

From: [Inman, Bob](#)
To: [Grizzle, Betty](#)
Subject: RE: Additional road crossing studies?
Date: Monday, June 19, 2017 10:51:20 AM
Attachments: [2014 Clevanger Wolverine Chapters.pdf](#)

Hello Betty,

I am not aware of other road crossing studies with the exception of the genetic based stuff from Canada that is attached. I thought I saw a published paper on this but don't have such in my files. Tony Clevenger's email is apclevenger@gmail.com. There were definitely some genetic lab analysis issues identified as part of this work, and I believe that came to surface after this report was written. So it would be essential to ask Tony what that was and how it might have affected the info in the report.

Hope you are well.

-Bob Inman

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From: Grizzle, Betty [mailto:betty_grizzle@fws.gov]
Sent: Friday, June 16, 2017 10:35 AM
To: Inman, Bob <bobinman@mt.gov>
Subject: Additional road crossing studies?

Hi Bob - I am reviewing your peer review comments and the Packila et al. 2007 paper. Do you know if additional studies have been conducted regarding road crossings or road crossing mortalities?
Thanks.

FYI - I believe a few Regional Office Staff (Region 6) will be attending the WAFWA meeting in July, perhaps others from our Headquarters office, not sure about Region 1.

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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 km² 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, F_{st} , 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.

