valley, the Kicking Horse Valley is sparsely populated, as Field (300 residents) is the only townsite within the national park.

Experimental Design and Sampling

For sampling purposes our survey area was delineated by creating a 30-km buffer around the TCH from Castle Junction (BNP) to the west boundary of YNP (Figure 1). We surveyed wolverine occurrence using a systematic sampling design consistent with past wolverine research (Fisher et al. 2013), enabling future data pooling and large, landscape-scale analyses. The survey area was divided into 12-km x 12-km grid cells. Hair traps and motion-detection cameras were used to sample wolverine occurrence (Fisher et al. 2013).

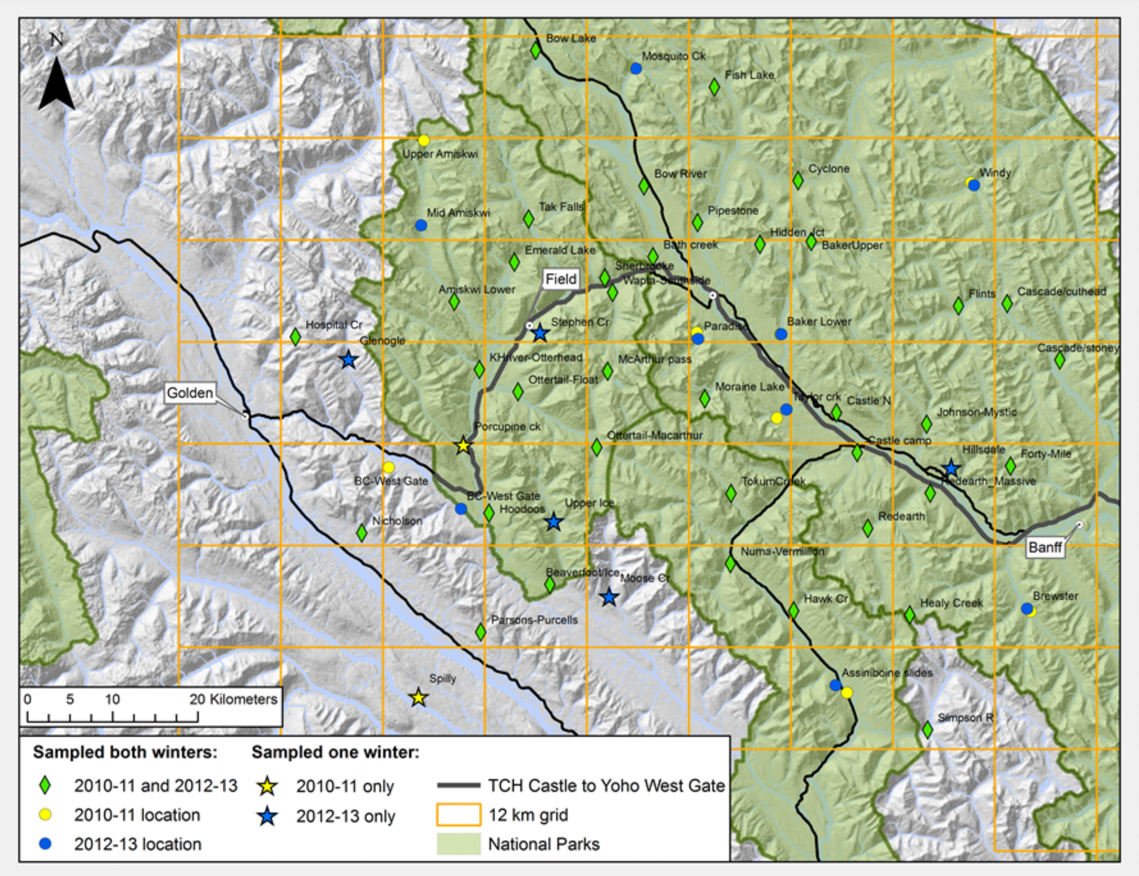

Figure 1. Map of study area in the Canadian Rocky Mountains centered on the Trans-Canada Highway with 12 x 12 km grid overlay. The area is bounded by Banff in the east, Bow Summit in the north, Golden, BC in the west, and Simpson River (Kootenay National Park) in the south. The study area encompasses approximately 7000 km2.

One sampling location was located in each grid cell. However, to increase probability of detection and movements within the TCH corridor an additional sampling site was placed in select grid cells that overlaid the TCH. Each sampling site was checked during 3, 30-day sessions between January and April. The three replicate monthly sessions allowed us to incorporate detection probability into occupation estimates (MacKenzie et al. 2002).

Our analysis uses camera trap data collected during winters of 2010-2011 and 2012-2013, including n=59 sites. We recorded observations of each mammal species within each month (January, February, March) and scored each species as present or absent monthly. We summed presences across 3 months to yield a 0-3 count of species occurrence at each site. This measure provides presence / absence information, as well as indexing residency at each site during the sampling period.

Quantifying Landscape Covariates

ESRI ArcGIS 9.3.1 software and digital map inventories (ABMI 2010, and National and Alberta Provincial Parks' geo-databases) were used to quantify explanatory variables. Variables were limited to the highest resolution spatial data available with continuous coverage across the study area. All natural and anthropogenic landscape measures were quantified by creating circular buffers around each sample location, across 20 spatial scales ranging from 500 m up to 10,000m. All measured values were standardized for accurate comparison of parameter effect size. A cross-scale analysis (N. Heim, unpublished data) shows that the 10,000-m radius results in best-supported models for wolverines, so landscape quantified at this scale was used for habitat selection analysis. To be consistent with previously quantified GIS data (A. Clevenger, unpublished data), the occupancy analysis used GIS data quantified at the 5000-m scale. Fisher et al. (2011) suggest that different scales provide different model fits, but the cross-scale analysis suggests we do not expect the variables selected as important for wolverines to differ among scales.

Landscape composition (habitat availability) was quantified using a LandSat thematic-mapped GIS land cover dataset incorporating a digital elevation model, with a habitat-identification algorithm that classified 16 landcover types (McDermid et al. 2009). The percent area of each class within the circular buffer described landcover around each camera site. Mean values within each buffer were calculated for other landscape variables described by raster datasets. . In addition, we quantified (1) topographic ruggedness, measured as the mean elevation difference over an area (Riley et al. 1999); and (2), persistent spring snowpack, calculated using 12 years (2000 to 2010) of classified moderate resolution imaging spectroradiometer (MODIS) satellite imagery from a 21-day composite (April 24 –May 15) at a 0.5-km2 resolution. This calculation followed work by Copeland et al. (2010) using MODIS satellite data to test the association of wolverine occurrence with persistent spring snow cover.

Available human footprint data (ABMI 2010) was accumulated into one polygon dataset. We grouped variables from these data by block and linear features. We calculated the mean values of these human footprint features in two different ways in order to represent the differences in landscape-scale impacts of block versus linear features. Block features were measured as percent area of two types, urban and industrial. Linear features were measured by the density (km/km^2) of three types, linear road, industrial, and recreation.

Independent Variable Reduction

The GIS analysis yielded dozens of variables describing the landscape. Some of these are variants of one another and therefore highly correlated; some were not sufficiently represented on the landscape to allow modelling; others were naturally correlated because of their co-occurrence on the landscape. We grouped variables together into sets – landcover, footprint, and species – and created correlation matrices to examine the degree of correlation between variables, and eliminated removed one variable from any pair having a correlation coefficient higher than 0.75 (Zuur et al. 2009).

Of the 16 landcover variables, only 9 were sufficiently represented to allow modelling. As we had no *a priori* hypotheses about which landcover variables might predict wolverine occurrence, we used the step-AIC function in R package MASS to reduce these variables. This procedure works like stepwise regression, iteratively fitting different variables within the candidate set, until the best-fit, most parsimonious model (based on AIC weight) is obtained. We used this same procedure to reduce correlated footprint, topographic, and persistent spring snow cover variables.

The final candidate set of independent variables were not correlated, and represent several competing hypotheses about the effects of landscape on wolverine occurrence.

Wolverine Occupancy Analysis

Species are often detected imperfectly, and detection often decreases with increasing rarity (MacKenzie 2005, Mackenzie et al. 2002, Mackenzie et al 2006). Species occupancy at a site (ψ) can be modelled in conjunction with its probability of detection (p): the probability of detecting that species if present. Occupancy is not a static measure; it is expected to change through time (MacKenzie et al. 2003). Sites without wolverines can become occupied in subsequent years, whereas sites with wolverines in one year may have no wolverines in the next. Examining how occupancy changes among years helps us to better understand the role of environmental conditions on wolverine distribution. We used multi-season occupancy models (MacKenzie et al. 2003, Mackenzie et al. 2006) to estimate the probability that a wolverine would be detected *via* cameras, and the probability of wolverine occupancy at sampling sites. Multi-season models assume that occupancy is constant within a season, but can change among seasons; empty sites can be colonized, and occupied sites can become extinct, among seasons. Thus, multiple surveys are nested within multiple seasons, similar to Pollock's robust design for mark-recapture (MacKenzie et al. 2003).

To ensure that any missed detections of wolverines by camera traps does not influence our conclusions about wolverine distribution in the study area, we estimated the probability of detecting wolverines given they were present at a site. If probability of detection is high, then camera data from across the entire park complex can be reliably combined in generalised linear models (GLMS) for the habitat selection analysis.

We used custom multiple-season hierarchical occupancy models in software PRESENCE v.4.9 (Hines 2006). Detection histories were comprised of monthly wolverine detections and non-detections at each site, repeated across three months. Models assumed occupancy was either constant, or varied with natural and anthropogenic landscape features. Models further assumed that p was either constant, or varied through time. Resulting models were ranked using an information-theoretic approach to model selection (Burnham and Anderson 2002), based on Akaike's Information Criterion (AIC) score and normalised AIC weights (AICw), which describe the weight of evidence in support of each model. We ranked models by AICw and calculated evidence ratios (ERs) to weigh support for each covariate (Burnham and Anderson 2002, Anderson 2008); ER = 2 suggests there is twice the evidence for inclusion of an explanatory variable, than for its exclusion. From per-survey estimates of p we calculated the probability of false absence (pfa) for a given survey duration as [1-p]t (Long and Zielinski 2008), with t=3 independent surveys.

Habitat Selection Analysis

We used generalised linear models (GLM) to test hypotheses about wolverines' relationship to landscape composition, since these are more flexible than occupancy models for this purpose, and model the more informative 0-3 residency index as opposed to simple presence / absence, like occupancy models do. GLMs were created in R statistical software (ver. 2.15.3; R Core Development Team 2011) with Poisson errors and log-link function (Crawley 2007). Resulting models were ranked by AIC weights. Models with high AIC weights suggest the variables within those models best describe variability in wolverine distribution across the study area.

Results

Wolverine Occupancy Analysis

The probability of detecting a wolverine at a sampling site given it was present (p) varied through time. This model was supported by 100% of the weight of evidence (Table 1). Estimated *p* increased from January through March in both years. In Year 1, p more than doubled from January to March. In Year 2, the increase was less marked, as overall detectability was higher in Year 2 than in Year 1 (Figure 2). Multiplying the probabilities of failing to detect wolverines within each survey (1-p), the probability of false absence in Year 1 was 0.5%, and in year 2 was 0.4%, meaning that we are 99.5% confident that we are detecting wolverines at cameras when they are present at a site. This lends great confidence in the results of the habitat models.

Table 1. Model selection of occupancy models testing hypotheses about the variability of probability of detection (p) through time. Estimated p could vary with SURVEY, YEAR, or remain constant (). All other variables were held constant.

Model	AIC	ΔAIC	AIC weight	Model Likelihood	no.Par.*	.-2ll**
psi,gamma(),eps(),p(SURVEY)	290.12	0	1	1	9	272.12
psi,gamma(),eps(),p(YEAR)	327.35	37.23	0	0	5	317.35
psi,gamma(),eps(),p()	328.91	38.79	0	0	4	320.91

*number of parameters in the model
**-2 log likelihood of the model (model fit)

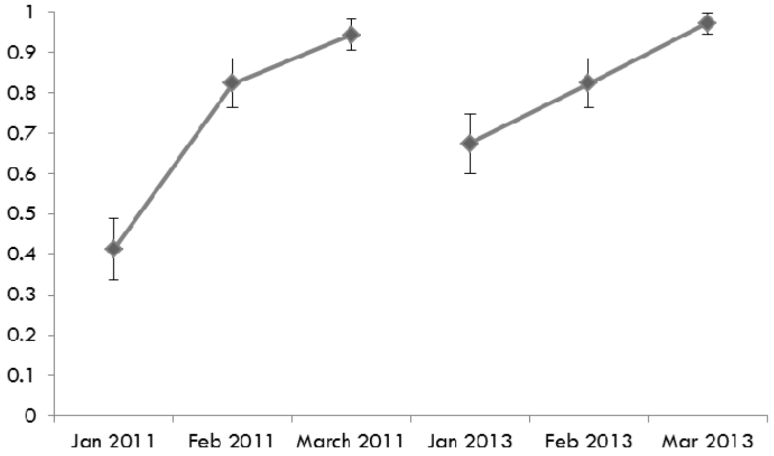

Figure 2. The probability of detecting a wolverine at a camera, given it was present at a site, increased from January through March in both years, and approached 1.0 at the end of surveying.

Given the strength of evidence that p varied among surveys, we assumed this condition for all remaining occupancy models, which tested hypotheses about the effect of landscape features on wolverine occurrence. The best-supported model, which carried 65% of the weight of evidence (AICw = 0.65), suggested the proportion of the landscape covered in snow and ice (as described by the McDermid et al. 2009 landcover data; SNOWICE) was the best predictor of wolverine occupancy (Table 2). All other variables, including the proportion of area covered in shrubby cover (SHRUB) or herbaceous alpine cover (HERB), topographic ruggedness (TRI), persistent spring snow through May (SNOW), the density of linear features (LINEAR), the density of non-motorized recreational trails (QUIET), and distance to highways (HWY), did not explain as much variability in wolverine occupancy. None of these variables explained any variability in the probability of site colonization (gamma) or the probability of site extinction (eps) from Year 1 to Year 2.

Table 2. Model selection of occupancy models relating the probability of wolverine occupancy (psi), site colonization (gamma), and site extinction (eps) to natural and anthropogenic landscape features.

Model	AIC	ΔAIC	AIC wgt	Model Likelihood	no.Par.*	.-2LL**
psi(SNOWICE),gamma(),eps(),p(SURVEY)	282.75	0.00	0.65	1.00	10.00	262.75
psi,gamma(SHRUB),eps(),p(SURVEY)	286.72	3.97	0.09	0.14	10.00	266.72

psi(TRI),gamma(),eps(),p(SURVEY)	287.20	4.45	0.07	0.11	10.00	267.20
psi(SHRUB),gamma(),eps(),p(SURVEY)	287.78	5.03	0.05	0.08	10.00	267.78
psi(SNOW),gamma(),eps(),p(SURVEY)	288.96	6.21	0.03	0.04	10.00	268.96
psi,gamma(),eps(),p(SURVEY)	290.12	7.37	0.02	0.03	9.00	272.12
psi,gamma(),eps(SNOWICE),p(SURVEY)	290.14	7.39	0.02	0.02	10.00	270.14
psi,gamma(SNOWICE),eps(),p(SURVEY)	290.49	7.74	0.01	0.02	10.00	270.49
psi,gamma(TRI),eps(),p(SURVEY)	290.62	7.87	0.01	0.02	10.00	270.62
psi,gamma(),eps(HERB),p(SURVEY)	291.67	8.92	0.01	0.01	10.00	271.67
psi,gamma(SNOW),eps(),p(SURVEY)	291.68	8.93	0.01	0.01	10.00	271.68
psi,gamma(LINEAR),eps(),p(SURVEY)	291.82	9.07	0.01	0.01	10.00	271.82
psi(LINEAR,gamma(),eps(),p(SURVEY)	291.94	9.19	0.01	0.01	10.00	271.94
psi,gamma(),eps(TRI),p(SURVEY)	292.02	9.27	0.01	0.01	10.00	272.02
psi,gamma(),eps(LINEAR),p(SURVEY)	292.04	9.29	0.01	0.01	10.00	272.04
psi,gamma(),eps(SHRUB),p(SURVEY)	292.05	9.30	0.01	0.01	10.00	272.05
psi(HWY),gamma(),eps(),p(SURVEY)	292.11	9.36	0.01	0.01	10.00	272.11
psi,gamma(HWY),eps(),p(SURVEY)	298.00	15.25	0.00	0.00	10.00	278.00
psi,gamma(HERB),eps(),p(SURVEY)	298.00	15.25	0.00	0.00	10.00	278.00
psi(QUIET),gamma(),eps(),p(SURVEY)	299.32	16.57	0.00	0.00	10.00	279.32
psi,gamma(QUIET),eps(),p(SURVEY)	299.82	17.07	0.00	0.00	10.00	279.82
psi,gamma(),eps(SNOW),p(SURVEY)	303.73	20.98	0.00	0.00	10.00	283.73
psi,gamma(),eps(HWY),p(SURVEY)	303.73	20.98	0.00	0.00	10.00	283.73
psi,gamma(),eps(QUIET),p(SURVEY)	303.73	20.98	0.00	0.00	10.00	283.73
psi(HERB),gamma(),eps(),p(SURVEY)	306.66	23.91	0.00	0.00	10.00	286.66

*number of parameters in the model; **-2 log likelihood of the model (model fit

This best-supported model suggested that the probability of wolverine occupancy ranged from 0.4 – 0.9 in landscapes without snow and ice cover within a 5000-m radius (such as valley bottoms), but quickly climbed to 1.0 if any of the landscape was covered in snow and ice (Figure 3). Wolverine occupancy appeared to be stable in the two years measured within this three-year period. The probability of site extinction (ε) was only 0.7 (s.e. = 0.04), indicating a very small chance that a site with a wolverine present in the first year would lose its wolverine in the last year. The probability that a wolverine would colonize an empty site (γ) was 0.33 (s.e. = 0.27). The "spatial growth parameter" (λ) ranged from 0.93 (95% CI = 0.85 – 1.00) to 1.33 (95% CI = 0.46 – 2.2) depending on the % of snow and ice in the landscape. As the confidence intervals of the spatial growth parameter overlap 1.0, there is no strong evidence that wolverine occupancy either declined or increased, indicating a stable distribution.

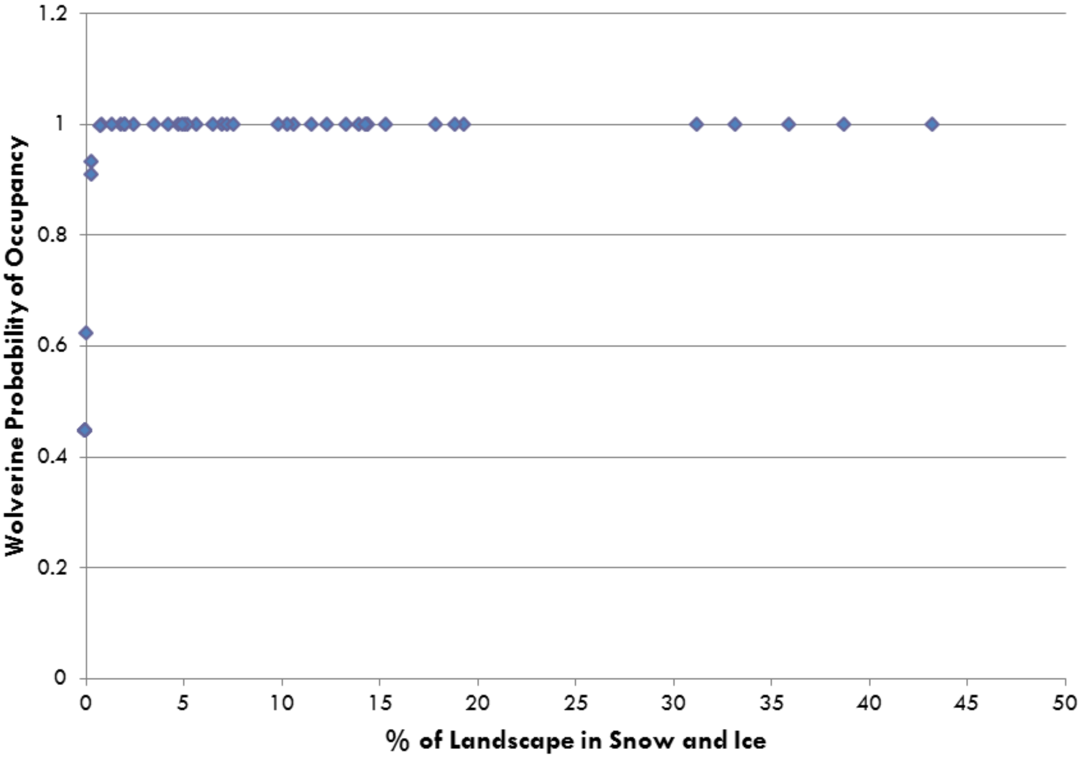

Figure 3. The probability of wolverine occupancy at a site increased markedly with the % of the landscape covered in ice and snow within a 5000-m radius of the camera site.

Habitat Selection Analysis

Given that the probability of detecting a wolverine if present approached 1.0, there is no evidence that missed detections may prevent us from reliably using wolverine detections across all three months within a year in generalized linear models. The best-supported of these models suggested two landcover variables – the proportion of shrub cover and the proportion of snow and ice within a 10-km radius – best described wolverine occurrence in our study area (Table 3). Both of these variables were positively related to wolverine occurrence (Table 4). The effect size of shrub cover was greater than that of snow and ice. The mean area of covered by persistent spring snowpack (through May 15) was the second-best supported model, but this variable did not explain sufficient additional variation to weight the AIC score. Topographic ruggedness and human footprint were *not* supported as explaining wolverine occurrence in the study area.

Table 3. The best-supported model suggested that landcover explained wolverine occurrence in the study area.

Model	Model variables	AIC score	ΔAIC	AIC weight	Residual deviance*	Degrees of freedom
Landcover	% shrub cover % snow and ice cover	182.73	0	0.69	45.36	55
Snow	years (0-12) of persistent spring snow through May 15th	184.66	1.93	0.26	49.29	56
TRI	topographic ruggedness index	188.68	5.95	0.04	53.30	56
Footprint	cumulative % cover of human footprint density of linear industrial features road density recreational trail density	190.44	7.71	0.01	53.43	53

*Null model deviance = 55.98, 57 degrees of freedom

Table 4. The best-supported model suggested that of the landcover variables, the % of shrub cover and the % of the landscape in snow and ice cover, best explained wolverine occurrence.

	Parameter Estimate	Std. Error	z value	P value
(Intercept)	-0.14	0.306	-0.48	0.633
% shrub cover	0.10	0.049	2.14	0.032
% snow and ice	0.02	0.010	2.22	0.026

Discussion

Wolverine detectability varied over time, but the extremely low probability of false absences suggests that we were successful at detecting wolverines when they were present at the sampling site. Fisher et al. (2013) and Fisher and Bradbury (in press) found similar detectability estimates that increased over time in the Willmore Wilderness and west-central Foothills of Alberta. The increasing probability of detection during winter may be explained by greater mobility in mid- to late-winter owing to more stable snow conditions, greater female movements during denning, or individuals discovering and then making repeat visits to the baited sites.

During the 3-year sampling period, it was highly unlikely that a site with a wolverine present during the first year would not have a wolverine present during the subsequent sampling year. The spatial growth parameter estimates viewed along with the modest likelihood of wolverines colonizing sites without previous detections indicate a reasonably static level of occupancy and stable population over the 3-year period. We recognize that the results of our 3-year study based on 2 sampling intervals cannot reliably measure population trend, however, it does present evidence that the population has not declined or increased between sampling years.

Wolverines were detected throughout most of the park complex, except for valley bottoms and at the margins of the national park boundaries distant from high elevation areas, rugged terrain and areas with snow and ice cover. Most sites had some degree of snow and ice cover in the landscape surrounding a sampling site, and there was a high probability of wolverine occurrence at these sites between January and March. At sampling sites lacking snow and ice cover within the surrounding landscape, wolverines could still be present, but with a probability of less than 50%. We are confident in these results, as the probability of detecting wolverines at sampling sites approached 100% by March of both sampling years, thus there is no evidence of any spurious result induced by detection error.

Similar to the results from our occupancy analysis, the habitat selection analysis also predicted that amount of shrub cover was the best correlate of wolverines' occurrence and areas of persistent spring snow cover. The association with areas covered in snow/ice and persistent spring snow may appear redundant, however the chronology of how the variables are measured suggests different biological requisites and possibly different habitat associations. The snow/ice cover class is from satellite imagery taken during the fall, thus depicting areas with year-round snow and ice cover (McDermid et al. 2009). Persistent spring snow cover, however, describes the presence of snow cover during the wolverine's reproductive denning period and their presumed obligate relationship of reproductive dens to areas that retain snow in the spring (Aubry et al. 2007, Schwartz et al. 2009, Copeland et al. 2010, McKelvey et al. 2011).

Our results are consistent with research primarily conducted in the contiguous United States inferring that wolverines are obligate habitat specialists that require spring snow cover. However, this ecological association with spring snow cover also extends to year-round locations throughout the species worldwide distribution (Copeland et al. 2010). Early research reviews reported that wolverines could persist in a broad array of habitat types (Pasitschniak-Arts and Lariviere 1995). More recently, this has been challenged as fine-scale research has documented wolverines associated with high elevation alpine and avalanche environments (Copeland et al. 2007, Krebs et al. 2007, Lofroth and Krebs 2007, Inman et al. 2012). Historical and recent records for western North America reveal little evidence of wolverine presence outside subalpine habitats in the U.S. (Aubry et al. 2007) although wolverines range across the flat boreal and Arctic landscape throughout Canada. In the Alberta boreal, wolverines continue to thrive in areas without persistent spring snow cover (S. Webb, unpublished data). The role of snow in wolverine distribution is therefore controversial and varies regionally, which suggests that snow itself is not the proximal mechanism influencing wolverine distribution, but rather some ecological process correlated with snow.

Avalanche paths are treeless areas consisting of low shrub vegetation (Veblen et al. 1994, Quinn and Phillips 2000) and many high elevations basins in the Rocky Mountains are avalanche-disturbed (Mowat 2000). Wolverines in our study area were strongly associated with areas of shrub cover and supports previous research documenting a consistent year-round association with avalanche path habitats by wolverines (Krebs et al. 2007). While wolverines do hunt, 60% of their food is carrion, often avalanche-buried carcasses (van Dijk et al. 2008, Andrén et al. 2011, Inman et al. 2012). Moose and caribou are commonly consumed winter prey of wolverines in mountainous environments elsewhere (Hornocker and Hash 1981, Landa et al. 1997, Lofroth et al. 2007), however, in our study area the former is extremely scarce and the latter is absent. Avalanche-killed ungulates, therefore, may constitute an important food resource during this period of reduced food availability (Lofroth et al. 2007, Inman et al. 2012).

Wolverine occurrence has been correlated with remoteness from human development (Rowland et al. 2003; Copeland et al. 2007, Krebs et al. 2007, May et al. 2008, Fisher et al. 2013). Notably, neither distance to highways, including the TCH, or any other anthropogenic footprint variable explained wolverine occurrence in our study area. This lack of an effect on wolverine occurrence suggests that human impacts may not be spatially extensive or strong enough to affect wolverine distribution in our largely protected study area.

The absence of a highway effect on wolverines' contrasts with previous research. A localized snowtracking survey in our study area (Kicking Horse Pass, Yoho National Park, BC) found that wolverines rarely crossed the TCH (Austin 1998) and other studies showed anecdotally that wolverines were averse to crossing two-lane highways with less traffic volume (Copeland 1996, Krebs and Lewis 2000, Packila et al. 2008). Although we were unable to detect a highway effect on wolverine distribution or habitat selection, the highway may nonetheless be affecting wolverine movement and dispersal, which this analysis does not consider. The results from our genetic sampling within the study area will help better understand the effects of the TCH on wolverine gene flow and population connectivity (A Clevenger and M Sawaya, unpublished data).

3. Wolverine Use of Wildlife Crossing Structures in Banff National Park

The results of this research have been published in the journal *Northwest Science* as "Mitigating Highways for a Ghost: Data Collection Challenges and Implications for Managing Wolverines and Transportation Corridor." The abstract is included here, and the full text is included as Appendix E.

Abstract

Research provides transportation agencies with evidence-based data to guide the planning and design of crossing structures that effectively link critical habitats and populations. To date, research has focused on a range of mammal species. However, for rare-occurring, wide-ranging species such as wolverines (*Gulo gulo*), collecting the required information can be challenging. Highway crossing structures have been recommended as a conservation strategy for wolverines in the northern U.S. Rocky Mountains. However, there is virtually no information describing wolverine response to crossing mitigation. I describe 15 years of continuous year-round monitoring (1996-2012) of wolverine response to highway mitigation in Banff National Park, Alberta. Crossing structures were monitored using track pads and cameras. Wolverines were detected using crossing structures 10 times. Nine crossings occurred at wildlife underpasses and one at a wildlife overpass. The first detected passage occurred in 2005. Three crossings were recorded during the same crossing check in 2010 and 2011, suggesting use by the same individual of the structures. Few conclusions can be drawn regarding the attributes of crossing structures that facilitate passage of wolverines. Given the scarcity of crossing structures within wolverine range, it will be difficult to collect sufficient information in the short term for this rare and elusive species. Given the proposal to list wolverines under the Endangered Species Act, transportation departments and land managers should begin proactively identifying critical habitat linkages across highways in wolverine range and opportunities for highway mitigation in the short and long term.

V. RESTORE HARLEQUIN DUCK MOVEMENTS ACROSS THE TRANS-CANADA HIGHWAY

Introduction

Harlequin ducks are an indicator of healthy aquatic ecosystems (Smith 2000). Three or four of the most important harlequin duck feeding and loafing concentration areas along the Bow River between Castle Junction and Lake Louise were possibly affected by the Trans-Canada Highway (TCH) Phase 3B twinning project. Moraine Creek is a tributary to the Bow River that is crossed by the Trans-Canada Highway (TCH) on Phase 3B where harlequin ducks are known to nest (Smith 2000, S. Humphries, Parks Canada, unpublished data). The previous Moraine Creek Bridge had insufficient clearance above high water (0.5 m) for passage of harlequin ducks (Golder Associates 2004). The reconstructed bridge was raised 5.0 m above low water and lengthened from 12 to 60 m to allow for greater wildlife movement.

The monitoring metrics to evaluate harlequin duck movements and highway mitigation were the following:

- Is harlequin duck movement affected by the twinned TCH phase 3B?
- For any given year of monitoring, do harlequin ducks nest on Moraine Creek?
- If nesting does occur, are adult females able to move between nest and the Bow River? How does movement between nest and the Bow River occur?
- Are adult females and brood able to move across the twinned TCH using the reconstructed Moraine Creek Bridge?

Methods

Observations were made of adult female and brood movements along Moraine Creek during the nesting and post-nesting/fledging period. Movements to and from the Bow River to the nesting areas occur during a 3-week period in late June and early July (Smith 2000, S. Humphries, Parks Canada, personal communication).

Results

Year 1

No work was initiated during the first year other than discussion with Parks Canada staff regarding the most suitable monitoring methods at Moraine Creek.

Year 2

Monitoring of potential female movements began on June 21, 2010 and was completed on July 9, 2010. The Banff National Park Volunteer Engagement Program was solicited to assist with monitoring harlequin duck movements. Volunteers monitored each day between the start and end date. No harlequin ducks were observed on the creek or flying above it. There was no evidence of female nesting in the Moraine Creek drainage above the TCH.

Year 3

We trained volunteers for monitoring harlequin duck movements on Moraine Creek during an evening on June 21, 2011. The following day we began monitoring in pairs. Monitoring lasted 3 weeks. A total of 31 volunteers participated by spending evenings from 7 pm -10:30 pm at the Moraine Creek underpass and watching for hens flying up and down stream. Approximately 54.5 hours of observations were totaled during 22 days of monitoring. No harlequins were sighted, however one grizzly bear was seen in the area three times.

Year 4

During Year 4 we monitored harlequin duck movements on Moraine Creek. Monitoring began earlier than the previous two years, starting on June 3 and lasting until July 14. A total of 18 volunteers participated (usually in pairs) by spending evenings from 7 pm -10:30 pm situated at the Moraine Creek underpass and watching for any hens flying up and down stream.

For the third year in a row, no harlequin ducks were observed at Moraine Creek. Given the diminished harlequin duck population in the Bow Valley (S. Humphries, Parks Canada, personal communication) and our inability to detect harlequins on Moraine Creek, we did not continue with this task in Year 5.

Discussion

We were unable to detect any harlequin duck activity on Moraine Creek during three years of intensive monitoring. We targeted the most likely time of reproductive season (mid-June to mid-July) and within that period the most propitious time for observing harlequin duck movement and activity on Moraine Creek and the Bow River. Moraine Creek is an important tributary to the Bow River that is crossed by the Trans-Canada Highway (TCH) on Phase 3B. Previous nesting studies have documented harlequin duck activity on Moraine Creek; however, this work was conducted over a decade ago and potential loss of breeding females that routinely nest on Moraine Creek may have disappeared from the population and/or changes in harlequin duck demographics may be responsible for a lack of nests on Moraine Creek.

The life span on open span bridges like Moraine Creek is 70-80 years. Although harlequin ducks are not currently nesting on Moraine Creek bridge, it is not an indication that there won't be any nesting activity during the life span of the bridge. Populations fluctuate over and redistribute themselves over time, sometimes widely and often unpredictably. Breeding females are capable of nesting on Moraine Creek even during demographic declines or shifts in distribution. When the harlequin duck population rebounds or a breeding female selects Moraine Creek for nesting, the conditions on the ground will be in place to facilitate feeding movements by hen and movements by hen and brood to the Bow River. Annual monitoring of the harlequin duck population is a management priority for the Banff and Lake Louise-Yoho-Kootenay Field Units. Given the need for the information we were unable to obtain during this short project, we recommend that the Field Units maintain annual surveys of the harlequin duck population to track population status and distribution. Should breeding females nest on Moraine Creek this will be an opportunity to determine whether nesting females can move between nest and Bow River, and whether hens and their brood are able to move across the twinned TCH using the widened Moraine Creek bridge.

The Moraine Creek bridge was designed exclusively for harlequin duck use. However, during the four years of monitoring we have found substantial amount of use by terrestrial mammals, large and small. Species such as lynx, wolves, moose and grizzly bears have been detected using the Moraine Creek underpass (see Chapter III.1.). During our Year 3 monitoring a grizzly bear appeared in the area. Our citizen scientist volunteers monitoring harlequin duck movements moved out of the area and allowed the bear to pass through the underpass. Despite the investment by Parks Canada to reconstruct the bridge for a single species, the tangential benefits of the underpass for non-target wildlife are of high conservation significance.

VI. ASSESS THE EFFECTIVENESS OF TEXAS GATES ON THE TRANS-CANADA HIGHWAY

Authors: Mirjam Barrueto and Anthony P. Clevenger

Introduction

Wildlife exclusion fencing is frequently used along highways to reduce wildlife-vehicle collisions (WVCs; Huijser et al. 2007, Putman 1997). While fencing is designed to prevent wildlife from accessing the highway right-of-way a problem arises when fencing crosses access roads that vehicles use on a regular basis. Swing gates are commonly used on roads with private access or infrequent traffic. Gates are not an option, however, for roads that have regular traffic or are common thoroughfares.

Texas gates (cattle guards) are installed where access roads intercept fences on roads with frequent traffic (Reed et al. 1974, Allen et al. 2013). Like fences, their function is to prevent wildlife from gaining access to the highway right-of-way. Little research has been dedicated to evaluating the efficacy of Texas gates (or variations of them) for multiple species of wildlife (Belant et al 1998, Seamans and Helon 2008, Allen et al. 2013). In addition to some species being capable of jumping over Texas gates (Reed et al. 1974, Allen et al. 2013), some species manage to walk over the gates with little difficulty (e.g., carnivores compared to ungulates). Snow compaction during winter can severely limit the effectiveness of Texas gates as wildlife are able to walk across without any difficulty.

The Trans-Canada Highway (TCH) is the major transportation corridor through Banff National Park, Alberta, covering roughly 80 km between the park's eastern and western boundaries. In the 1970s, safety issues compelled planners to upgrade the TCH within Banff from two to four lanes, beginning from the eastern boundary and working west (Ford et al. 2010). Large animals were excluded from the road with a 2.4-m-high fence erected on both sides of the highway, and underpasses were built to allow wildlife safe passage across the road. The occurrence of carnivores accessing the right-of-way on mitigated sections of the TCH and being killed in collisions with vehicles suggests that these intrusions are a result of wildlife climbing the exclusion fence or passing over Texas gates.

Like fences, Texas gates need to be impermeable to wildlife passage in order to keep road-related mortality to a minimum and for highway mitigation measures to be effective in reducing wildlife-vehicle collisions (Huijser et al. 2007). Texas gates that allow wildlife intrusions to the highway right-of-way result in reduced wildlife use of crossing structures and a greater risk of wildlife mortality on highways.

The purpose of this study was to evaluate the effectiveness of Texas gates and electrified mats (hereafter referred to as electro-mats) in preventing wildlife crossings to the highway right-of-way. We wanted to know what species approach Texas gates and electro-mats and what proportion of approaches result in animals not passing over the exclusion devices.

Methods

Study Area

Our study was carried out in Banff National Park, Alberta approximately 150 km west of Calgary. The study area is characterized by continental climate with long winters and short summers (Holland and Coen 1983). The TCH is the major transportation corridor through Banff (park length = 83 km) carrying an estimated annual average daily traffic volume of 17,000 vehicles per day, with peaks of more than 30,000 vehicles per day during summer, (Highway Service Center, Parks Canada, unpublished data). Upgrading the TCH from 2 to 4 lanes has progressed in phases. Along each phase highway mitigation measures consisting of wildlife exclusion fencing and crossing structures were installed (McGuire and Morrall 2000; Clevenger and Waltho 2000, 2005). Where wildlife fencing intersects access roads leading to the TCH, Texas gates and electro-mats have been placed in the road to keep wildlife from entering right-of-ways (Belant et al 1998, Seamans and Helon 2008).

Data Collection

A total of 14 Texas gates and electro-mats were identified as being candidates for monitoring during the study period: Highway 93 N junction-Niblock, Whitehorn Avenue North and South (Lk Louise), Km 69 entrance to borrow pit, Castle Camp-93S, Sunshine Road, 5-Mile Bridge South, 5-Mile Bridge North, Norquay North, Norquay South, Banff Industrial Compound, Minnewanka interchange North, Mannix Pit, and Minnewanka interchange South. All Texas gates were the same design and dimensions (5 m long and spanning road width). Electro mats were 1.21 m (4 ft) long and spanned the entire road width. Voltage on the electro-mats was to be maintained at 9000V-12,000V 24 hrs per day.

Some of the abovementioned Texas gates were not monitored since they were considered not likely problematic for wildlife intrusions due to the regularity and high volume of traffic, e.g., Minnewanka South, Norquay South, Whitehorn South.

We monitored the following Texas gates and electro-mats:

- Highway 93N-Niblock (Texas Gate and Electro-mat; year-round)
- Km 69 (Electro-mat, seasonal)
- Castle Camp (Texas gate, seasonal)
- Sunshine (Texas gate; year-round)
- 5-Mile North (Texas gate; year-round)

- 5-Mile South (Texas gate; year-round)
- Banff Industrial Compound (Texas gate; year-round)

Remote cameras were placed at Texas gates and electro-mats that were most likely to have wildlife visits and possible intrusions, thus maximizing data collection to help determine the efficacy of the gates and mats. To maximize the number of wildlife photographed at the gates and mats we configured the cameras to operate 24-hrs per day. This resulted in a large amount of photographs to review and classify. All cameras were placed in security boxes to minimize risk of vandalism.

Results and Discussion

A total of five Texas gates and two electro-mats were monitored from as early as June 2011 until as late as December 2013 (Table 1). Cameras were positioned but not operating for a total of 716 site-days (1 site-day=1 camera-day at a Texas gate or electro-mat site), while there were a total of 2708 operative site-days during the 2.5-year period. Cameras were able to detect a minimum of eight species (including "deer spp.") at the gates and mats. Coyotes were most frequently detected at the gates and mats (n=40) followed by wolves (n=9), elk (n=7), grizzly bears (n=6), deer spp. (n=5) and black bears (n=3).

Of the 72 approaches made by the eight species towards the gates and mats there were 52 (72%) crossings. There were only three approaches to the electro-mats, two of the three resulted in no passage across the mats. One grizzly bear was not detected by the camera at Km 69, yet was observed by highway construction personnel running across the mat out towards the highway.

The crossing rates shown in Table 1 are based on extremely low sample sizes. Of the sites with a minimum of 10 approaches, crossing rates were lowest at the 5-Mile South Texas gate (0.583), followed by 5-Mile North (0.714), Banff Compound (0.800), and Sunshine1 (0.875).

Our study confirmed that there are high passage rates of wildlife at Texas gates indicating that they are not effective at keeping wildlife from entering highway right-of-ways. Only one Texas gate (5-Mile South) deterred roughly half of the approaches and attempts by wildlife to cross. It is unclear why this gate performed better than other gates. Improved monitoring could help understand the reasons why some gates perform better than others. There was only one detected passages by wildlife over the two electro-mats; however, the sample size of approaches (n=3) of both sites is extremely small, thus the result is meaningless until the mats can be tested over a longer period with a larger sample size.

Table 1. Summary of wildlife activity and crossings at five Texas gates and two electro-mats (underlined) in Banff National Park, Alberta, 2011-13. Sunshine 1 and 2 represent camera monitoring data from one Texas gate. Species counts are number of detections at or in vicinity of gates and mats. Approaches are attempts to move towards or across gates and mats. Crossings (in brackets) are successful passages over gates and mats.

	5-Mile S	5-Mile N	Banff Cmpd	Castle Camp	Sunshine1	Sunshine2	93 North	Km69	Total Approaches	Total Crossings	**Cross rate[b]**
Date/start	Jun 2011	Jul 2011	Jun 2011	Jun 2011	Sep 2011	Jul 2012	Jul 2011	Jul 2011			
Date/end	Oct 2013	Nov 2013	Nov 2013	Aug 2013	Oct 2013	Aug 2013	Dec 2013	Sep 2012			
Days-no schedule	28	0	55	145	183	97	208	0	716		
Days-scheduled	501	577	197	129	202	114	157	115	1992		
Total days	**529**	**577**	**252**	**274**	**385**	**211**	**365**	**115**	**2708**		
Coyote	7(7)	14(13)	9 (8)	2 (2)	5 (4)	2(2)	0	1 (0)	40	35	**0.875**
Wolf	2 (0)	1 (1)	0	1 (1)	5 (4)	0	0	0	9	7	**0.777**
Cougar	0	0	0	0	1 (1)	0	0	0	1	1	**1.000**
Grizzly bear	1 (0)	0	0	1 (1)	4 (4)	0	0	0	6	5	**0.833**
Black bear	0	1 (1)	0	0	1 (1)	1 (1)	0	0	3	3	**1.000**
Elk	1 (0)	3 (0)	0	2 (0)	0	0	1 (1)	0	7	1	**0.142**
Moose	0	0	0	1 (0)	0	0	0	0	1	0	**0.000**
Deer	1 (0)	2 (0)	1 (0)	0	0	0	0	1 (0)	5	0	**0.000**
Approaches	12	21	10	7	16	3	1	2	72		
Crossings[a]	7	15	8	4	14	3	1	0		52	
Cross rate[b]	**0.583**	**0.714**	**0.800**	**0.571**	**0.875**	**1.000**	**1.000**	**0.000**	**0.722**		
Events[c]	8378	27,663	21,863	3334	18,899	17,274	38,370	10,966	146,747		

[a] All animals.

[b] Crossing rate = Crossings/approaches.

[c] Events = Number of photos/5.

There is an obvious need to continue monitoring of Texas gates and electro-mats in Banff National Park and elsewhere for a more rigorous assessment of how well these measures perform year-round, and in areas of high snowfall such as the Canadian Rocky Mountains. Millions dollar investments are made to mitigate highways for wildlife and Texas gates and electro-mats need to perform in order for the entire mitigation to be functional. Gates and mats that do not function as designed will render an entire multi-million dollar mitigation complex like that of Banff National Park's as little or no conservation value; particularly if high-profile carnivores are literally slipping through the cracks in the system.

Our monitoring method was rudimentary and not the most effective for our monitoring objective. We used infrared-operated cameras powered by AA cell batteries that photographed everything that moved in front of the camera over a 24-hour period. On some roads such as Highway 93 North and the Sunshine Road during winter, hundreds of cars would pass each day and be photographed, resulting in many thousands of photographs to upload and review every two weeks. Our monitoring of gates and mats could have been improved by using better technology.

Future monitoring of Texas gates and electro-mats is needed to better understand how effective these measures are in preventing wildlife intrusions and potentially road-related mortalities. Monitoring up until now has been conducted using an relatively ineffective method that could be improved by investment in the emerging systems that utilize "animal recognition software" using digital signature technology, micro-wave detection systems and camera technology (still or video) that more accurately detect and track animal movement and behaviour within the vicinity of Texas gates and electro-mats.

Research and monitoring would also be improved by increasing the sample size of gates and especially electro-mats, and testing wildlife response to mats that are of varying length, all longer than the 1.21 m (4 ft) electro-mat length currently being used. If it is not possible to increase sample size in Banff National Park, then efforts should be made to conduct a "meta-monitoring" and meta-analysis combining efforts with other researchers elsewhere investigating Texas gate and electro-mat designs.

VII. TECHNOLOGY TRANSFER

This section lists articles that have been published on the highway mitigation research led by Dr Clevenger between 1996-2014, many of which are based on the 17-year Banff research project. Also listed are other technology transfer activities (workshops, professional presentations etc.) that have been developed based on the research from this project.

Published (or Accepted for Publication)

Clevenger, AP, Barrueto, M, Gunson, K, Caryl, F., Ford, AT. In press. Context-dependent effects on spatial variation in deer-vehicle collisions. *Ecosphere.*

Barrueto, M., A.T. Ford, A.P. Clevenger. 2014. Anthropogenic effects on activity patterns of wildlife at crossing structures. *Ecosphere* 5(3):27. http://dx.doi.org/10.1890/ES13-00382.1

Sawaya, M, S Kalinowski, AP Clevenger. 2014. Genetic connectivity for two bear species at wildlife crossing structures in Banff National Park*. Proceedings of the Royal Society B: Biological Sciences 281:201131705.*

McKelvey, K.S., K.B. Aubry, N.J. Anderson, A.P. Clevenger, J.P. Copeland, K.S. Heinemeyer, R.M. Inman, J. Squires, J.S. Waller, K. Pilgrim, M.K. Schwartz. 2014. Recovery of wolverines in the Western United States: Recent extirpation and re-colonization or range retraction and expansion? *Journal of Wildlife Management 78:325-334.*

Clevenger, AP, A Kociolek. 2013. Potential impacts of highway median barriers on wildlife: State of practice and gap analysis. *Environmental Management 52:1299-1312.*

Clevenger AP. 2013. Mitigating highways for a ghost: Data collection challenges and implications for managing wolverines and transportation corridors. *Northwest Science 87:256-264*.

Sawaya, M, AP Clevenger, S Kalinowski. 2013. Wildlife crossing structures connect Ursid populations in Banff National Park. *Conservation Biology 27:721-730*.

Ascensao, F, AP Clevenger, M Santos-Reis, P Urbano, N Jackson. 2013. Wildlife-vehicle collision mitigation: IS partial fencing the answer? An agent-based model approach. *Ecological Modelling 257:36-43.*

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APPENDICES

Appendix A: Context-dependent Effects on Spatial Variation in Deer-Vehicle Collisions (Article)

Appendix B: Anthropogenic Effects on Activity Patterns of Wildlife at Crossing Structures (Article)

Appendix C: Supplementary Tables for Section III, Chapter 6 (Factors Affecting Passage by Small and Medium-sized Mammals at Culverts)

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APPENDICES

Appendix A: Context-dependent Effects on Spatial Variation in Deer-Vehicle Collisions (Article)

Title: The effect of scale on analysis of deer-vehicle collisions

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Abstract. Identifying strategic locations for mitigating highways has been a key focus of road ecologists. Generally areas with the highest probability of wildlife-vehicle collisions (WVC) are targeted for mitigation measures like warning signs or crossing structures. These high-risk areas arise because of correlated processes that affect the probability of collisions. There are few generalities stemming from studies identifying the landscape and road-related factors contributing to WVCs. The incorporation of large-scale biophysical variables into predictions of WVC locations s remains a significant knowledge gap, principally because data collection efforts are often constrained by political boundaries. Such boundaries encompass landscapes with different biophysical characteristics, masking important large- and local-scale processes affecting the probability of WVCs. We contrasted variables explaining WVCs between five contiguous study areas defined by biophysical boundaries. Our goal was to quantify the extent to which localized processes are general both among and within study areas. We used long-term data from spatially-accurate WVCs locations collected over an 11,400 km^2 area. The factors predicting WVC occurrence varied greatly between and within individual study areas, suggesting that factors explaining WVCs are context dependent, with a strong interaction between local- and large-scale biophysical processes. The lack of generality in our models suggests that efforts to better understand the causes and consequences of WVCs may require field data derived from individual road sections. For transportation and land managers to effectively mitigate highways for wildlife, will require an understanding of the mechanisms giving rise to WVCs. Until these mechanisms are better addressed through additional field studies and meta-analytical methods, additional tools will be required to best identify where to mitigate highways for wildlife.

Key words: Canadian Rocky Mountains, deer-vehicle collisions, highway, mitigation, *Odocoileus hemionus*, *Odocoileus virginianus*, predictive model, road ecology, scale, traffic safety, wildlife

Introduction

Roads, highways and railways are pervasive features of industrialized societies, occurring in the cities, rural areas and remote landscapes of most countries (Davenport and Davenport 2006). This infrastructure and the vehicles on them can have pronounced impacts on the abiotic (e.g., chemical effluents, hydrology, land forms) and biological processes in nearby ecosystems (Forman et al. 2003). One of the more obvious impacts of roads arises from wildlife-vehicle collisions (WVCs). For example, there are an estimated 1.5 million collisions per year between vehicles and wildlife in the USA (Conover et al. 1995; L-P Tardiff and Associates 2003; Huijser et al. 2007a). Not surprisingly then, much effort has been made to ensure motorist safety and the persistence of wildlife in areas where large, free-roaming animals occur near roads (Beckmann et al. 2010). Transportation, safety and wildlife managers have created an array of tools to meet these safety goals, including mitigation structures (e.g., wildlife-exclosure fencing, crossing structures), early warning systems (e.g., signs, radar), and citizen scientist monitoring (Huijser et al. 2007a; Lee et al. 2006; Gagnon et al. 2011). Identifying the areas where these mitigation measures should be implemented has been a key focus for road ecologists in the recent decades.

A common first step to siting mitigation measures is to identify areas with the highest probability of WVCs (Litvaitis and Tash 2008; Santos et al. 2011), though other areas may be priorities for mitigation as well (Eberhardt et al. 2013). WVCs are typically clustered along roads and these clusters arise because of correlated processes that affect the probability of 1) an animal encountering a road, 2) a vehicle travelling on the road at that time, and 3) a motorist’s ability to avoid a collision (Stanley et al. 2006). Hypothetically, areas with the highest probability of WVCs occur where large numbers of wildlife cross roads that have high traffic volumes and poor motorist visibility (Finder et al. 1999; Hubbard et al. 2000; Saeki and Macdonald 2004).

Identifying which factors lead to this heightened probability has been the subject of several studies, typically by monitoring the location of WVC incidents and associating these locations with landscape and road-related variables (Romin and Bissonette 1996; Nielsen et al. 2003; Malo et al. 2004; Seiler 2005). However, few generalities can be taken from these results, reviewed in (Gunson et al. 2011). For example, the amount of forest cover increased deer collisions in Illinois and Iowa, but not in Minnesota (Finder et al. 1999; Hubbard et al. 2000; Nielsen et al. 2003). If factors predicting WVCs are largely idiosyncratic to a given study area, then accurate predictions of WVC locations can only be derived from local data, potentially requiring extensive monitoring efforts in larger regions.

To help develop a general understanding of factors predicting WVCs, researchers need to address contingencies giving rise to these idiosyncratic results. These contingencies may include: measurement error (Gunson et al. 2009), differences in data collection protocols by researchers (Huijser et al. 2007b) or large-scale (i.e., landscape or region) biophysical differences among study areas (National Research Council 2005). The former two contingencies arise from methodological differences and are readily addressed through consistent study designs (Huijser et al. 2007a; Gunson et al. 2009); however, incorporating large-scale biophysical variables into studies on WVCs remains a significant gap in road ecology research. One reason why large-scale biophysical variables are challenging to address in WVC studies is that data collection efforts are often constrained by political boundaries. Typically, such boundaries are cast over landscapes with different biophysical characteristics, masking important large- and local-scale processes affecting the probability of WVCs. Large-scale processes include general land use patterns (e.g., urban, rural, wilderness), watershed boundaries, human population growth and wildlife population density (Forman 1995; Collinge 2009). Local-scale processes can include road visibility, traffic volume, vehicle speed and habitat types and topography (Forman et al. 2003).

Understanding how processes acting under these large and local scales interact with one another requires study area boundaries congruent with biophysical processes (Reiners and Driese 2004).

Using data from a long-term study collected over an 11,400 km^2 area, we contrasted variables explaining WVCs between five contiguous study areas defined by biophysical boundaries in the Rocky Mountains of Canada. Our goal is to quantify the extent to which localized processes are general both among and within study areas. We tested the hypotheses that factors predicting WVC occurrence will be consistent among study areas with similar biophysical characteristics. We contrasted this hypothesis with the null expectation that WVCs are idiosyncratic and exhibit high residual spatial auto-correlation in statistical models.

Methods

Study Area

The study area includes the mountainous landscapes of Banff, Kootenay and Yoho National Parks and adjacent Alberta provincial lands (50˚49'11" to 51˚23'38"N, 115˚9'46" to 116˚ 29'7"W). The climate is continental and characterized by long winters and short summers (Holland and Coen 1983; Figure 1). We divided the landscape into five contiguous study areas, each with a major highway running along the valley bottom, and whose boundaries were derived from major watersheds (i.e., the continental divide) or abrupt transitions along biophysical gradients (elevation, valley width, valley orientation) (Table 1). The Trans-Canada Highway (TCH) is aligned west to east and transects two watersheds on either side of the Continental Divide, the Kicking Horse Valley and the Bow Valley (Banff National Park [BNP]). Highway 93 is aligned north to south in the Kootenay River drainage and Highway 40 runs in a north-south direction in the Kananaskis River Valley to the east of national park lands. Because of climatic differences between national park and non-national park lands we divided the Bow Valley into two regions: Bow-West in BNP and Bow-East outside BNP. Bow-West is characterized by higher elevation, greater precipitation, and lower human population density than Bow-East. At the time of data collection, there were both 2- and 4-lane highways and no wildlife exclosure fencing or wildlife crossing structures (Clevenger and Waltho 2005).

Wildlife-Vehicle Collision Data

In January 1997, we collaborated with wildlife and highway managers in each study area to standardize WVC data collection. During regular operations, workers marked each WVC they encountered and reported the location to us. We subsequently visited the site and obtained a Universal Transverse Mercator coordinate using a differentially corrected global positioning system (GPS) unit (error <3 m; Trimble Navigation Ltd., Sunnyvale, California, USA). We collected data on WVC locations for five ungulate species, and a total of 546 ungulate vehicle collisions were reported between August 1997 and November 2003. However, we focused our analysis on deer (*Odocoileus* spp.) because they were distributed similarly across the region, whereas the distribution of other species was highly variable among study areas. We grouped collision data from mule deer (*O. hemionus*) and white-tailed deer (*O. virginianus*). Both deer species were prevalent in all study areas, they made up the majority (53%) of WVCs and we observed that these species have similar habitat requirements in our area. We verified that deer-vehicle collisions (hereafter referred to as WVCs) co-occurred using the Williamson overlap index (Williamson 1993). The overlap index was 2.94, indicating that vehicle collisions with the two species were spatially correlated along each highway in study areas and thus could be grouped together.

Predictor Variables

We identified 17 field and geographic information system (GIS)-derived variables that have been shown to affect WVCs in previous studies (Gunson et al. 2011) and measured these variables at 289 observed WVC locations and 721 random locations (Table 2). The number of random locations was proportionate to the number of observed WVC locations of the original, multi-ungulate dataset in each study area. Measurement of field variables was obtained by first relocating each WVC and random location with a handheld GPS unit between April 2003 and February 2004. We used a rangefinder (Yardage Pro® 1000, Bushnell® Denver, CO) to quantify visibility measurements variables in the field and an optical reading clinometer to measure slope.

Statistical Analysis

We measured collinearity of explanatory variables for each study area separately and calculated variance inflation factors (VIF). We removed variables with a VIF ≥ 3.0 (Zuur et al. 2010), including: percentage of forest cover, shrub cover, and open area; in-line (5 m) visibility, angular visibility, and presence of barriers. We applied log and square-root transformations to normalize distributions of all variables except for inline-visibility (Tabachnik and Fidell 2013). Exploratory line fitting of these data suggested that most predictor variables had non-linear relationships with the response variable. We therefore used Generalized Additive Models (GAM) to address these non-linear relationships, with cubic spline smoothing functions for all variables, and a logit link function with location type (i.e., observed or random) as the response variable.

We were not only interested in which local-scale factors predicted the location of WVCs, but the extent to which these factors were general within and between study areas. Thus, we first analysed WVCs at the regional scale and examined how different methods of subdividing these data changed model fit. We incorporated all non-collinear predictors, created models using all combinations of predictors and ranked model fit using Akaike's Information Criterion (AICc) [(Burnham and Anderson 2002). We defined the null model as the best-fitting model of the regional scale data. Next we considered how the fit of the null model is affected by: a) a factor for study area, b) a two-dimensional smoother for spatial coordinates, and c) an interaction of study area and spatial coordinates. The study area factor was used to quantify support for our initial characterization of the biophysical drivers of WVCs across this region; if our characterization was accurate and these large-scale processes mattered, then this factor should improve the null model. The model including spatial coordinates addressed the extent to which WVCs were the result of spatially-autocorrelated processes at the local scale. For example, we did not attempt to quantify the distribution of deer or deer habitat along the highways, which could lead to heighted WVC rates along some stretches of highway. However, levels of deer abundance were expected to be highly variable and spatially correlated, and to influence WVC occurrence. If factors predicting WVCs are highly localized, spatial coordinates should significantly improve model fit over the null model and the model containing a factor for study area. The model containing an interaction of the terms for study-area and spatial coordinates addressed a synergy between regional biophysical and localized processes giving rise to WVCs.

Finally, to address the extent to which the factors predicting WVCs were general among study areas, when species and field data collection methods are held constant, we subdivided the regional data by study area and used model-selection procedures to identify the best-fitting model of the non-covarying predictors for each area. We calculated and compared a measure of relative importance of each variable (RI) as the sum of model weights across all possible models containing each variable, but only reported models with ΔAICc <2 (Anderson 2008).

Results

Collision Summary Data

Most of the 289 WVCs we detected occurred in Bow-East (47%), followed by Kananaskis (18%), Bow-West (12%), Kootenay (12%), and Kicking Horse (10%). As a function of road-length and vehicle traffic (unit = 1000 annual average daily traffic volume [AADT]), the highest collision rate also occurred in Bow-East watershed (4.0 collisions/km - 0.24 collisions/km*1000AADT), followed by Bow-West (1.1 collisions/km - 0.14 collisions/km*1000AADT), Kananaskis (0.7 collision/km - 0.19 collisions/km*1000AADT), Kicking Horse (0.6 collisions/km - 0.13 collisions/km*1000AADT), and Kootenay (0.3 collisions/km - 0.15 collisions/km*1000AADT).

Regional Factors Influencing WVC Occurrence

The best-fitting null model for the regional analysis included six covariates, including road design (i.e., width and distance to barrier) and habitat structure (i.e., cover, topography, distance to water, and distance to human disturbance; Table 3; see Table S1 for full results). The inclusion of a term in this model for local study area improved the fit (ΔAICc vs. null >22), indicating that the biophysical boundaries we defined were associated with factors influencing WVCs (see Figure S1). When we removed this factor for study area and instead used a term for spatial coordinates the fit of the model improved yet again (ΔAICc vs. null >43), suggesting that WVCs are better predicted by factors operating on fine scales. However, the best fitting model (ΔAICc vs. null >48) was created from an interaction of biophysical study area and spatial coordinates, indicating that large-scale biophysical processes influences the effect of localized factors, i.e., the drivers of WVC occurrence are not constant within our study areas.

Local-scale Factors Influencing WVC Occurrence

Factors predicting WVC occurrence varied greatly between individual study areas (Table 3). Distance to water (drainage) was an important predictor of WVCs in 3 of the 5 study areas, while other variables (i.e., distance to barrier, slope, road width) had modest importance in only 2 of the 5 study areas. Topography, habitat, distance to cover and human use, and in-line visibility had little or no relative importance in any of the individual study area watershed models. When we included a smoothing term for coordinates in the best-fitting model of each study area, there were meaningful (ΔAICc ≥ 2 improvements in 3 of the 5 study areas. This result indicates that the predictor variables for the best-fitting models in these three study areas contained unexplained variation that could be accounted for by proximity alone.

Spatial Autocorrelation

We tested for residual spatial autocorrelation (RSA) using spline correlograms (Bjornstad 2001), using Pearson's residuals from the fitted best models (ncf package; (Bjornstad 2012). In the best-fitting model for the regional analysis, we found significant RSA for data points within 15-20 m of each other (see Figure S2). RSA was reduced in the best-fitting regional model, however, when including spatial coordinates (see Figure S2). We found no significant RSA in the best-fitting models for the individual study areas (with spatial coordinates included in the Bow-East and Kootenay models), suggesting that spatial dependencies between data points were accounted for appropriately in these models (see Figures S2, S3).

Model Validation

To validate the adequacy of our models, we used Q-Q plots modified for analysis of logistic regression (Landwehr et al. 1984; Zuur et al. 2009). We simulated 1000 data sets from the fitted models, and plotted the fitted residuals from the original model fit against the median simulated ordered residuals. Points outside of the 95% confidence intervals indicated possible outliers, while major deviations from the 1:1 line with points outside the confidence bands indicated departures from the model assumptions. The empirical probability plots for the best models in each watershed were all within the confidence intervals and showed reasonably straight lines (see Figure S4), with the possible exception of the Kootenay and Kicking Horse models (see Figures S5, S6, S7, S8, S9), where low sample sizes (and thus wide confidence bands) made it difficult to determine if the apparent departure from a straight line was problematic or not.

Discussion

We found compelling evidence that factors predicting WVCs are context dependent, with a strong interaction between local- and large-scale biophysical processes. We expected to find greater agreement in the composition of models among the five study areas for the following reasons: 1) study areas were contiguous and shared many important ecosystem properties, such as climatic envelope, levels of human disturbance, and the composition of plant and animal communities; 2) our monitoring focused on the same taxa; 3) field data were collected using consistent methods among study areas. The lack of generality in our models suggests that efforts to better understand the causes and consequences of WVCs may require field data derived from individual road sections.

Road ecology theory predicts that WVCs arise from the occurrence of wildlife on the road, driver behavior and traffic volume (Forman et al. 2003). The relationships between habitat and animal or population demographics are complex, varying with a number of local-scale and large-scale processes (Garshelis 2000; Frair et al. 2005; Johnson et al. 2006; Fryxell et al. 2008). Traffic volume can also be highly patchy along otherwise homogenous stretches of road because of the emergent properties and stochasticity of driver behavior (Drew 1968; Leutzbach 1988; Van Langevelde and Jaarsma 2004). Moreover, most WVC studies, ours included, do little to consider how these predictive factors vary over time. A legacy of high WVCs occurrence in an area may depress local population abundance, thereby lowering the probability of wildlife on the road, and generating 'cold spots' of WVC occurrence (Litvaitis and Tash 2008; Eberhardt et al. 2013). This temporal component of WVC occurrence may further explain some of the contingencies observed in WVC studies conducted at a regional scale. Given the complexity of these factors contributing towards WVC occurrence, we urge researchers to uncover the mechanistic pathways by which wildlife behaviour and abundance, traffic volume and driver behavior give rise to WVC occurrence. Until these mechanisms are better addressed through additional field studies and meta-analytical methods, additional tools are required to best identify the location of mitigation measures. For example, expert opinion, least-cost analysis, radio-telemetry, linkage mapping and centrality analysis have also proven useful in guiding restoration and prioritizing areas for future road mitigation (Clevenger and Wierzchowski 2006; Beier et al. 2008; Chetkiewicz and Boyce 2006; Landguth et al. 2013). Developing models from WVC data should be recognized as only one of a number of tools available to to identify locations on roads for mitigating road-related mortality and increasing safe passage of wildlife.

While the model best fitting models varied among our study areas, a few variables were important factors in more than one watershed. Specifically, distance to water (drainage) was a key predictor of WVCs in the regional watershed model and three of five study areas. Typically, risk of WVC was greatest at or beyond 2000 m from a drainage. The distance with lowest risk of WVC depended on the study area. Though drainages are associated with WVC occurrence, we note that conditions along and among highways varied in ways that could affect WVC occurrences, including road grades, topographies, hydrologic flows, and the presence of road-related features such as bridges (Hubbard et al. 2000; Malo et al. 2004; Dussault et al. 2006). In the two watersheds where distance to drainage was relatively unimportant, the topography along these highways was more homogenous, suggesting that road visibility or animal movement behaviour maybe correlated with risk of WVCs near drainages. Surprisingly, however, our field measurement for a driver's ability to detect an animal on the road, road visibility, was not an important variable in any study area. Additionally, in many areas, particularly mountainous landscapes such as our study areas, large animals often follow riparian areas through the landscape, likely to minimize the energetic costs of movement (Chruszcz et al. 2003; Dickson et al. 2005; Brost and Beier 2013). This suggests that drainages increase WVC occurrence by concentrating wildlife movement across roads, such that mitigation measures aimed at changing driver awareness may be less effective than measures focusing on the safe passage of animals across the road.

In addition to factors that concentrate animal movements over particular stretches of highway, factors that increase the time required to cross a highway by wildlife appear to be particularly risky in areas with high traffic volumes. For example, in Bow East, which as 100% more traffic than then next busiest highway (Bow West), barriers and road width increased probability of WVC occurrence, but these variables were less important on highways with lower traffic volumes. These results are consistent with theoretical models that consider how animal body size, movement speed, traffic volume and road width influence WVC (Van Langevelde and

Jaarsma 2004). Mitigation measures along high traffic volume areas should focus on deterring wildlife access to the road surface using exclusion fencing and wildlife crossing structures (Clevenger et al. 2001; Olsson and Widen 2008; McCollister and VanManen 2010; Gagnon et al. 2011).

There is increasing interest worldwide in sustainable road systems and the ecological effects of expanding transportation infrastructure (Sanderson et al. 2002; Ritters and Wickham 2003; Laurance et al. 2009). Road networks, wildlife corridors and mitigation measures will increasingly play an important role in ensuring that the dual needs of motorist safety and safe wildlife passage are met. In order to effectively mitigate highways for wildlife and motorist safety, transportation and land managers need to reliably identify and then predict the root causes of WVCs. Understanding the interactive effects of large and local-scale processes contributing to the occurrence of WVCs is a critical next step in developing this understanding.

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Author contribution

Conceived and designed the experiments: AC, KG, BC, AF. Performed the experiments: KG, BC, FC, CM. Analyzed the data: MB, AF. Wrote the paper: AC, MB, AF. Provided funding for data collection and analysis: AC.

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Table 1. Description of highways and traffic in five study areas of the Canadian Rocky Mountains.

Highway	Study area	Political jurisdiction	Length (Km)	Traffic volume (AADT[a])	Posted speed (Km/hr)
Trans-Canada Highway	Bow-East	Province of Alberta, (east of Banff National Park)	35.1	16,960	110
Trans-Canada Highway	Bow-West	Banff National Park, Alberta (Highway 93 South junction to Yoho National Park boundary)	32.2	8000	90
Trans-Canada Highway	Kicking Horse	Yoho National Park, British Columbia	45.6	4600	90
Highway 40	Kananaskis	Province of Alberta (east of Banff National Park)	79.1	3075[b]	90
Highway 93 South	Kootenay	Kootenay National Park, British Columbia	102.6	2000	90

[aA]AADT: 2005 annual average daily traffic volume (Parks Canada Agency and Alberta Transportation, unpublished data).

[b]1999 summer average daily traffic volume (Alberta Transportation, unpublished data).

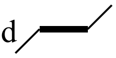
Table 2. Definition and description of variables selected to model occurrence of deer-vehicle collisions in five contiguous study areas of the Canadian Rocky Mountains.

Predictor variable	Definition
Continuous	
Forest[a]	Mean percentage (%) of continuous forest cover (trees >1m height) in a 100 m transect perpendicular to highway, on both sides of highway.
Shrub[a]	Mean percentage (%) of shrub cover (trees and shrubs <1 m high) in a 100 m transect perpendicular to highway, on both sides of highway.
Open[a]	Mean percentage (%) of area devoid of vegetation (rock, gravel, water, pavement etc.) in a 100 m transect perpendicular to highway, on both sides of highway.
Cover[a]	Mean distance (m) to vegetative cover (trees and shrubs >1 m high) on both sides of highway.
Human use[b]	Distance (m) to nearest human use feature along highway.
Barrier[b]	Distance (m) to nearest jersey or guardrail barrier.
Water[b]	Distance (m) to nearest transverse waterway, i.e. drainage (river, stream, or creek).
Road slope[a]	Mean slope (°) of land 0-5 m perpendicular to pavement edge, on both sides of highway.
Verge slope[a]	Mean slope (°) of land 5-10 m perpendicular to the pavement edge on both sides of highway.
Adjacent slope[a]	Mean slope (°) of land 10-30 m perpendicular to the pavement edge on

	both sides of highway.
In-line visibility[a]	Mean distance observer at the pavement edge no longer sees passing vehicles, taken from each direction on both sides of highway.
In-line visibility 5m[a]	Mean distance at which observer at 5 m from pavement edge no longer sees passing vehicles, taken from each direction on both sides of highway.
Angular visibility[a]	Mean distance at which observer at 10 m from the pavement edge no longer sees passing vehicles, taken from each direction on both sides of highway.
Road width[a]	Distance (m) between outer edges of road pavement.
Categorical	
Habitat[a]	Dominant habitat within a 100 m radius on both sides of highway measured as forest (coniferous or deciduous forest); open-forest mix; open (fields, meadows, or barren ground); open-water area (wetland, lake, parallel stream or floodplain); riparian (perpendicular drainage), or rock.
Topography[a,c]	Adjacent terrain measured as level (1); completely raised and or buried (2, 3, 4), and partially raised or buried (5, 6)
Barrier presence[a]	Number of concrete barriers and guard rails at site measured as 0, >1

[a] Variable in field.

[b] Variable measured from GIS.

[c] (1) level  (2) raised  (3) buried-raised 

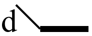
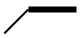
(4) buried  (5) part-buried  (6) part-raised 

Table 3. A summary of models for each watershed analysis of deer-vehicle collisions with relative importance (RI) scores of nine explanatory variables. RI scores were calculated as the sum of model weights of all models containing a variable. RI scores are color-coded ranging from high (red) to moderate (orange) to low (green).

Study area	Distance to:				Slope	Visibility	Road		
	Water	Cover	Human use	Barrier	angle	In-line	width	Habitat	Topography
Bow West	0.92	0.26	0.31	0.41	0.9	0.34	0.52	0.08	0.11
Kananaskis	0.28	0.27	0.27	0.46	0.31	0.29	0.35	0.61	0.49
Kootenay	0.22	0.64	0.42	0.68	0.54	0.68	0.44	*	0.12
Kicking Horse	0.96	0.4	0.24	0.48	0.84	0.24	0.29	*	0.18
Bow East	0.58	0.44	0.48	0.99	0.08	0.68	0.94	0.02	0.18
All areas	0.98	0.11	0.14	0.99	0.19	0.22	0.65	0.3	0.09
Mean	0.65	0.35	0.31	0.66	0.47	0.41	0.53	0.25	0.19
SD	0.34	0.18	0.12	0.26	0.34	0.21	0.23	0.26	0.14
CV	0.53	0.51	0.39	0.39	0.71	0.52	0.44	1.05	0.76

Appendix B: Anthropogenic Effects on Activity Patterns of Wildlife at Crossing Structures (Article)

esa ECOSPHERE

Anthropogenic effects on activity patterns of wildlife at crossing structures

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Abstract. Despite the popular perception of protected areas as vestiges of remnant wilderness, the behavior and activity patterns of wildlife in these areas are still subject to many forms of anthropogenic disturbances, such as roads, recreation and resource extraction. In Banff National Park, Alberta, efforts to mitigate the effects of roads on wildlife using wildlife crossing structures (WC) have been successful for a number of large mammal species, when measured as a reduction in mortality from vehicle collisions or the restoration of population connectivity; however, a comprehensive view of mitigation success should also account for the restoration of animal behavior and activity patterns. We evaluated the general hypothesis that existing WC have mitigated the effects of anthropogenic disturbance on wildlife activity, and predicted that the activity patterns of wildlife at WC should be similar to those in areas characterized by little or no human disturbance. We collected data from a long-term monitoring program of activity patterns, in an assemblage of large mammal species, using a network of camera traps throughout Banff National Park. We quantified the inter- and intra-specific overlap of diel activity patterns at 39 engineered wildlife crossings, varying in design (e.g., over and underpasses) and age. We compared activity at WC to baseline conditions at 126 backcountry sites (BC). In general, activity patterns at WC were found to closely match those at BC. Of the eight species we examined, only elk and coyotes showed significantly different peaks in activity. Activity between WC depended on the time of day, the amount of human use and age of the crossing structure; however, the impact of these factors varied among carnivores and ungulates. Our work demonstrates that the impact of people on wildlife activity at WC is highly context dependent and that the restoration of native patterns of activity within protected areas will require management of human activity, even in relatively remote areas.

Key words: activity patterns; anthropogenic disturbance; Banff National Park; camera traps; large mammals; traffic; Trans-Canada Highway; wildlife crossing structures.

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INTRODUCTION

National parks and other protected areas were typically created and managed for the preservation of natural heritage and conservation of biodiversity. However, recreation, tourism and human infrastructure within these refuges areas can have negative consequences on wildlife populations (Taylor and Knight 2003, Hebblewhite et al. 2005, Brown et al. 2012; Hansen et al., *in press*). Across southern Canada and the conterminous USA, most of the land designated as a protected area occurs in mountainous landscapes. The complex topography of these ecosystems is characterized by a natural pattern of fragmentation entailing productive and speciose habitats at lower elevations, that are interspersed with largely low quality habitats of steep rocks, snow and ice at higher elevations. It is in these biologically-rich valley bottoms where anthropogenic activity is also concentrated, including disturbances from recreational activity, residential developments, resource extraction and transportation corridors (Theobald et al. 1997, Hansen et al. 2002). Despite the popular perception of these protected areas as vestiges of remnant wilderness, the behavior and activity patterns of wildlife moving through mountainous protected areas can be affected by a number of anthropogenic disturbances. These sub-lethal changes in wildlife activity can emerge as changes in animal physiology (Wasser et al. 1997, Millspaugh et al. 2001), the probability of human-wildlife conflict (Woodroffe et al. 2005), and inter-specific interactions (Hebblewhite et al. 2005, Berger and Gese 2007, Ford and Clevenger 2010, Muhley et al. 2013). To ensure the safe and sustainable co-existence of people and wildlife in mountainous areas, there is a pressing need to better understand how wildlife activity changes in response to human activity.

Previous studies have shown that both vehicle and foot traffic can alter wildlife behavior up to several kilometers away from the disturbance site for a number of large mammal species, including wolves (*Canis lupus*; Karlsson et al. 2007, Rogala et al. 2011), elk (*Cervus elaphus*; Cassirer et al. 1992, Naylor et al. 2009, Rogala et al. 2011), bears (*Ursus* sp.; McLellan and Shackleton 1988, Gibeau et al. 2002, Moen et al. 2012) and bighorn sheep (*Ovis* sp.; Longshore et al. 2013). At the same time, wildlife can become habituated to such disturbances and adjust their behavior to minimize encounters with people (Schultz and Bailey 1978, Burson et al. 2000, Brown et al. 2012); perhaps with little consequence to the demographic vital rates of wildlife populations. For example, wildlife typically cross highways at night when traffic volumes are low (Tigas et al. 2002, Chruszcz et al. 2003, Waller and Servheen 2005, Graves et al. 2006, Meisingset et al. 2013), suggesting that these labile responses are an important component of wildlife survival in human-occupied landscapes.

One of the most expensive and well-documented efforts to mitigate anthropogenic disturbances to wildlife occurs in Canada's national parks, where a series of fences and crossing structures have been built to facilitate the movement of large mammals across a major highway (Ford et al. 2010). In spite of this major highway, over 150,000 wildlife crossings have been recorded at these structures (Clevenger et al. 2009), rates of wildlife-vehicle collisions have dropped off (Clevenger et al. 2001), and demographic and genetic connectivity continues (Sawaya et al. 2013, 2014). However, a clear picture of how these mitigation measures have restored wildlife activity has not yet emerged. Understanding the extent to which vehicle traffic and human activity alters wildlife movement near highways will increase our ability to design more effective wildlife crossing structures (WC) and reduce the negative effects of habitat fragmentation in mountain ecosystems (Barber et al. 2011, Leblond et al. 2013).

To address this knowledge gap, we evaluated the general hypothesis that WC buffer the effects of anthropogenic disturbance on wildlife activity, and predict that the activity patterns of large mammals at WC should be similar to activity patterns in areas characterized by little or no human disturbance. We employed a long-term monitoring program (>4 years) to measure activity patterns for an assemblage of large mammal species, using a network of motion-activated cameras (camera traps) in Banff National Park, Alberta. We quantified the overlap of wildlife activity at 39 WC, with 126 sites that were undisturbed by transportation and human activity, located >2 km from transportation infrastructure (hereafter referred to as backcountry [BC]). Specifically, we first established species-specific patterns of diel activity and then analyzed (1) if the differences in diel activity between WC and BC sites are greater for some species groups (i.e., carnivores) than others (i.e., ungulates) (Hebblewhite et al. 2005, Ford and Clevenger 2010), and (2) if human use of WC and their novelty change the diel activity of wildlife (Clevenger and Waltho 2000). We examined the role of factors that can further explain these relationships, such as the design of the WC (e.g., over or underpass), fluxes in daily traffic volume

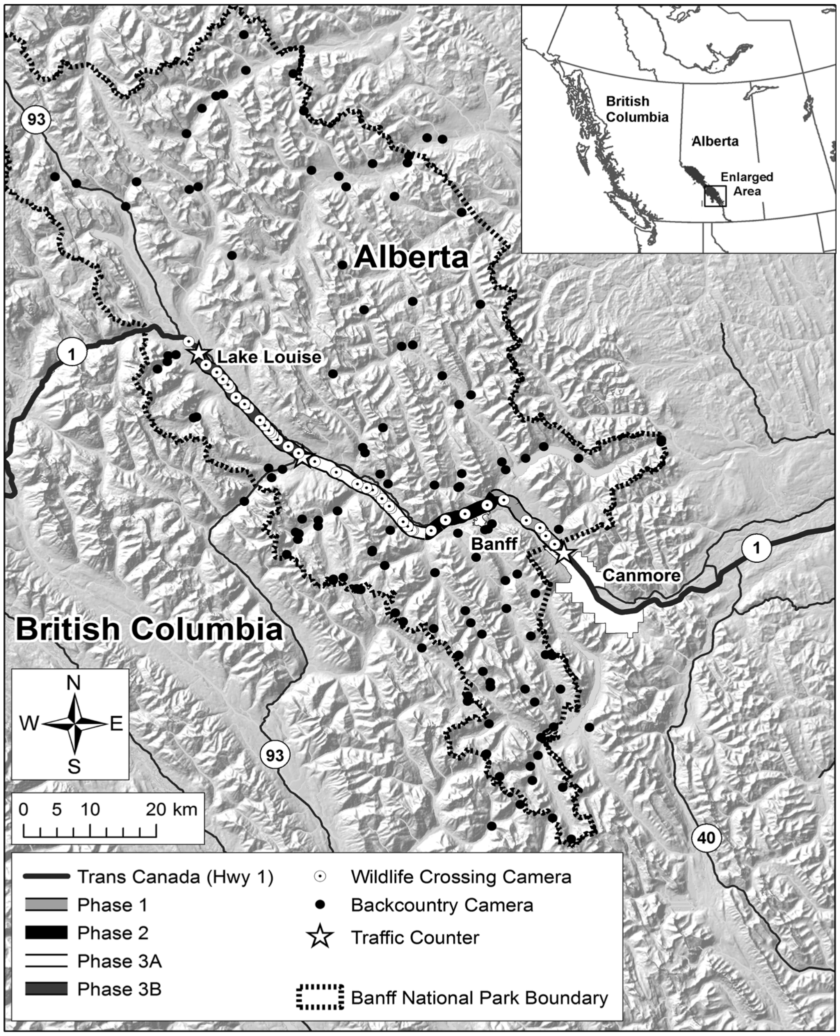

Fig. 1. Study area in Banff National Park, Alberta. White circles with black dots in center are the location of camera sites at wildlife crossings (WC) along the Trans-Canada Highway (TCH). Solid black dots are locations of backcountry cameras (BC). Stars represent the location of traffic counters along the TCH. The different phases of highway mitigation (1, 2, 3A, 3B) are shown spanning from east to west.

and the age of the WC. Our results will assist transportation and wildlife managers in devising appropriate strategies for human use of WC and in designing WC structures to minimize changes in wildlife behavior.

METHODS

Study area

The study area, located in Banff National Park, is situated approximately 150 km west of Calgary, Alberta, in the Bow River Valley, along the Trans-Canada Highway (TCH; Fig. 1). The study area is characterized by mountainous landscapes, with a continental climate consisting of long winters and short summers (Holland and Coen 1983). Vegetation characteristic of the montane and subalpine ecoregions consists of open forests dominated by lodgepole pine (*Pinus contorta*), Douglas-fir (*Pseudotsuga menziesii*), white spruce (*Picea glauca*), Englemann spruce (*Picea englemannii*), trembling aspen (*Populus tremuloides*), and natural grasslands.

With the exception of bison (*Bison bison*) and caribou (*Rangifer tarandus*), Banff National Park retains the full complement of native large mammal species. We focused on camera images of wolves, coyotes (*C. latrans*), cougars (*Puma concolor*), black bears (*U. americanus*), grizzly bears (*U. arctos*), mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), elk, and moose (*Alces alces*). The two *Odocoileus* species (hereafter referred to as "deer spp.") were pooled due to similarities in habitat use, life-history, and the occasional difficulties in distinguishing the two species, particularly in some of the low-quality nighttime photos.

The TCH is the major transportation corridor through Banff National Park, covering roughly 80 km between the park's eastern and western boundaries. Traffic volume along the TCH is relatively high for the region, with an average of 17,970 vehicles per day in 2008 and increasing at a rate of 2.5% per year (Highway Service Centre, Parks Canada, Banff, Alberta).

In the 1970s, safety issues compelled planners to upgrade the TCH within Banff from two to four lanes, beginning from the eastern boundary and working west (Ford et al. 2010). Large animals were excluded from the road with a 2.4-m-high fence erected on both sides of the highway, and underpasses were built to allow wildlife safe passage across the road. The first 27 km of highway twinning (Phases 1 and 2) included 10 wildlife underpasses and was completed in 1988 (Fig. 1). Fencing and WC on the next 18 km section (Phase 3A) was completed in late 1997 with 11 additional wildlife underpasses and two 50-m wide wildlife overpasses (Clevenger and Waltho 2000, 2005). The final 30 km of four-lane highway to the western park boundary (Phase 3B) includes 21 crossing structures, including four, 60-m wide wildlife overpasses and was completed in 2013.

Animal activity

To quantify animal activity, we employed motion-activated cameras to record the movement of large mammals: (1) at 39 WC along the TCH between 2007 and 2012; (2) throughout the BC of Banff National Park between 2008 and 2012 (Fig. 1). We define activity as an independent camera trap event at both WC and BC sites, which consists of passage by an individual, or group of the same species. We distinguished sequential events by a lapse in activity at the camera lasting longer than 2 minutes. Prolonged feeding or resting behavior was not recorded as activity because cameras would typically record multiple images of the same individuals under 2 minutes. Thus, at both WC and BC sites, our activity data represent the travelling behavior of large mammals. At WC sites we also estimated the direction of travel and whether animals moved through the WC or turned back without crossing. We only used images captured between 1 May to 31 October to minimize seasonal bias caused by migration patterns (e.g., elk; Hebblewhite et al. 2002) or torpor (e.g., black and grizzly bears). This period also coincides with the highest levels of human use and traffic volumes in Banff National Park.

Since 2005, cameras were used to monitor wildlife use of the WC (Clevenger and Waltho 2000, 2005, Ford et al. 2009). WC cameras were located within or adjacent to (<10 m away) wildlife underpasses and centered on top of wildlife overpasses. Every 2–3 weeks, we inspected camera operation and downloaded images.

Since 2008, Parks Canada has used camera traps to monitor wildlife activity in BC areas of Banff National Park. At the local scale, BC cameras were set up to maximize detection of wildlife, given presence, but at the scale of the study area these sites were randomized across high- and low-use hiking trails, elevation and habitat types. BC cameras were checked 2–3 times during the calendar year.

Compared to direct observation, camera traps provide a relatively low-impact means of monitoring behavior and facilitate data collection on a continuous basis across diel periods (O'Brien 2010, McCallum 2012). All cameras used in this study were made by the same manufacturer (Reconyx, Holmen, Wisconsin, USA) and provided information on date, time and ambient temperature during each camera trap event. Cameras were operable 24 h/day, year-round, with occasional periods of malfunction or premature battery failure. We determined camera-sampling effort (camera-days) at WC and BC sites by calculating the number of days that cameras were operational.

We compared the number of camera trap events between WC and BC sites, by taxa, over a 24-hr cycle (0 to 2300 h MST). We monitored

WC using cameras and other methods almost continuously since 2008, and found in a previous analysis that cameras reliably detect crossing events (Ford et al. 2009).

Traffic volume data

Traffic volume data were obtained from three counters that measured the mean hourly traffic along the TCH (Highway Service Centre, *unpublished data*) from 2007 to 2012 (Fig. 1). We associated each WC with the data from the nearest traffic counter. Weekend traffic is typically higher than weekday traffic because of recreational use in this area (Rogala et al. 2011), creating a weekly periodicity of vehicle traffic (see Appendix: Fig. A1). We partitioned these data into high (weekend, Friday to Sunday) and low (weekday, Monday to Thursday) categories. We did not expect these two categories to impact wildlife beyond a potential effect of the higher traffic volumes on weekends.

Statistical analysis

To quantify overlap in inter-specific activity patterns, we compared the diel pattern of camera trap events for all species-pair combinations using two-sample Kolmogorov-Smirnov (KS) tests, separately for the WC and for the BC data. We defined a non-significant result from the KS test as a matching activity pattern, and a significant (at the 0.05 level) result as a non-matching activity pattern. The KS test has the advantage of making no assumption about the distribution of data, i.e., is non-parametric and distribution free, and can be used when sample sizes are unequal (Justel et al. 1997, Zar 1999). We then measured the overlap of intra-specific activity patterns between WC and BC sites, again using two-sample KS tests.

To quantify the potential effects of human (i.e., foot traffic) activity on wildlife at WC, we used KS tests to compare overlap of intra-specific activity patterns between WC with high and low human use. High human use WC were defined as those with >50 human events per year (reference years were 2010 to 2012), while WC with low human use had <50 human events per year. This cut-off was chosen because approximately 75% of WC had <50 human crossing events each year and there was a clear separation of WC with high use (mean = 255, min = 53, max = 1046) and the rest receiving relatively low use (mean = 14.2, min = 0, max = 47). Because human use was confounded by WC design and age (e.g., overpasses and newer WC were virtually off-limits to people), we also performed this analysis on a subset of WC that had the same design and were built >15 years before this study began (i.e., Phase 1, Fig.1).

If wildlife habituation to roads increases their use of WC, we would expect to see changes in the activity patterns and frequency of use at WC varying in age, assuming that wildlife populations in the adjacent areas are the same. We used KS tests to determine if the novelty of WC played a role in wildlife activity patterns by pooling data from older WC built >15 years ago (Phases 1, 2, 3A) and comparing these activity patterns with novel (1–3 years old) WC along Phase 3B.

Finally, we assessed the impact of vehicle traffic on animal activity at WC. For the previous analyses we had pooled data across years and sites, and measured differences in resulting activity patterns with KS tests. To detect an effect of vehicle traffic volume on use of WC, while accounting for the time of day, required greater analytical resolution than the discrete- KS tests could provide. Exploratory analysis of the relationship between hour of day and activity was identified as non-linear, and based on earlier research, variation between behavior at the different sites was also expected. We used generalized additive mixed effects models (GAMMs) to take these non-linear and random effects into account (Wood 2006, Zuur et al. 2009). We used the number of successful crossing events per hour at each crossing structure as a function of vehicle traffic volume, time of day, human use of crossing structure, and age of crossing structure. Based on the expectation that changes in behavior occurred over the years, we also included interactions between hour of day and age of crossing structure, as well as an interaction of human use and age of crossing structure. Because wildlife response to hourly variation in traffic volume may depend on ambient or baseline traffic conditions, we partitioned our analysis into *high* (weekend) and *low* (week day) ambient vehicle traffic volumes. However, we did not expect the weekday factor to have an impact on animal behavior beyond the potential effect of increased traffic volumes seen on weekends. Thus, we did not include the weekday factor itself as a covariate in the models. All species were analysed separately.

For all models, we used a Poisson distribution and log-link function (global model shown in Eq. 1).

$$\begin{aligned}&\text{Events}_{is} \sim \text{Poisson}(\mu_{is})\\&\eta_{is} = \alpha + f_{\text{Phase}}(\text{Hour}) + f(\text{Mean traffic volume})\\&\quad + \beta_1 \times \text{Phase} + \beta_2 \times \text{Human} + \beta_3 \times \text{Phase}\\&\quad \times \text{Human} + \text{LEffort} + a \qquad (1)\\&a_i \sim N(0, \sigma_a^2)\\&\log(\mu_{is}) = \eta_{is}\end{aligned}$$

We defined Events as the cumulative amount of activity (i.e., number of successful crossing events) at each WC(i) pooled across all years for each hour (s). Mean traffic volume was defined as the number of vehicles passing at each hour, averaged across all years. Human use (Human) was defined by a factor for 'high' (>50 crossings by humans) and 'low' (≤50 human crossing events). Age of crossing structures was defined by Phase with the four levels 1, 2, 3A and 3B, referring to the highway mitigation phases (Fig. 1). We treated WC as a random factor (a), and included the number of camera days (LEffort) at each WC as an offset, to account for unequal monitoring effort. Finally, the covariate Hour accounted for the strong diel activity patterns displayed by most species. To account for the circular nature of Hour, we used cyclic cubic regression splines for the smoothers. We created a Global model and performed step-wise variable removal until all covariates remaining were significant at the 0.05 level (Burnham and Anderson 2002). We returned variables to the resulting model to address heteroscedasticity in residuals. For a given species, we only included WC where at least one detection occurred. All modelling was performed with R (version 3.0.1; R Development Core Team 2008) using the mgcv package (Wood 2006) for the GAMMs.

RESULTS

Sampling effort

We captured >194,000 images at WC and >254,000 of images at the BC, resulting in a total of 33,732 and 6577 events for our eight focal species, respectively. Most of these images consisted of deer and elk (>75% of events at WC and >45% at BC). The total sampling effort was 31,750 camera-days at 39 WC sites and 19,097 at 126 BC sites.

Diel activity patterns

Most inter-specific pairs had non-matching activity distributions at WC and BC (Table 1). The only species pairs with matching activity patterns at both WC and BC sites were grizzly bear-black bear and elk-cougar, suggesting that WC buffers changes to probability of interspecific interactions. Four additional species pairs had matching activity patterns at BC sites only (Table 1) and no species had matching activity at WC sites only.

Intra-specific activity patterns at WC closely matched those at BC sites (Fig. 2), with the exception of elk and coyotes (Table 2). For elk, the activity peaks at the WC sites were one hour earlier in the morning and one hour later in the evening. Coyote activity peaked at 0900 h in the BC and at 0200 h at WC. Generally, at both WC and BC, deer, elk, moose, wolves and grizzly and black bears exhibited strong crepuscular activity patterns (Fig. 2). Cougar activity was primarily nocturnal at both WC and BC sites (Fig. 2).

The effect of human-activity on wildlife use of WC was significant for four species (Table 3). Black bears, deer sp., elk and wolves had significantly different activity at WC with high levels of human use compared to WC with low human use. Black bears were more active in the morning and less active in the afternoon and evening at high human use WC. Deer showed more nocturnal and less morning activity at high human use WC and elk were less nocturnal at high human use WC (Fig. 3). When we looked at just a subset of WC sites with identical designs, wolves and elk were still more nocturnal at high human use sites, but not black bears and deer (Table 4). This suggests that WC design may buffer human activity to shape when some species attempt to use WC.

Patterns of adaptation to WC varied among species. At novel WC, black bears concentrated activity during the crepuscular periods; while at established WC they were primarily active during the day (Fig. 4). Coyotes shifted their activity to mostly diurnal use at novel WC, while their activity was relatively constant during the night and day at old WC. Similar shifts towards more diurnal activity patterns at novel WC were seen for wolves. Moose activity at novel WC peaked earlier in the morning and later at night, while deer were more active at night at novel WC.

Table 1. Results of comparisons of inter-specific activity patterns at wildlife crossing structures and backcountry sites using two sample Kolmogorov-Smirnov tests. Activity (N) is defined as the number of independent camera events per species. Non-significant ($P > 0.05$) comparisons indicate matching activity patterns. D is the maximum vertical deviation between the two distribution curves.

Species 1 (N)	Species 2 (N)	D	P
Wildlife crossing structures			
Black bear (522)	Cougar (254)	0.2975	<0.001
	Coyote (719)	0.2246	<0.001
	Deer (16,225)	0.1826	<0.001
	Elk (6410)	0.3208	<0.001
	Grizzly (622)	0.0563	0.329
	Moose (245)	0.1570	0.005
	Wolf (1161)	0.2311	<0.001
Cougar (254)	Coyote	0.1383	0.001
	Deer	0.1923	<0.001
	Elk	0.0598	0.347
	Grizzly	0.2879	<0.001
	Moose	0.2065	<0.001
	Wolf	0.1066	0.017
Coyote (719)	Deer	0.1188	<0.001
	Elk	0.1317	<0.001
	Grizzly	0.2227	<0.001
	Moose	0.1363	0.002
	Wolf	0.0509	0.201
Deer (16,225)	Elk	0.2093	<0.001
	Grizzly	0.1325	<0.001
	Moose	0.1014	0.013
	Wolf	0.0966	<0.001
Elk (6410)	Grizzly	0.3125	<0.001
	Moose	0.2106	<0.001
	Wolf	0.1127	<0.001
Grizzly (622)	Moose	0.1199	0.012
	Wolf	0.2005	<0.001
Moose (245)	Wolf	0.0999	0.035
Backcountry			
Black bear (165)	Cougar (91)	0.2865	<0.001
	Coyote (354)	0.1626	0.005
	Deer (2025)	0.2070	<0.001
	Elk (853)	0.2074	<0.001
	Grizzly (715)	0.0830	0.314
	Moose (293)	0.1763	0.002
	Wolf (544)	0.2529	<0.001
Cougar (91)	Coyote (354)	0.1781	0.020
	Deer	0.1831	0.005
	Elk	0.1191	0.189
	Grizzly	0.2809	<0.001
	Moose	0.1430	0.116
	Wolf	0.1199	0.212
Coyote (354)	Deer	0.619	0.198
	Elk	0.1371	<0.001
	Grizzly	0.1306	<0.001
	Moose	0.1073	0.005
	Wolf	0.1505	<0.001
Deer (2025)	Elk	0.1830	<0.001
	Grizzly	0.1495	<0.001
	Moose	0.1469	<0.001
	Wolf	0.1199	<0.001
Elk (853)	Grizzly	0.1972	<0.001
	Moose	0.0593	0.427
	Wolf	0.1277	<0.001
Grizzly (715)	Moose	0.1643	<0.001
	Wolf	0.2332	<0.001
Moose (293)	Wolf	0.1375	0.0015

Effect of vehicle traffic, human use, age of structure and hour of day on wildlife crossing structure use

Wildlife demonstrated marked interspecific variation in diel patterns of WC use, but periodicity in activity was present for all species. Time of day was a strong factor in determining crossing events of elk in all Phases except 3A (Fig. 5; see Appendix: Table A1 for full results). Elk activity in Phases 1, 2 and 3B showed two activity peaks in the morning and evening hours (around 0600 and 2100 h) and low activity during the late morning and afternoon (1000 to 1600 h). At Phases 1 and 2, there was also a second period of low activity at night (0000 to 0300 h). WC along Phases 1 and 2 had higher numbers of elk crossings than those of Phases 3A and 3B.

Time of day was the most important covariate for deer, with all crossing events in all Phases exhibiting one peak in the morning (between 0600 and 1000 h), and a second, smaller peak around 2000 h (Fig. 5; see Appendix: Table A2 for full results). Deer activity was lowest at 1500 h and 0200 h. Age of structure also increased deer crossing events, with Phase 1 having more events per hour than Phases 3A and 3B.

For wolves, time of day interacted with age of WC and was a key driver of crossing events for wolves (Fig. 5; see Appendix: Table A3 for full results). While time of day was not significant in Phase 1, it was highly significant for Phase 2, with a distinct spike in crossing events at night (0500 h) and low activity during the day (1500 h); wolves moving along Phase 3A increased crossing events in the early morning hours (0500 h) and evening hours (2100 h). Traffic volume negatively affected crossing events across all phases. Human activity at WC also interacted with age of structure: crossing events were greater at low human use structures in Phase 1, but number of events declined at low human use structures WC along Phases 3A and 3B. In Phase 2, human use was not significant.

For coyotes, at high human use structures, hour was highly significant, with a peak at 0100 h

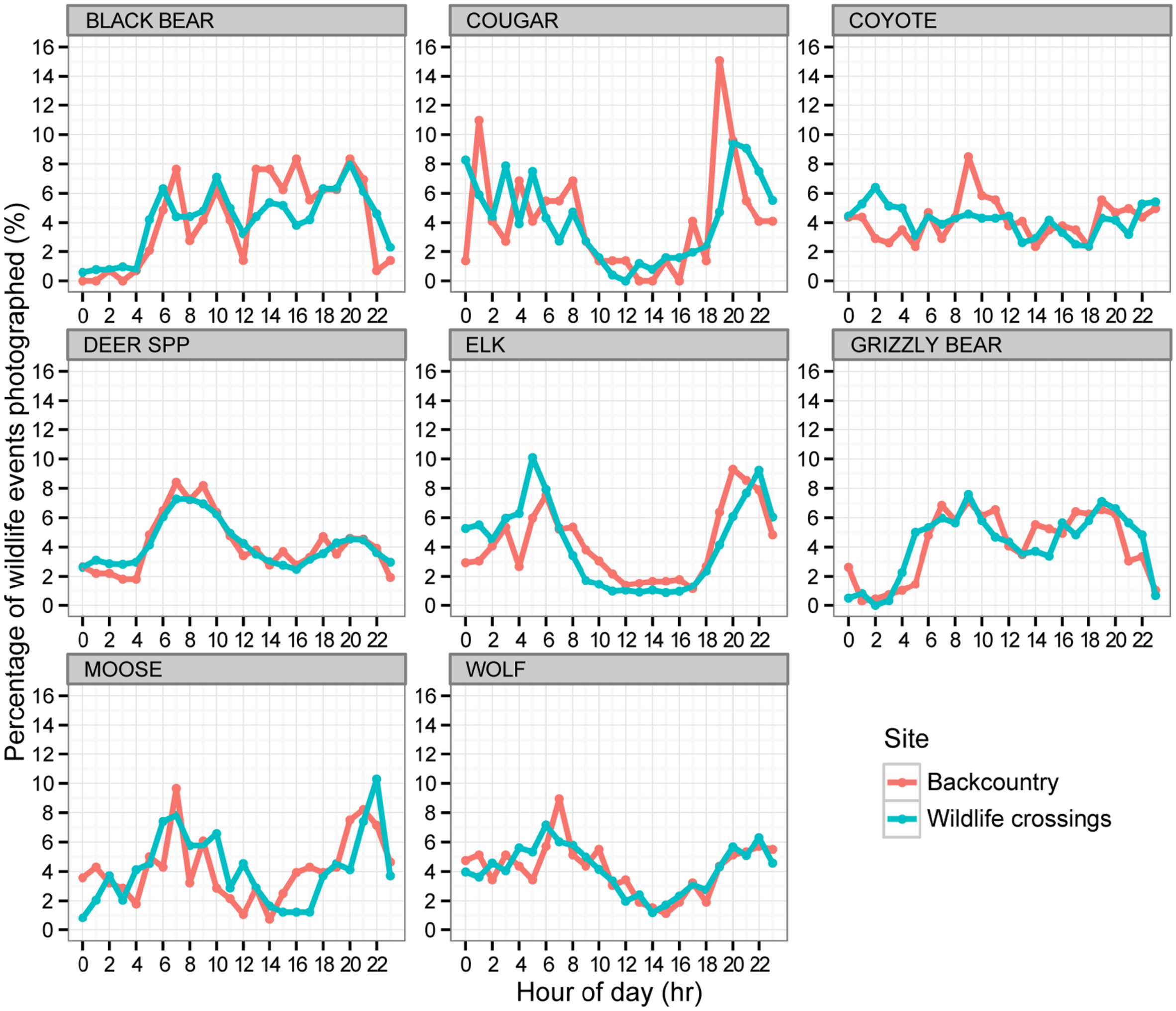

Fig. 2. Diel activity patterns of large mammals at wildlife crossings (WC) and backcountry (BC) sites in Banff National Park, Alberta. Activity is based on the percentage of wildlife events photographed at WC (turquoise solid line) and at BC sites (red solid line).

Table 2. Results of two sample Kolmogorov-Smirnov tests for intra-specific activity at wildlife crossing structure (WC) and backcountry (BC) camera sites. Listed are the number of camera events by species at WC and BC sites used in the analysis. Significant ($P < 0.05$) comparisons indicate different activity patterns. D is maximum vertical deviation between the two distribution curves.

	Camera location			
Species	BC	WC	D	P
Cougar	91	254	0.0622	0.957
Coyote	354	719	0.1057	0.010
Wolf	544	1161	0.0274	0.943
Grizzly bear	715	622	0.0420	0.600
Black bear	165	522	0.0532	0.870
Deer sp.	2026	16,255	0.0305	0.069
Elk	853	6410	0.1437	<0.001
Moose	293	245	0.0955	0.175

Table 3. Results of two sample Kolmogorov-Smirnov tests for activity patterns at wildlife crossing structures with high and low human use in Banff National Park, Alberta. Values for high and low refer to crossing events detected by motion-activated cameras at 39 sites. Significant ($P < 0.05$) comparisons indicate different activity patterns. D is the maximum vertical deviation between the two distribution curves.

	Human use			
Species	High	Low	D	P
Cougar	83	171	0.0613	0.984
Coyote	358	361	0.0714	0.318
Wolf	172	989	0.1231	0.023
Grizzly bear	183	439	0.0950	0.193
Black bear	152	370	0.1345	0.041
Deer sp.	4374	11,850	0.0425	<0.001
Elk	2761	3649	0.0799	<0.001
Moose	43	202	0.1171	0.716

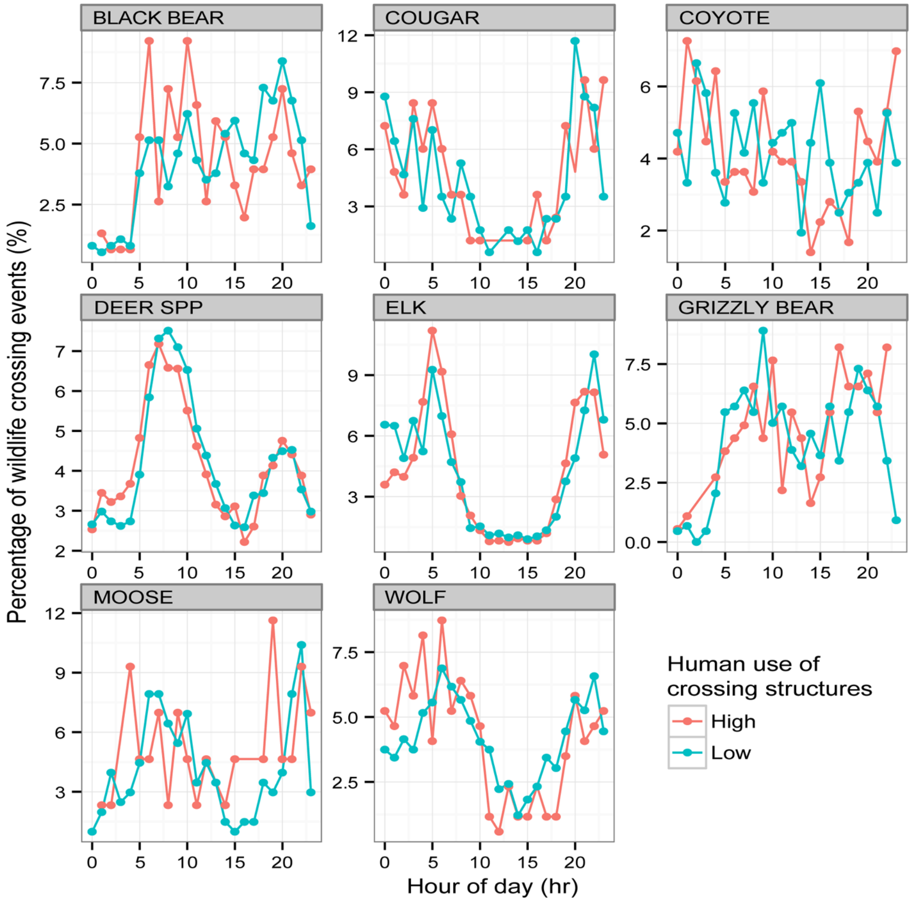

Fig. 3. Diel activity patterns of large mammals at high human-use and low human-use wildlife crossings in Banff National Park, Alberta. Activity is based on the percentage of wildlife events photographed at high human use WC (red solid line) and low human use WC (turquoise solid line).

Table 4. Results of two-sample Kolmogorov-Smirnov tests between activity patterns at wildlife crossing (WC) structures with high and low human use, standardized by open-span design type. Listed are the number (N) of camera events by species at high and low human use sites used in the analysis. Significant ($P < 0.05$) comparisons indicate different activity patterns. D is the maximum vertical deviation between the two distribution curves.

	Human activity			
Species	High use (N)	Low use (N)	D	P
Cougar	54	110	0.1350	0.523
Coyote	283	52	0.1309	0.438
Wolf	41	442	0.3290	<0.001
Grizzly bear	34	136	0.1029	0.935
Black bear	126	183	0.1556	0.053
Deer sp.	1336	4487	0.0330	0.213
Elk	2557	2735	0.1048	<0.001
Moose	6	14		. . .

Note: Insufficient data for moose to test.

and a low at 1500 h (Fig. 6; see Appendix: Table A4 for full results). At low human use WC coyotes showed no temporal variation in crossing events, as hour was not a significant predictor. Phases 1 and 2 had significantly more crossings than Phase 3B and Phase 1 also had more crossings than Phase 3A. The interaction of phase and human use on number of crossing events was highly significant, with high human use leading to fewer crossings in the newer Phases 3A and 3B, and to more crossing events in the older Phases 1 and 2.

For grizzly bears, we pooled weekend and weekday data due to low overall detections. Within these pooled data, both time of day and traffic volume were significant factors with activity peaking during the day (0600 to 1900 h), but otherwise decreasing with traffic volume (Fig. 6; see Appendix: Table A5 for full results).

As with grizzly bears, we pooled weekend and weekday data for cougars. Time of day was significant for both high and low human use WC, with more crossing events during the night and fewest around 1200 h (Fig. 6; see Appendix: Table A6 for full results). Phase 1 had more crossing events than Phase 2 or Phase 3A, while the newer Phase 3B had no crossings by cougars at all.

For black bears, as with grizzly bears and cougars, we pooled weekend and weekday. Time of day was an important explanatory variable, with decreasing number crossing events during the night (between 2100 and 0400 h) and a nearly uniform probability of crossing events during the remainder of the day (Fig. 6; see Appendix: Table A7 for full results). At low human use structures, the number of events was highest in the evening (2000 h), while at high human use structures, there was a dip in crossing events in the afternoon (1500 to 1600 h) and there were more events at Phase 1 than at all other phases.

Discussion

Our results demonstrated marked variation in the effect of anthropogenic disturbances on wildlife, including changes to the timing of interspecific interactions and the allocation of activity over daily cycles. The activity patterns of all species at WC showed some response to human activity. However, some species (deer, elk, coyotes, black bears) were sensitive to specific types of human activities, whereas large carnivores (wolves, grizzly bears, cougars) were sensitive to all forms of human disturbance that we measured.

While efforts to mitigate disturbance to wildlife arising from transportation infrastructure can be costly (McGuire and Morrall 2000, Huijser et al. 2009), this effort is leading to the restoration of animal movement (Gagnon et al. 2011, Van Manen et al. 2012, Sawaya et al. 2013, Sawyer et al. 2013) and genetic flows (Sawaya et al. 2014) across the landscape and a reduction in the risk of wildlife-vehicle collisions (Clevenger et al. 2001, McCollister and Van Manen 2010, Found and Boyce 2011). Indeed, the large number of wildlife using WC in our study area (Clevenger et al. 2009) may be interpreted by some observers

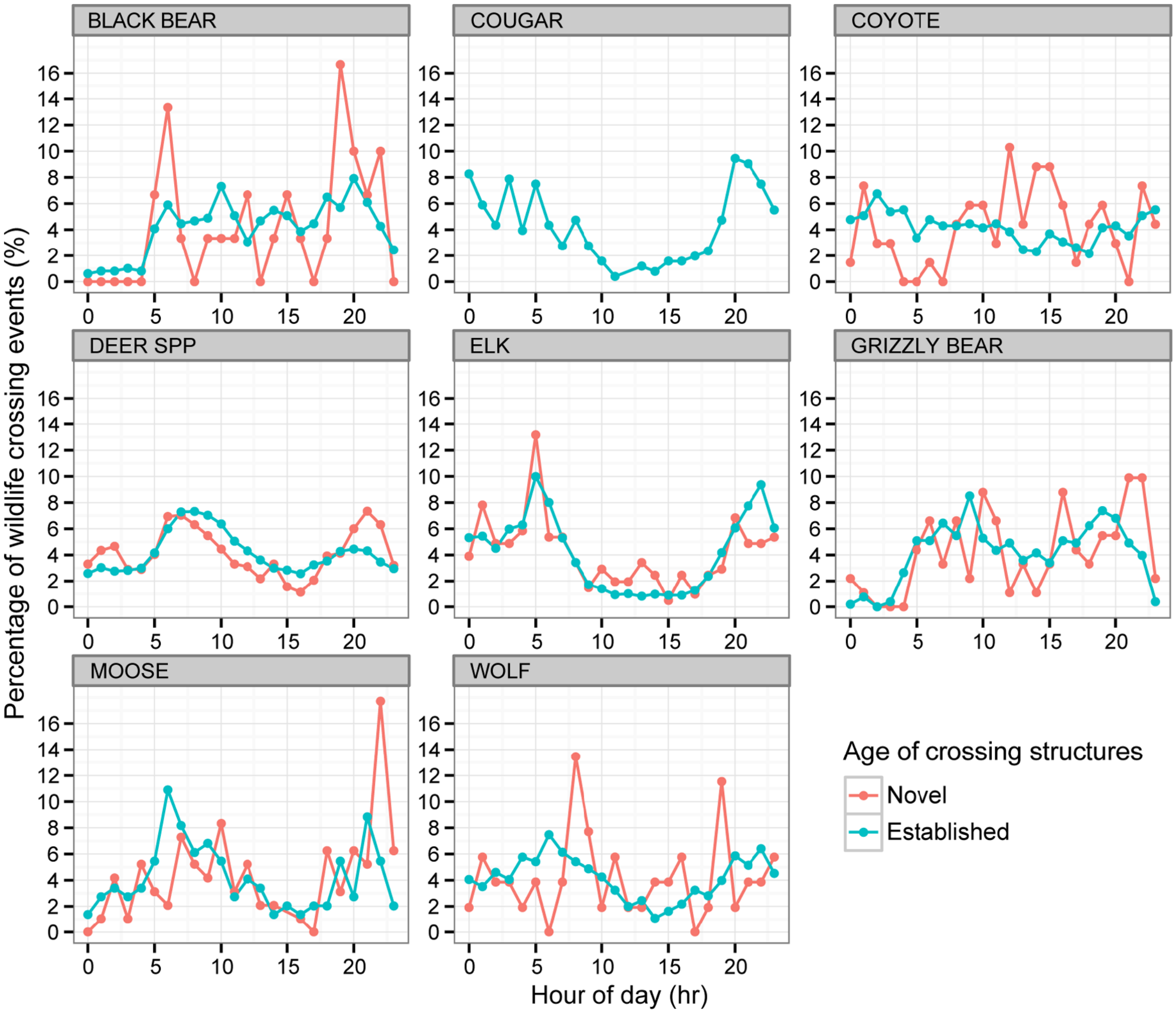

Fig. 4. Diel activity patterns of large mammals at novel vs. established wildlife crossings in Banff National Park, Alberta. Activity is based on the percentage of wildlife events photographed at novel WC (red solid line) and established WC (turquoise solid line). No data were obtained from cougars using novel wildlife crossings during the study period.

as a successful restoration of critical ecological flows across this human-occupied landscape. Less appreciated by these levels of wildlife use are the sub-lethal effects of highways on wildlife behavior and the extent to which mitigation buffers these effects.

Understanding the behavioral response of wildlife to people is an information gap with critical conservation and management implications (Buchholz 2007, Caro 2007, Blumstein and Fernandez-Juricic 2010). Previous studies have shown that large mammals can adjust their location and timing of certain behaviors to avoid interacting with people, including hikers (Rogala et al. 2011, Longshore et al. 2013), skiers (Ferguson and Keith 1982, Cassirer et al. 1992), aircraft (Weisenberger et al. 1996, Krausman et al. 1998) and vehicles (Burson et al. 2000, Brown et al. 2012). Some of these behaviors generate cascading effects on other human-wildlife interactions. For example, deer are more vulnerable to collisions with vehicles during hunting season, but only in areas where hunting is permitted (Sudharsan et al. 2006). Here we have shown that wildlife adjust their behavior in response to variation in human activity, and that this

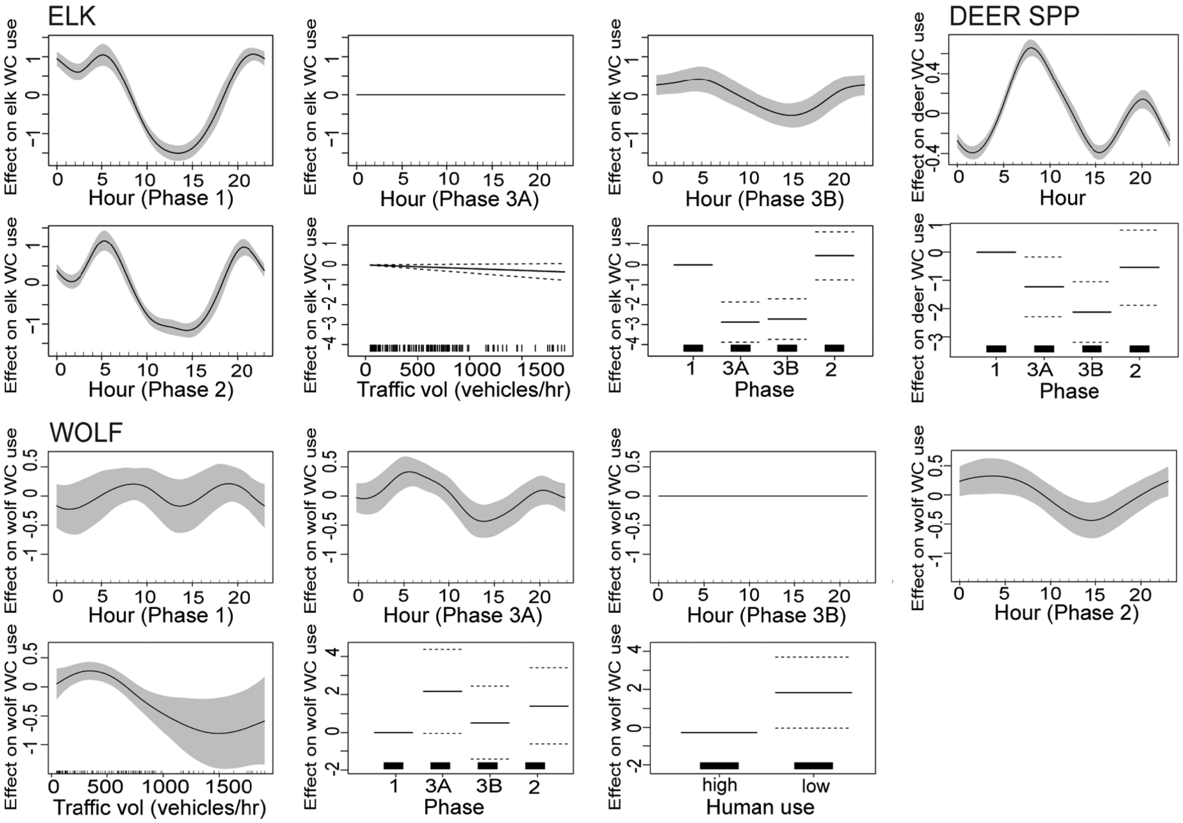

Fig. 5. Plots showing the smooth functions of continuous covariates and term plots of parametric terms of the best GAMM models for elk, deer and wolves in Banff National Park, Alberta. The x-axes of all smooth function plots show the covariate values, the x-axes of the term plots show the factor levels. In all plots, the y-axis is the covariate effect on the mean response, which is the number of animals per hour using an 'average' crossing structure. Values on the y-axis are on the linear predictor scale.

response depends on the baseline levels of human activity in the area. For instance, traffic volume negatively affected crossing count of wolves at all Phases, but the amount of wolf activity at WC depended on how many people also used the WC. Our results are consistent with others (e.g., Ng et al. 2004, Mata et al. 2005, Grilo et al. 2008) showing that the restoration of pre-disturbance activity patterns of wildlife living near highways will depend on the management of human use at WC.

Though our results showed that human use of WC affected wildlife activity, we found congruent overall activity patterns for most species among WC and BC sites. This result suggests that wildlife can habituate to some types of disturbances (e.g., vehicle traffic) but remain sensitive to others (e.g., foot traffic at WC), and that the WC designs used at our study site are capable of buffering at least some of the potentially aversive stimulus (e.g., noise, chemosensory emissions, light) produced by roads and traffic (Barber et al. 2009, Brown et al. 2012, McClure et al. 2013). If wildlife habituation to roads increases use of WC, we predicted the frequency of crossing events would increase with age of WC, which was the case for all species but wolves and grizzly bears. Gagnon et al. (2011) also found an adaptive response of elk and deer to WC in Arizona over a 4-year period and Ford et al. (2010) present data suggesting adaptive responses by grizzly bears to use of WC. These adaptive responses by wildlife support the use of long-term monitoring (e.g., ≥4years) to fully understand the effectiveness of mitigation (Clevenger et al. 2009), at least for long-lived, wide-

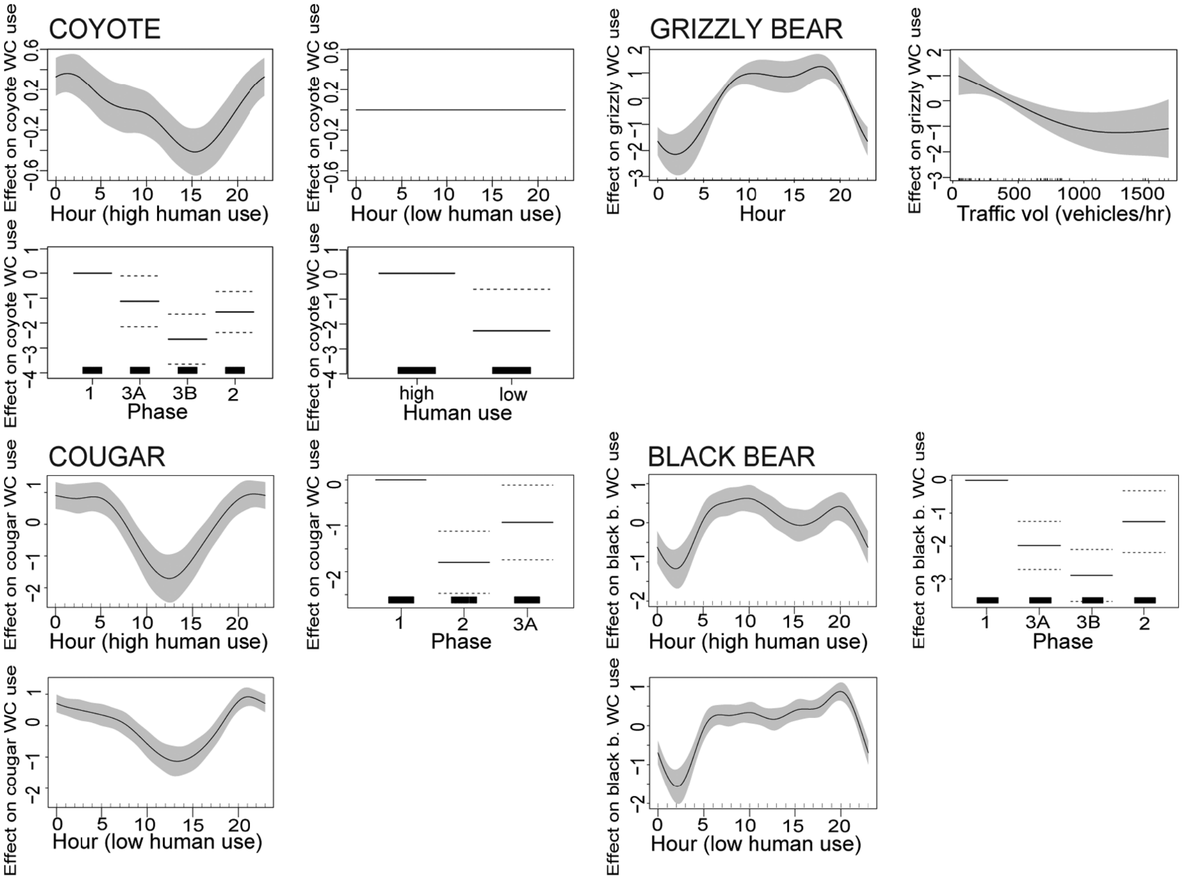

Fig. 6. Plots showing the smooth functions of continuous covariates and term plots of parametric terms of the best GAMM models for coyotes, grizzly bears, cougars and black bears in Banff National Park, Alberta. The x-axes of all smooth function plots show the covariate values, the x-axes of the term plots show the factor levels. In all plots, the y-axis is the covariate effect on the mean response, which is the number of animals per hour using an 'average' crossing structure. Values on the y-axis are on the linear predictor scale.

ranging species like large terrestrial mammals.

Protected areas are one of the most widely used approaches to conserving wildlife; however, conservation goals can be compromised when people reside and continue to use protected areas for resource extraction, transportation and recreation (Woodroffe and Ginsberg 1998, Ament et al. 2008). In an effort to restore ecosystem processes and structures, a central focus for the management of protected areas has been to mitigate the effects of people on wildlife movement and mortality (McNeely et al. 1990, Cooperrider and Noss 1994). Transportation and land managers should be cognizant of the potential negative effects of anthropogenic disturbances compromising the ecological and conservation value of WC. Rigorous long-term monitoring of WC and anthropogenic disturbances associated with them will provide sound information for managers responsible for ensuring the efficacy of WC. Furthermore, information on the relationship between wildlife and anthropogenic disturbance will aid in assessing the performance of mitigation efforts aimed at increasing landscape connectivity, reducing the risk of human-wildlife conflict and conserving wildlife populations.

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SUPPLEMENTAL MATERIAL

APPENDIX

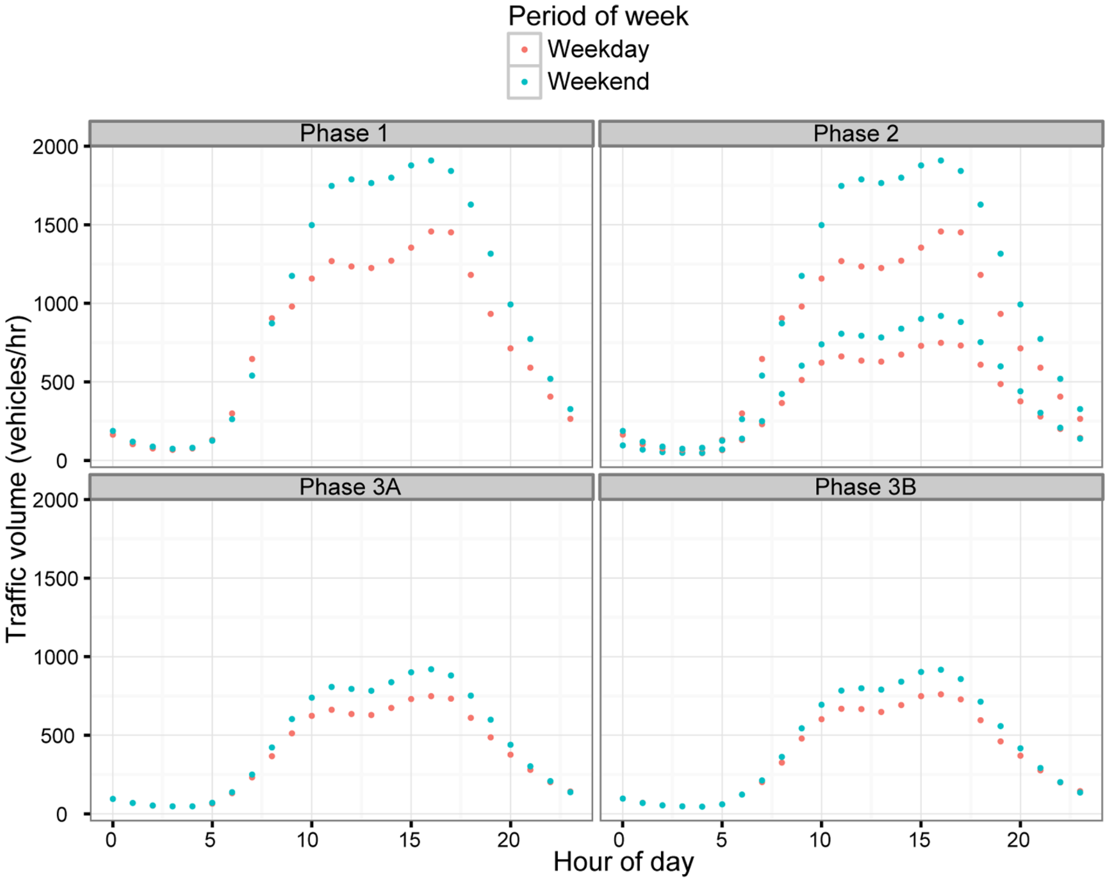


Fig. A1. Plots of traffic volume in average number of vehicles/hour obtained from three traffic counters on the Trans-Canada Highway (TCH) in Banff National Park, Alberta. Traffic volume data are shown for the four phases of the TCH from 2007–2013. Red solid dots are weekday (Monday–Thursday) traffic, while turquoise solid dots are weekend (Friday–Sunday) traffic volumes.

Table A1. Best generalized additive mixed models (GAMMs) for elk. $N = 1632$, $R^2(\text{adj}) = 0.514$. ICC = Intra-class correlation. Smooth terms are denoted with s(). σ_i^2 = variance of the random intercept; σ_r^2 = variance of the (working) residuals.

Effect	Variable	Coefficient	SE	*t*	Estimated df	*F*	*P*	σ_i^2	σ_r^2	ICC
Fixed	Intercept	−4.210	0.419	−10.046			<0.001			
Fixed	Traffic†	0.000	0.000	−1.678			0.094			
Fixed	Phase 3A	−2.873	0.507	−5.667			<0.001			
Fixed	Phase 3B	−2.721	0.510	−5.338			<0.001			
Fixed	Phase 2	0.467	0.612	0.762			0.446			
Fixed	s(hr): Phase 1				7.129	43.799	<0.001			
Fixed	s(hr): Phase 3A				0.000	0.000	0.436			
Fixed	s(hr): Phase 3B				3.024	1.885	<0.001			
Fixed	s(hr): Phase 2				7.417	37.275	<0.001			
Random	Crossing structure							0.815	1.535	0.347

Notes: Traffic (indicated with †) was modeled as a smooth term first, but was found to be equal to a linear effect. Estimated df = 1. An ANOVA for the parametric coefficient Phase resulted in a *P* value of <0.001, with df = 3 and *F* = 22.069.

Table A2. Best generalized additive mixed models (GAMMs) for deer spp. $N = 1680$, $R^2(\text{adj}) = 0.293$. ICC = Intra-class correlation. Smooth terms are denoted with s().σ_i^2 = variance of the random intercept; σ_r^2 = variance of the (working) residuals.

Effect	Variable	Coefficient	SE	t	Estimated df	F	P	σ_i^2	σ_r^2	ICC
Fixed	Intercept	−3.482	0.447	−7.791			<0.001			
Fixed	Phase 3A	−1.229	0.528	−2.327			0.020			
Fixed	Phase 3B	−2.123	0.537	−3.953			<0.001			
Fixed	Phase 2	−0.541	0.671	−0.806			0.420			
Fixed	s(hr): Phase 1				3.540	0.939	0.045			
Fixed	s(hr): Phase 3A				4.504	2.932	<0.001			
Fixed	s(hr): Phase 3B				0.000	0.000	0.953			
Fixed	s(hr): Phase 2				2.439	1.086	0.006			
Fixed	s(Traffic)				3.960	4.391	0.002			
Random	Crossing structure							0.987	1.881	0.344

Note: An ANOVA for the parametric coefficient *Phase* resulted in a P value of <0.001, with df = 3 and $F = 22.069$.

Table A3. Best generalized additive mixed models (GAMMs) for wolf. $N = 1440$, $R^2(\text{adj}) = 0.351$. ICC = Intra-class correlation. Smooth terms are denoted with s().σ_i^2 = variance of the random intercept; σ_r^2 = variance of the (working) residuals. HumanL = Low human use.

Effect	Variable	Coefficient	SE	t	Estimated df	F	P	σ_i^2	σ_r^2	ICC
Fixed	Intercept	−8.454	0.870	−9.717			<0.001			
Fixed	Phase 3A	2.163	1.103	1.961			0.050			
Fixed	Phase 3B	0.510	0.966	0.528			0.598			
Fixed	Phase 2	1.387	1.009	1.375			0.170			
Fixed	HumanL	2.100	0.934	2.249			0.025			
Fixed	Phase 3A: HumanL	−2.616	1.170	−2.236			0.026			
Fixed	Phase 3B: HumanL	−2.468	1.086	−2.273			0.023			
Fixed	Phase 2: HumanL	−0.016	1.255	−0.013			0.990			
Fixed	s(hr): Phase 1				3.540	0.939	0.045			
Fixed	s(hr): Phase 3A				4.504	2.932	<0.001			
Fixed	s(hr): Phase 3B				0.000	0.000	0.953			
Fixed	s(hr): Phase 2				2.439	1.086	0.006			
Fixed	s(Traffic)				3.960	4.391	0.002			
Random	Crossing structure							0.440	0.994	0.307

Notes: An ANOVA for the parametric coefficient Phase resulted in a P value of 0.099, with df = 3 and $F = 2.096$. An ANOVA for the parametric coefficient Human resulted in a P value of 0.025, with df = 1 and $F = 5.059$. An ANOVA for the interaction of Phase and Human resulted in a P value of 0.012, with df = 3 and $F = 3.649$.

Table A4. Best generalized additive mixed models (GAMMs) for coyote. $N = 1536$, $R^2(\text{adj}) = 0.277$. ICC = Intra-class correlation. Smooth terms are denoted with s().σ_i^2 = variance of the random intercept; σ_r^2 = variance of the (working) residuals. HumanL = Low human use. HumanH = High human use.

Effect	Variable	Coefficient	SE	t	Estimated df	F	P	σ_i^2	σ_r^2	ICC
Fixed	Intercept	−5.684	0.354	−16.044			<0.001			
Fixed	Phase 3A	−1.128	0.509	−2.217			0.027			
Fixed	Phase 3B	−2.647	0.501	−5.281			<0.001			
Fixed	Phase 2	0.022	0.411	0.053			0.958			
Fixed	HumanL	−1.472	0.417	−3.534			0.000			
Fixed	Phase 3A: HumanL	1.054	0.570	1.850			0.064			
Fixed	Phase 3B: HumanL	2.184	0.590	3.701			0.000			
Fixed	Phase 2: HumanL	−0.078	0.639	−0.123			0.902			
Fixed	s(hr): HumanH				3.277	2.617	<0.001			
Fixed	s(hr): HumanL				0.000	0.000	0.463			
Random	Crossing structure							0.106	1.040	0.092

Notes: An ANOVA for the parametric coefficient Phase resulted in a P value of <0.001, with df = 3 and $F = 15.692$. An ANOVA for the parametric coefficient Human resulted in a P value of <0.001, with df = 1 and $F = 12.489$. An ANOVA for the interaction of Phase and Human resulted in a P value of <0.001, with df = 3 and $F = 6.094$.

Table A5. Best generalized additive mixed models (GAMMs) for grizzly bear. $N = 768$, $R^2(\text{adj}) = 0.188$. ICC = Intra-class correlation. Smooth terms are denoted with s().σ_i^2 = variance of the random intercept; σ_r^2 = variance of the (working) residuals. HumanL = Low human use. HumanH = High human use.

Effect	Variable	Coefficient	SE	*t*	Estimated df	*F*	*P*	σ_i^2	σ_r^2	ICC
Fixed	Intercept	−7.690	0.159	−48.470			<0.001			
Fixed	s(hr)				4.704	13.553	<0.001			
Fixed	s(Traffic)				2.573	5.551	0.002			
Random	Crossing structure							0.649	1.008	0.391

Table A6. Best generalized additive mixed models (GAMMs) for cougar. $N = 360$, $R^2(\text{adj}) = 0.325$. ICC = Intra-class correlation. Smooth terms are denoted with s().σ_i^2 = variance of the random intercept; σ_r^2 = variance of the (working) residuals. HumanL = Low human use. HumanH = High human use.

Effect	Variable	Coefficient	SE	*t*	Estimated df	*F*	*P*	σ_i^2	σ_r^2	ICC
Fixed	Intercept	−6.929	0.239	−29.004			<0.001			
Fixed	Phase 3A	−1.796	0.339	−5.302			<0.001			
Fixed	Phase 2	−0.925	0.407	−2.273			0.024			
Fixed	s(hr): HumanH				4.039	4.269	<0.001			
Fixed	s(hr): HumanL				4.536	7.090	0.732			
Random	Crossing structure							0.238	0.923	0.205

Note: An ANOVA for the parametric coefficient Phase resulted in a *P* value of <0.001, with df = 2 and *F* = 14.070.

Table A7. Best generalized additive mixed models (GAMMs) for black bear. $N = 696$, $R^2(\text{adj}) = 0.395$. ICC = Intra-class correlation. Smooth terms are denoted with s().σ_i^2 = variance of the random intercept; σ_r^2 = variance of the (working) residuals. HumanL = Low human use. HumanH = High human use.

Effect	Variable	Coefficient	SE	*t*	Estimated df	*F*	*P*	σ_i^2	σ_r^2	ICC
Fixed	Intercept	−6.264	0.247	−25.366			<0.001			
Fixed	Phase 3A	−1.960	0.306	−6.405			<0.001			
Fixed	Phase 3B	−2.168	0.366	−5.927			<0.001			
Fixed	Phase 2	−1.210	0.392	−3.088			0.002			
Fixed	s(hr): HumanH				5.039	3.280	<0.001			
Fixed	s(hr): HumanL				6.657	9.208	<0.001			
Random	Crossing structure							0.276	0.945	0.226

Note: An ANOVA for the parametric coefficient *Phase* resulted in a *P* value of <0.001, with df = 3 and *F* = 16.770.

Appendix C: Supplementary Tables for Section III, Chapter 6 (Factors Affecting Passage by Small and Medium-sized Mammals at Culverts)

Supplementary Tables for Section III, Chapter 6 (Factors Affecting Passage by Small and Medium-sized Mammals at Culverts)

Table 1. American marten. AIC and BIC values. In bold are values with ΔAIC or ΔBIC <6.

Rank	Model	AIC	ΔAIC	Model	BIC	ΔBIC
1	**M8**	**236.1**	**0**	**M8**	**251.2**	**0**
2	M9	243.0	6.9	**M9**	**255.0**	**3.9**
3	M13	243.1	7.0	M14	261.8	10.7
4	M7	251.8	15.7	M7	266.9	15.7
5	M14	252.8	16.7	M16	267.8	16.7
6	M3	254.9	18.8	M15	272.6	21.4
7	M11	255.1	19.0	M3	272.9	21.8
8	M10	256.3	20.2	M11	273.2	22.0
9	M12	257.7	21.6	M10	274.3	23.2
10	M16	261.8	25.7	M12	275.7	24.6
11	M15	263.5	27.4	M1	279.5	28.3
12	M1	264.4	28.3	M2	279.7	28.6
13	M2	264.7	28.6	M6	279.8	28.7
14	M6	264.8	28.7	M13	282.2	31.1
15	M4	266.5	30.4	M4	284.6	33.4
16	M5	268.4	32.3	M5	289.5	38.3

Table 2. Red squirrel models. AIC and BIC values. In bold are values with ΔAIC or ΔBIC <6.

Rank	Model	AIC	ΔAIC	Model	BIC	ΔBIC
1	**M13**	**266.3**	**0.0**	**M6**	**287.0**	**0.0**
2	**M6**	**272.0**	**5.6**	M16	294.5	7.5
3	M2	281.3	15.0	M2	296.3	9.3
4	M4	282.6	16.3	M1	298.0	11.0
5	M1	283.0	16.6	M15	298.0	11.0
6	M5	284.6	18.3	M14	299.5	12.4
7	M3	284.8	18.5	M4	300.7	13.6
8	M16	288.5	22.2	M3	302.8	15.8
9	M15	289.0	22.7	M9	304.4	17.4
10	M14	290.4	24.1	M13	305.4	18.4
11	M9	292.4	26.1	M5	305.7	18.6
12	M7	292.7	26.3	M7	307.7	20.7
13	M12	293.2	26.9	M8	308.8	21.8
14	M8	293.8	27.5	M12	311.2	24.2
15	M11	294.3	28.0	M11	312.3	25.3
16	M10	295.6	29.3	M10	313.7	26.7

Table 3 Chipmunk (TAMI). AIC and BIC values. In bold are values with ΔAIC or ΔBIC <6.

Rank	Model	AIC	ΔAIC	Model	BIC	ΔBIC
1	**M10**	**127.8**	**0.0**	**M13**	**135.2**	**0.0**
2	**M13**	**128.7**	**0.8**	**M14**	**135.3**	**0.1**
3	**M4**	**129.9**	**2.1**	**M10**	**138.6**	**3.5**
4	**M14**	**131.0**	**3.1**	**M8**	**139.1**	**4.0**
5	**M8**	**132.7**	**4.8**	M5	142.1	6.9
6	**M5**	**133.4**	**5.6**	M7	143.1	8.0
7	M7	134.5	6.7	M4	145.0	9.9
8	M3	135.0	7.1	M6	146.0	10.9
9	M6	135.3	7.4	M9	146.3	11.2
10	M9	135.5	7.7	M11	146.4	11.3
11	M11	135.6	7.8	M1	146.7	11.6
12	M1	135.9	8.1	M2	147.7	12.6
13	M2	136.9	9.1	M3	147.9	12.8
14	M12	139.1	11.3	M12	158.6	23.4

Table 4 Weasel species (*Mustela* spp.) models. AIC and BIC values. In bold are values with ΔAIC or ΔBIC <6.

Rank	Model	AIC	ΔAIC	Model	BIC	ΔBIC
1	**M11**	**191.7**	**0.0**	**M14**	**203.8**	**0.0**
2	**M12**	**193.5**	**1.9**	**M15**	**206.4**	**2.7**
3	**M13**	**194.0**	**2.4**	**M9**	**206.7**	**3.0**
4	**M9**	**194.7**	**3.0**	**M16**	**207.1**	**3.4**
5	**M14**	**194.7**	**3.1**	**M3**	**207.6**	**3.9**
6	**M10**	**195.6**	**3.9**	M11	209.7	6.0
7	**M3**	**195.6**	**3.9**	M1	210.6	6.9
8	**M8**	**196.1**	**4.5**	M8	211.2	7.4
9	**M4**	**197.2**	**5.6**	M12	211.6	7.8
10	**M15**	**197.4**	**5.7**	M10	213.6	9.9
11	M5	200.9	9.2	M4	215.3	11.5
12	M16	201.1	9.5	M5	215.9	12.1
13	M1	201.6	9.9	M7	216.8	13.1
14	M7	201.8	10.1	M2	218.1	14.3
15	M0	202.4	10.7	M6	219.1	15.4
16	M2	203.0	11.4	M0	220.5	16.7
17	M6	204.1	12.4	M13	230.2	26.4

Table 5 Mice and voles. AIC and BIC values. In bold are values with ΔAIC or ΔBIC <6.

Rank	Model	AIC	ΔAIC	Model	BIC	ΔBIC
1	**M13**	**937.9**	**0.0**	**M14**	**954.6**	**0.0**
2	**M14**	**939.6**	**1.7**	**M13**	**955.9**	**1.3**
3	**M9**	**942.5**	**4.7**	M9	963.6	9.0
4	M12	951.7	13.8	M12	963.7	9.1
5	M3	954.8	17.0	M10	971.2	16.5
6	M16	958.7	20.9	M4	971.2	16.6
7	M10	959.1	21.3	M3	972.9	18.3
8	M4	959.2	21.3	M6	979.5	24.9
9	M6	961.5	23.6	M5	980.6	26.0
10	M5	962.5	24.7	M11	981.0	26.3
11	M11	962.9	25.0	M16	997.9	43.2
12	M2	1178.6	240.8	M15	1190.7	236.0
13	M15	1184.6	246.8	M2	1193.7	239.1
14	M7	1185.0	247.2	M1	1197.9	243.3
15	M1	1185.9	248.1	M7	1200.1	245.5
16	M8	1187.5	249.6	M8	1202.5	247.9

Table 6 Shrew spp. AIC and BIC values. In bold are values with ΔAIC or ΔBIC <6.

Rank	Model	AIC	ΔAIC	Model	BIC	ΔBIC
1	**M5**	**160.1**	**0.0**	**M4**	**174.7**	**0.0**
2	**M11**	**162.7**	**2.6**	**M5**	**178.2**	**3.4**
3	**M4**	**162.7**	**2.6**	**M1**	**179.1**	**4.4**
4	**M7**	**165.5**	**5.4**	**M7**	**180.6**	**5.8**
5	M3	166.4	6.3	M11	180.7	6.0
6	M1	167.1	7.0	M15	183.3	8.6
7	M6	168.2	8.1	M2	184.1	9.4
8	M2	169.0	8.9	M3	184.4	9.7
9	M16	171.4	11.3	M12	184.9	10.2
10	M12	172.9	12.8	M6	186.3	11.5
11	M13	175.9	15.8	M10	188.1	13.4
12	M10	176.1	16.0	M14	193.5	18.7
13	M15	177.3	17.2	M13	194.0	19.2
14	M14	178.4	18.3	M8	196.9	22.1
15	M9	180.9	20.8	M9	202.0	27.3
16	M8	181.8	21.7	M16	210.5	35.8

Appendix D: Supplementary Tables for Section IV, Chapter 1 (Effects of Transportation Infrastructure on Fine-Scale Genetic Structure of Wolverines in Banff and Yoho National Parks)

Supplementary Tables for Section IV, Chapter 1 (Effects of Transportation Infrastructure on Fine-Scale Genetic Structure of Wolverines in Banff and Yoho National Parks)

Figure A.1: Pooled DNA-based detection locations for wolverine F002 that span the Trans-Canada Highway in Banff and Yoho National Parks between 2011 and 2013.

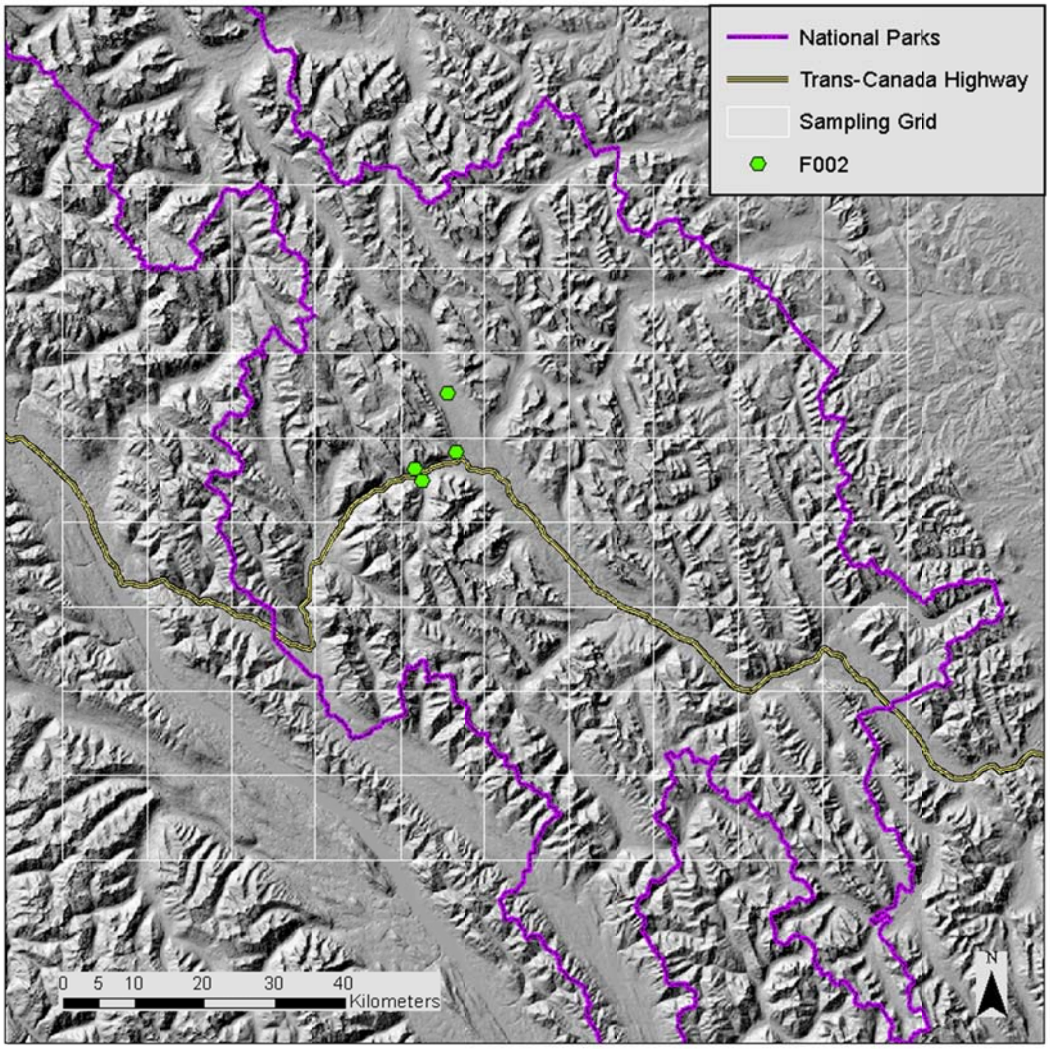


Figure A.6: Pooled DNA-based detection locations for wolverine M032 that span the Trans-Canada Highway in Banff and Yoho National Parks between 2011 and 2013.

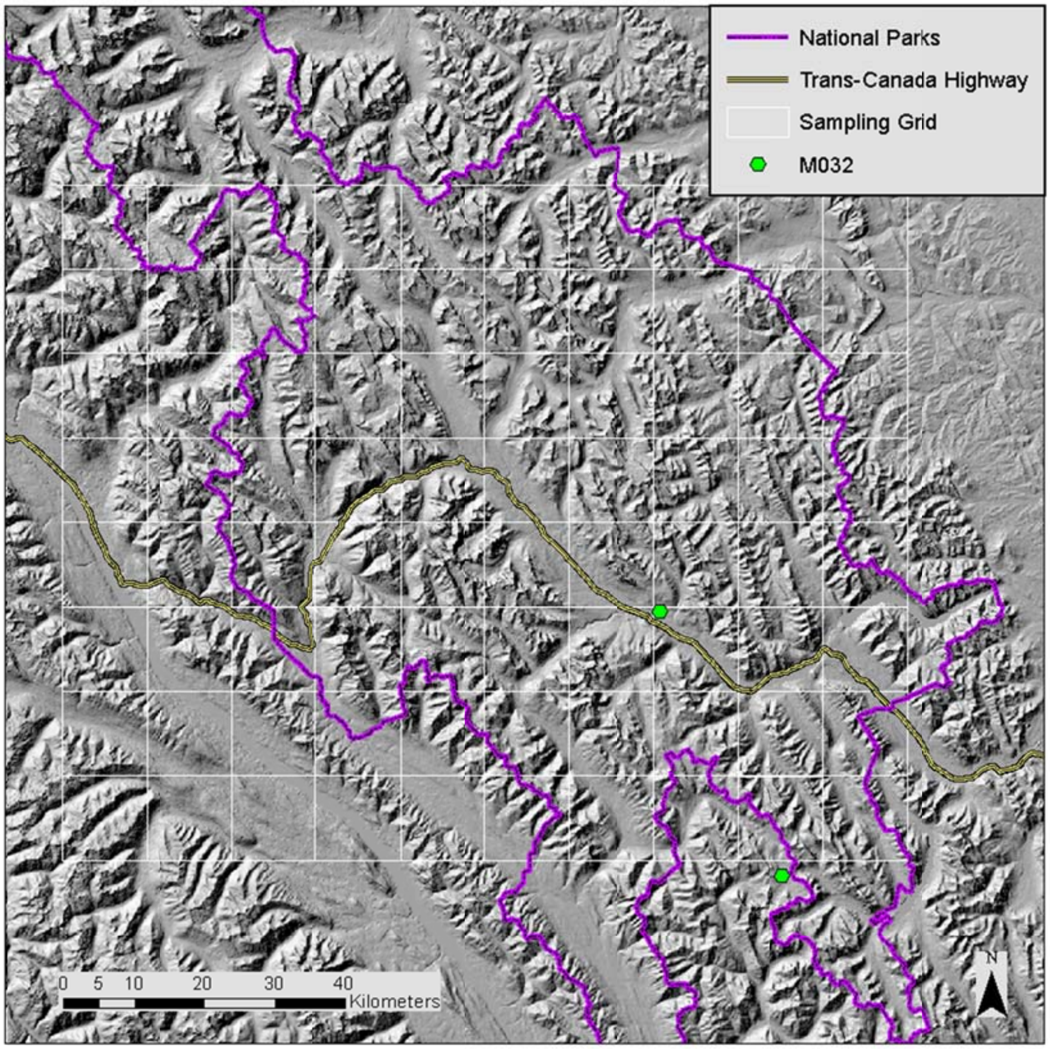


Figure A.2: Pooled DNA-based detection locations for wolverine F015 that span the Trans-Canada Highway in Banff and Yoho National Parks between 2011 and 2013.

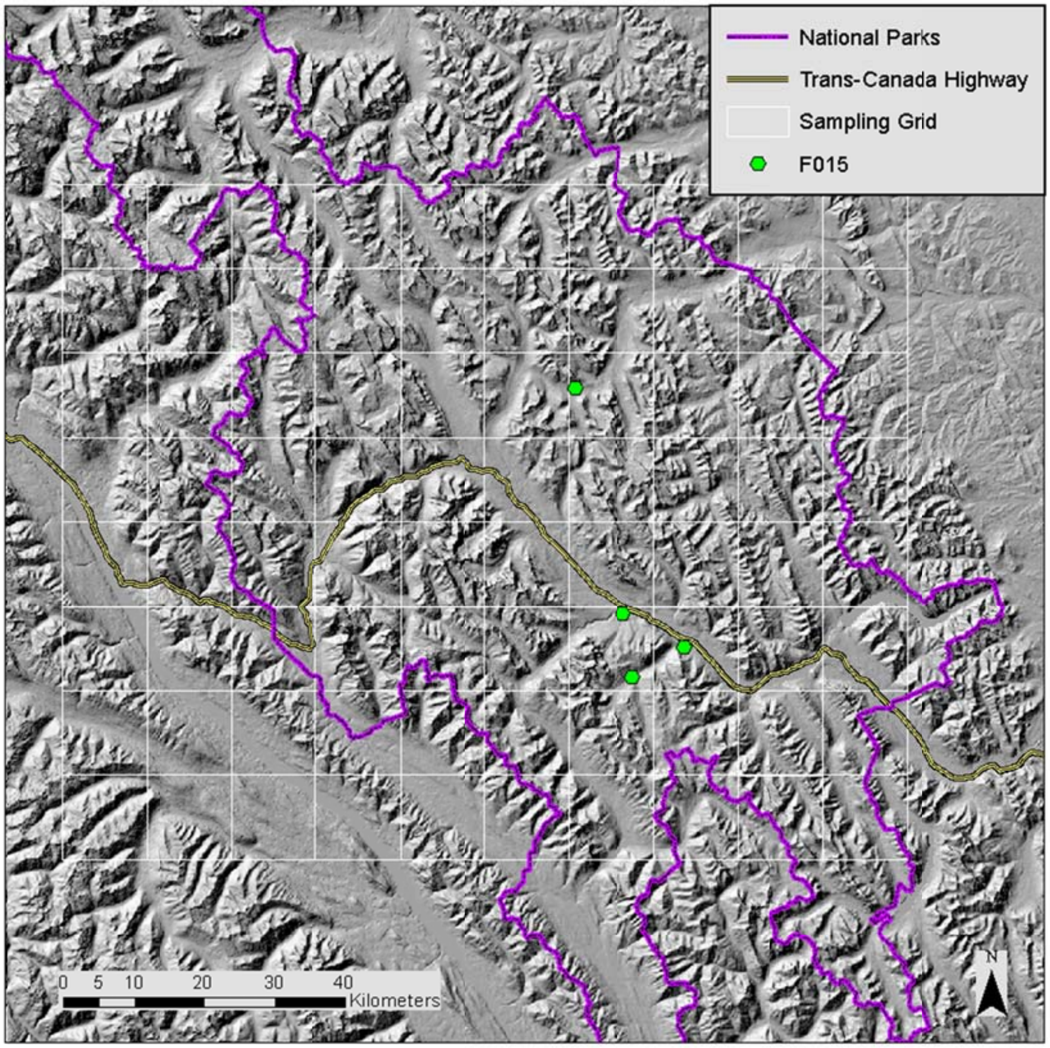


Figure A.3: Pooled DNA-based detection locations for wolverine M007 that span the Trans-Canada Highway in Banff and Yoho National Parks between 2011 and 2013.

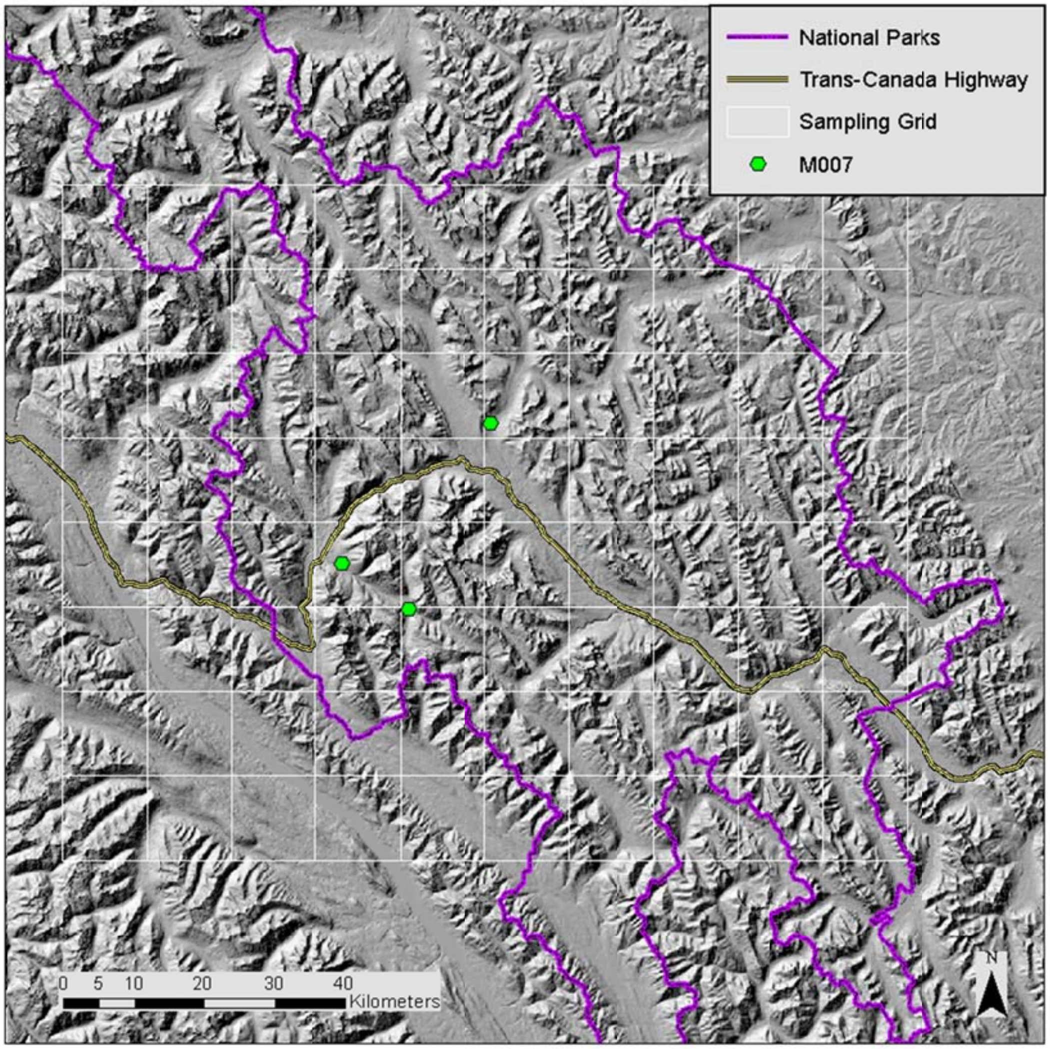


Figure A.4: Pooled DNA-based detection locations for wolverine M017 that span the Trans-Canada Highway in Banff and Yoho National Parks between 2011 and 2013.

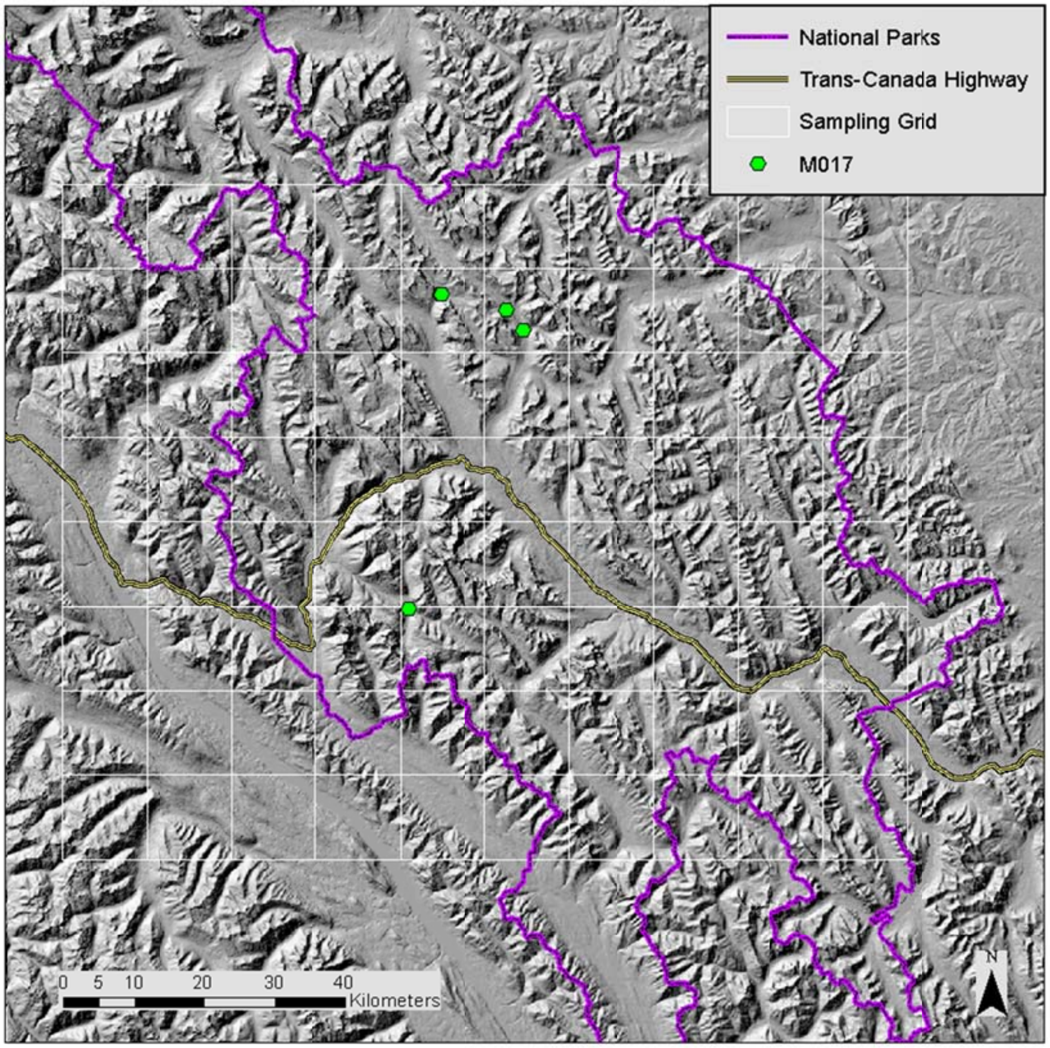


Figure A.5: Pooled DNA-based detection locations for wolverine M018 that span the Trans-Canada Highway in Banff and Yoho National Parks between 2011 and 2013.

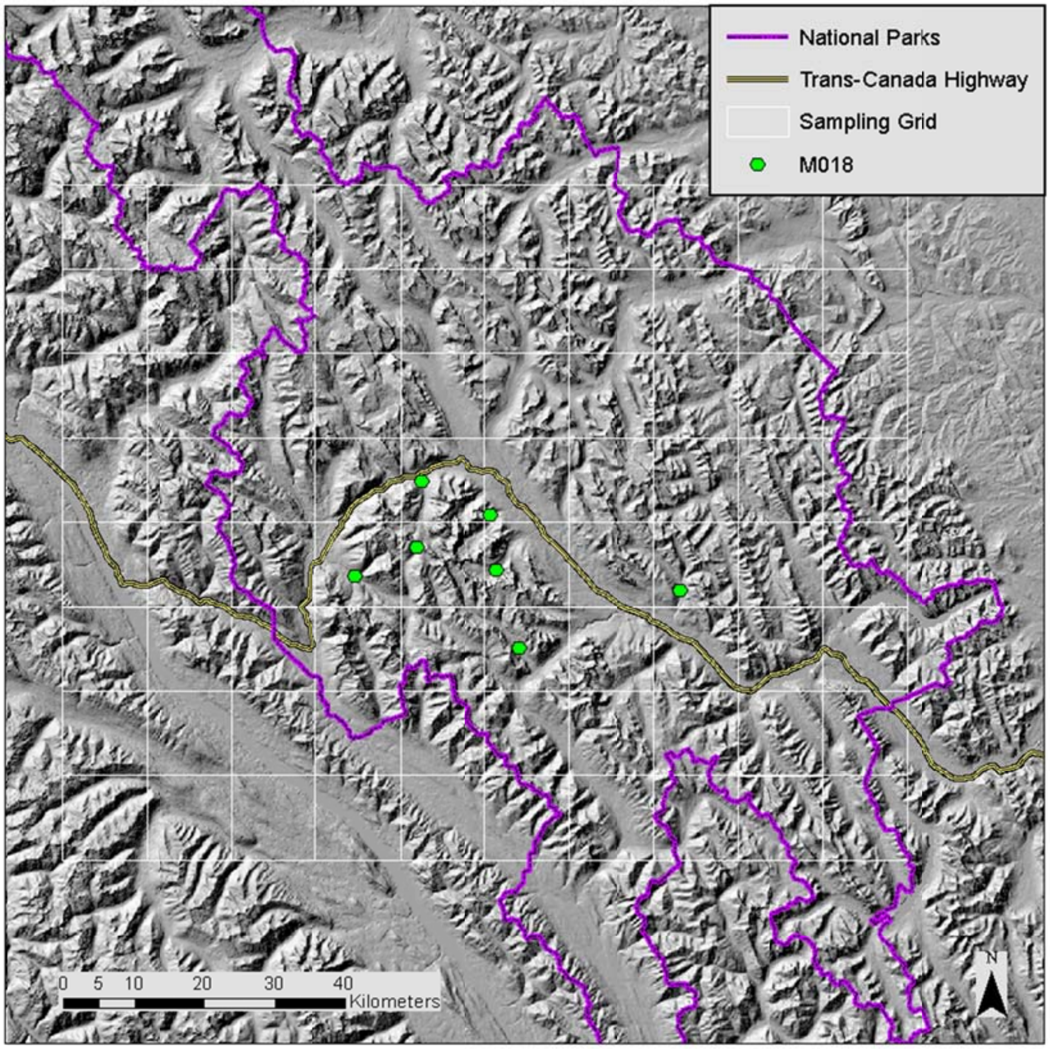


Figure A.7: Pooled DNA-based detection locations for wolverine M052 that span the Trans-Canada Highway in Banff and Yoho National Parks between 2011 and 2013.

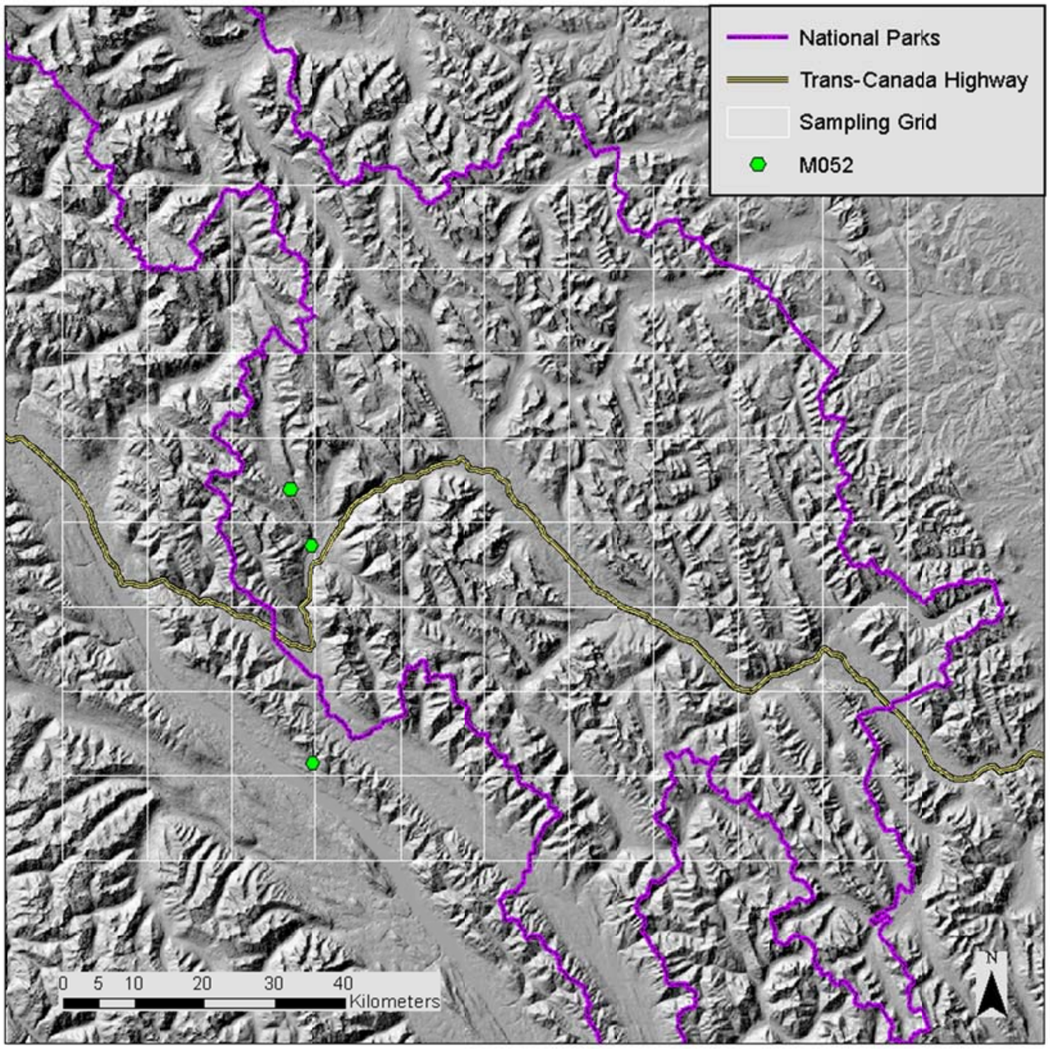
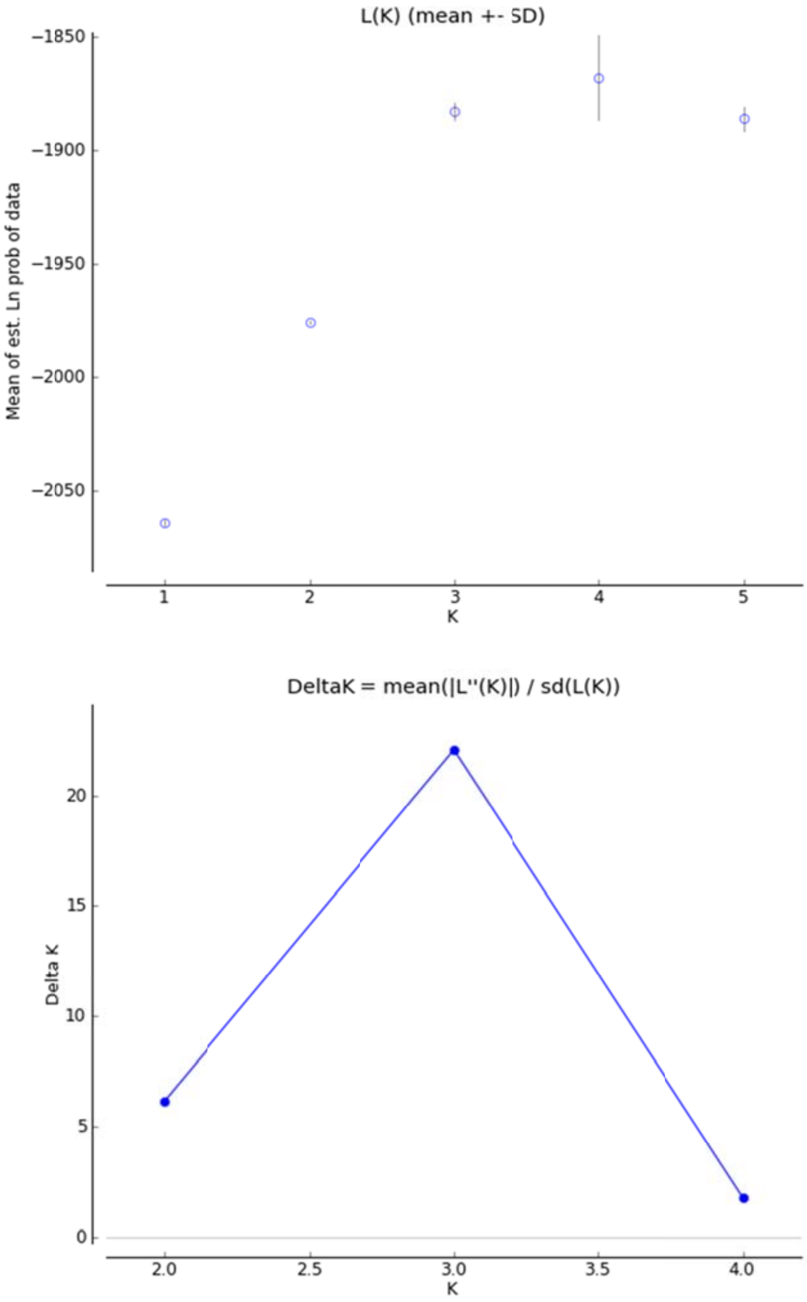


Figure B.1. Program STRUCTURE (Pritchard et al. 2000) output extracted using program STRUCTURE HARVESTER [Earl and vonHoldt 2012] showing (a) the posterior probability of the data for K (lnP(K), and (b) the second-order rate of change of log probability of the data between successive values of K (ΔK) [Evanno et al. 2005] for grizzly bears in Banff National Park, Alberta, Canada.



Appendix E: Mitigating Highways for a Ghost: Data Collection Challenges and Implications for Managing Wolverines and Transportation Corridor (Article)

Northwest Science Notes

The purpose of Notes is to publish papers typically less than five pages long. No specific format or content is required for articles published as Notes, but all will be peer-reviewed and must be scientifically credible. Authors may contact the Editor about the suitability of manuscripts for this section.

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Mitigating Highways for a Ghost: Data Collection Challenges and Implications for Managing Wolverines and Transportation Corridor

Abstract

Research provides transportation agencies with evidence-based data to guide the planning and design of crossing structures that effectively link critical habitats and populations. To date, research has focused on a range of mammal species. However, for rare-occurring, wide-ranging species such as wolverines (*Gulo gulo*), collecting the required information can be challenging. Highway crossing structures have been recommended as a conservation strategy for wolverines in the northern U.S. Rocky Mountains. However, there is virtually no information describing wolverine response to crossing mitigation. I describe 15 years of continuous year-round monitoring (1996-2012) of wolverine response to highway mitigation in Banff National Park, Alberta. Crossing structures were monitored using track pads and cameras. Wolverines were detected using crossing structures 10 times. Nine crossings occurred at wildlife underpasses and one at a wildlife overpass. The first detected passage occurred in 2005. Three crossings were recorded during the same crossing check in 2010 and 2011, suggesting use by the same individual of the structures. Few conclusions can be drawn regarding the attributes of crossing structures that facilitate passage of wolverines. Given the scarcity of crossing structures within wolverine range, it will be difficult to collect sufficient information in the short term for this rare and elusive species. Given the proposal to list wolverines under the Endangered Species Act, transportation departments and land managers should begin proactively identifying critical habitat linkages across highways in wolverine range and opportunities for highway mitigation in the short and long term.

Keywords: Banff National Park, *Gulo gulo*, roads, wildlife crossing structures, wolverine

Introduction

Ecological connectivity at a landscape scale is becoming increasingly important in the face of a changing climate (Heller and Zavaleta 2009). Local-scale corridors such as wildlife crossing structures may play an important role in allowing animals to adapt and respond to a warming climate. Research that identifies important attributes of wildlife crossing structures (underpasses and overpasses) that facilitate connectivity and dispersal for key fragmentation-sensitive species is needed to ensure local-scale habitat linkages will be able to mitigate continental-scale bottlenecks (Crooks and Sanjayan 2006, Clevenger 2012).

Monitoring and research provides transportation agencies with evidence-based data to guide the planning and design of crossing structures that effectively link critical habitats and populations (Clevenger and Huijser 2011, Gagnon et al. 2011, Van Manen et al. 2012). To date, research has focused on a range of migratory and non-migratory mammals in different landscapes and biomes including Florida panthers (*Felis concolor*

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coryi, Jansen et al. 2010), bobcats (*Lynx rufus*, Cain et al. 2003), cougars (*F. concolor*, Beier 1995), moose (*Alces alces*, Olsson and Widen 2008), bears (*Ursus* sp.; Clevenger and Wierzchowski 2006, Lewis et al. 2011, Van Manen et al. 2012) elk (*Cervus elaphus*, Gagnon et al. 2011) and others (Van Wieren and Worm 2001, Bond and Jones 2008). However, for rare-occurring, wide-ranging species, collecting the required information with sufficient sample sizes to draw inference-based conclusions can be exceptionally difficult and time-consuming.

Wolverines (*Gulo gulo*) naturally occur in low numbers and have some of the lowest rates of reproduction of any terrestrial mammal species (Banci and Harestad 1990, Inman et al. 2012). Because of their low-densities and association with rugged and remote habitats (Copeland et al. 2007, Krebs et al. 2007), obtaining information on wolverine occurrence and ecological requisites has proved challenging (Ruggiero et al. 2007). Wolverines are becoming recognized as genuine indicators of healthy, connected ecosystems due to their sensitivity to human disturbance and needs for large areas and intact habitats. (Schwartz et al. 2009, Copeland et al. 2010). Further, in February 2013, the U.S. Fish and Wildlife Service proposed to list wolverines in the contiguous United States as threatened (U.S. Fish and Wildlife Service 2013).

Highway expansion projects are occurring at a rapid pace within wolverine range in the northern U.S. Rocky Mountains. Similarly, road and highway upgrades are planned for energy development activities within their range in Alberta and British Columbia (Province of British Columbia 2011, Government of Alberta 2012). Highway crossing structures have been identified as one of three recommended conservation strategies for the future conservation of the wolverine metapopulation in the northern U.S. Rocky Mountains (Inman 2013). I am not aware of published literature (peer-reviewed or grey) anywhere in the world describing wolverine response to highway mitigation measures, such as wildlife crossing structures and fencing.

There are at least two reasons for the dearth of information. First, although wildlife crossing structures are becoming more common on North American highways, not all are systematically monitored for wildlife use. Monitoring is rarely conducted for more than 1-2 years; thus, sufficient time scales for wolverine use to occur haven been inadequate. Second, within wolverine range there are very few highways with wildlife crossing structures, and only one is located in core wolverine habitat as defined by persistent snow pack modeling (Copeland et al. 2010, McKelvey et al. 2011). Given the species low density and tendency to avoid transportation infrastructure (Austin 1998, Copeland 1996, Packila et al. 2007), collecting information on wolverine use of crossing structures now or in the future will be challenging at best and inevitably result in extremely small samples sizes. The Trans-Canada Highway (TCH) in Banff National Park (BNP), Alberta is one of the few places in the world today where wolverines may be detected using wildlife crossing structures.

Understanding how highways affect wolverine dispersal and means of successfully mitigating road impacts will be a critical part of local and continental scale conservation strategies (Clevenger 2012). Information on wolverine use of crossing structures, albeit sparse, will be of value to transportation and natural resource agency decision makers responsible for mitigating transportation projects within wolverine range today and in the future. My purpose of this paper is to describe long-term, year-round monitoring of wolverine response to highway mitigation measures (crossing structures and fencing) in a critical fracture zone where maintaining highway permeability is a conservation concern (Weaver et al. 1996).

Study Area

The TCH in the Canadian Rocky Mountains has long been recognized as a lethal barrier to wildlife and a potential bottleneck for population connectivity at local and trans-boundary scales (Weaver et al. 1996, Proctor et al. 2012). Over 30 years ago, safety and logistical considerations compelled planners to upgrade the TCH within BNP from two to four lanes (i.e., twinning), beginning from the eastern boundary of the park and working west (Clevenger and Waltho 2005).

In each phase, large mammals were excluded from the road with a 2.4-m-high fence erected on both sides of the highway. Underpasses were also built to allow wildlife to cross the road. The first 27 km of highway twinning included 11 wildlife underpasses and was completed by 1988 (Figure 1). The next 18 km section was completed in late 1997 with 10 additional wildlife underpasses and 2 wildlife overpasses (Ford et al. 2010). The final 38 km of twinning to the western park boundary at the

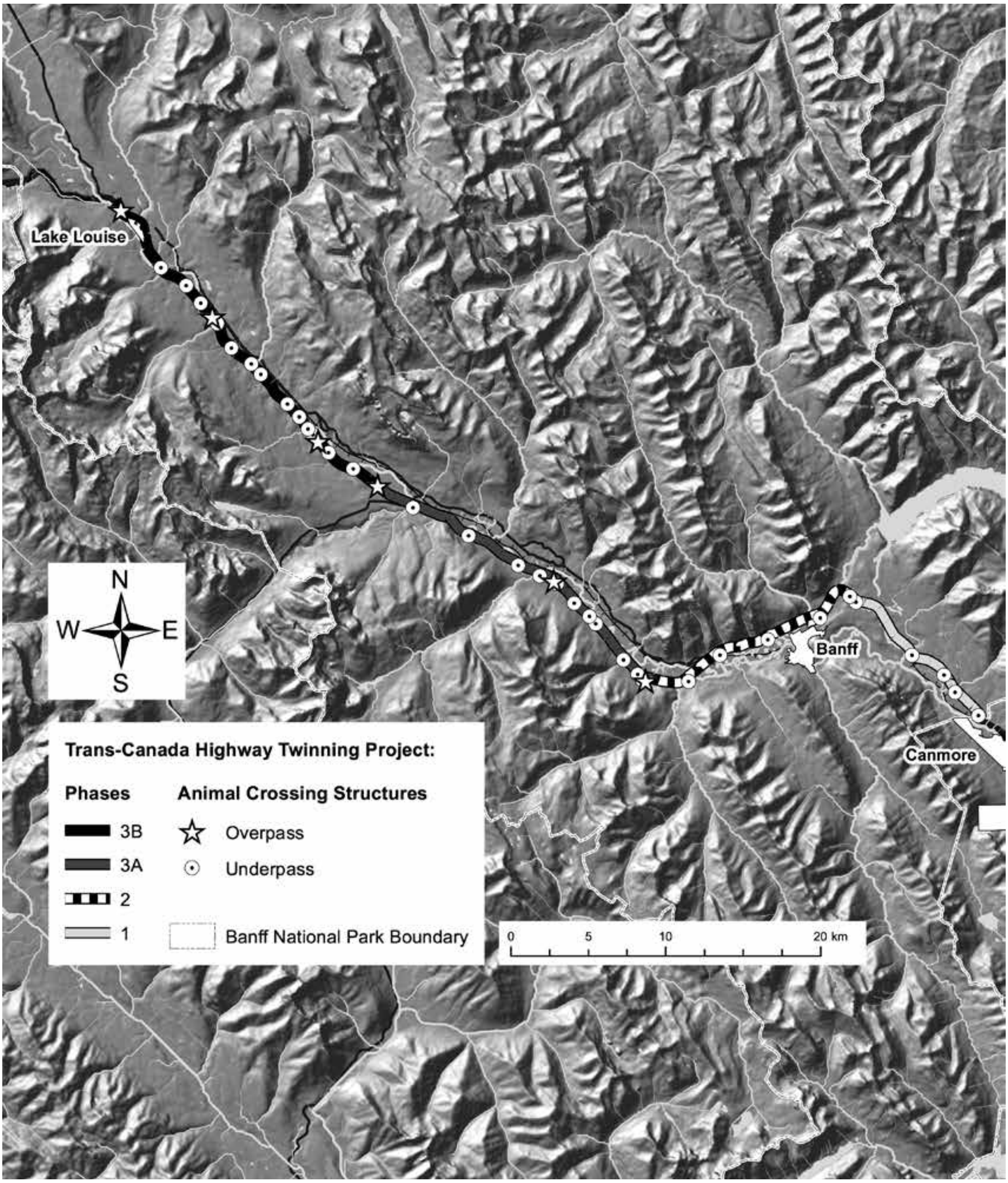

Figure 1. Wildlife crossing structures and their respective highway twinning phases along the Trans-Canada Highway in Banff National Park, Alberta.

Continental Divide and British Columbia-Alberta border will be completed in 2013 and consist of 21 additional wildlife crossing structures, including four 60-m wide wildlife overpasses.

BNP is unrivalled in terms of the number and diversity of wildlife crossing structures and associated biological data on wildlife distribution, movement and ecology. Eleven species of large mammals have been detected using the crossing structures more than 130,000 times during more than 15 years of systematic year-round monitoring (Clevenger et al. 2012). Mitigation efforts during the last 25 years have helped restore habitat connectivity across large sections of this major transportation corridor. The measures have been effective at reducing highway-related mortality of large mammals (Clevenger et al. 2001), contributing to dispersal and gene flow among grizzly (*U. arctos*) and black bears (*U. americanus*; Sawaya et al. [*in press*]) and provided evidence-based guidelines for future crossing structure designs in BNP and elsewhere (Clevenger and Waltho 2005; Clevenger and Huijser 2011).

Methods

Systematic year-round monitoring of the BNP crossing structures began in November 1996 (Clevenger and Waltho 2005). Monitoring consisted of checking the crossing structures and recording animal movement across raked track pads. Track pads spanned the width of the wildlife underpasses, were generally ≈2 m wide, and were set perpendicular to the direction of animal movement. At wildlife overpasses a single, 4-m-wide track pad was set across the center and motion-sensitive cameras were used to supplement track pad data. Tracking material consisted of a dry, loamy mixture of sand, silt and clay, 1-4 cm deep. Each crossing structure was visited every two to four days throughout the year. Observers identified tracks to species, estimated the number of individuals, their direction of travel (northbound or southbound across the TCH) and whether they moved through the crossing structure. Since 2005, motion-sensitive cameras were increasingly used to supplement track pads to monitor species use of the crossing structures (Ford et al. 2009). These cameras (Reconyx Inc., Holmen, Wisconsin) also provide information on time, animal behavior, and ambient temperature during each crossing event. Information on wolverine road-related mortalities and fence intrusions within the study area were collected opportunistically during the study period and with the help of the Parks Canada staff.

Results

Wolverines have been detected using the BNP crossing structures 10 times in the last 15 years. Nine of the recorded crossings occurred at wildlife underpasses, while one occurred at a wildlife overpass (Table 1). The first recorded passages (n=3) were detected during one monitoring check on 23 December 2005 at the Redearth Creek underpass (northbound and southbound) and Copper underpass (northbound). Three years later the fourth crossing was detected on 25 April 2008 at the Wolverine Creek underpass (southbound). In 2010, three wolverine crossings were

TABLE 1. Attributes of crossing structures where wolverines have been detected crossing the Trans-Canada Highway, Banff National Park, Alberta. All structures span four lanes of highway.

Crossing structure	Location-Km #	Design	Dimensions (width x height)	Number of detections
Wolverine overpass	27	Overpass	50-m wide	1
Wolverine Creek	29	Creek bridge underpass	11 m x 2.5 m	2
Pilot	34	Box culvert underpass	3.0 m x 2.4 m	1
Redearth Creek	37	Creek bridge underpass	11.4 m x 2.2 m	2
Copper	39	Elliptical culvert underpass	7.0 m x 4.0 m	1
Johnston	42	Box culvert underpass	2.4 m x 3.0 m	1
Castle	44	Elliptical culvert underpass	7.0 m x 4.0 m	1
Moraine Creek	64	Creek bridge underpass	16.0 m x 2.0 m	1

observed during one monitoring check (12 April) at Wolverine Creek underpass (southbound), Pilot underpass (northbound) and Johnston underpass (southbound; Figure 1). Three crossings were detected in 2011: 16 February at Castle underpass (northbound), 25 February at Moraine Creek underpass (southbound) and 16 November at Wolverine Overpass (northbound).

Parks Canada records of wildlife mortalities indicate that since 1980, five wolverines have died on highways in Banff and Kootenay National Parks; two adult males on the unmitigated TCH (1988, 1989), a subadult female near Marble Canyon (2012) and one of unknown gender and age on Highway 93 South near Vermilion Pass (1981). There have been four known incidents where wolverines have been documented climbing the TCH fence to cross or access the TCH right-of-way (three in 2011, one in 2012). All of the intrusions have occurred within 700 m of the nearest crossing structure.

Discussion

Of the 10 detected passages so far, we are unable to identify the number of individuals and gender of wolverines using the TCH crossing structures. The two monitoring checks (23 December 2005, 12 April 2010) where three passages were detected at the crossing structures suggest these were likely made by the same individual moving back and forth across the TCH. The tracks appeared to be the same age and moved in alternating directions through the structures.

The majority of 15+ years of monitoring occurred on the first 45 km of TCH (Phase 1, 2, 3A, Figure 1). Unlike the final 38-km section located near the Continental Divide (Phase 3B, Figure 1), this section lies in low-elevation montane habitat not previously considered optimal wolverine habitat according to the BNP ecological land classification map (Holryod and Van Tighem 1983). This map was created in the 1970s and was based on anecdotal data and what little was known about wolverine habitat at that time. Wolverines have been detected on both sides of the TCH, and relatively close to it, as part of a park-wide noninvasive wolverine survey from 2010-2013 (A. Clevenger, unpublished data).

These survey and crossing data suggest that wolverines avoid or seldom use wildlife crossing structures (possibly at random). Low use up until now may be attributed to avoidance of the TCH corridor or potential interactions with wolf packs occupying the Bow Valley (Inman et al. 2012). Future monitoring of the Phase 3B crossing structures will provide needed clarity on whether wolverines will use crossing structures and the effects of habitat and interspecific interactions.

Despite the small sample size we present after 15 years of Banff research, we are acutely aware of their limitations but also their uniqueness and value for practitioners and decision makers charged with highway mitigation schemes in wolverine range. The TCH has been mitigated in successive phases from 1982 to present. During that time there have been no wolverine mortalities on the mitigated highway, although two reported mortalities occurred in 1988 and 1997 while it was unfenced and unmitigated. Fencing does not preclude animals from occasionally climbing the highway fence (Clevenger et al. 2001). There have been four known incidents where wolverines were documented climbing the TCH fence to cross or access the TCH right-of-way. The relatively low incidence of mortality and fence-climbing may in part be due to their aversion to roads and highway corridors. Ongoing research in Banff, Yoho, and Kootenay National Parks will help to better understand the population-level effects of the TCH on wolverine dispersal, population genetics, and landscape connectivity (A. Clevenger, unpublished data).

As the construction of TCH crossing structures proceeds further west and ultimately into Yoho National Park, British Columbia, it enters subalpine habitats and will become the first attempt ever in North America to introduce highway mitigation at the Continental Divide, in core wolverine habitat according to snow persistence models (Copeland et al. 2010). This high-elevation ecosystem is doubly important given it is acutely affected by a warming climate and its north-south axis is bisected by east-west transportation corridors here and in other parts of the Rocky Mountain cordillera in Canada and the United States (Graumlich and Francis 2010). The need for this information is particularly critical given current highway expansion plans in wolverine habitat in the northern U.S. Rocky Mountains.

From the relatively sparse data we have collected over 15 years, we are unable to draw any sound conclusions or even analyze generally the attributes that facilitate passage of wolverines, as we have done for other large mammals previously (Clevenger and Waltho 2005). We may never have sufficient data from BNP alone to conduct a robust analysis, and it is unlikely that other study areas will be available in the near future. The difficulty lies in finding highway study sites within wolverine range having crossing structures and being monitored over sufficient time periods to collect robust sample sizes. Given the difficulties of securing data on wolverine response to crossing structures, a meta-analysis using data collected from multiple highway monitoring sites within wolverine range will likely best provide information to identify crossing structure needs for this rare and elusive species.

The current lack of information and urgency for information is of increasing concern, given the 2013 proposed listing under the Endangered Species Act (ESA; U.S. Fish and Wildlife Service 2013) and the possible reintroduction to Colorado (R. Inman, Wildlife Conservation Society, personal communication). Should wolverines become listed under the ESA and/or reintroduced into Colorado, transportation departments will be required to mitigate their projects for wolverine movement. Maintaining wolverine populations in the largest remaining areas of contiguous habitat in the southern portion of their range and facilitating connectivity among habitat patches is a recommended conservation measure to help sustain a viable wolverine population in the U.S. (McKelvey et al. 2011). Transportation departments and land managers should begin proactively identifying critical dispersal corridors across highways in the remaining areas of contiguous habitat, adjacent land securement issues and any potential opportunities for highway mitigation in the short and long term.

Acknowledgements

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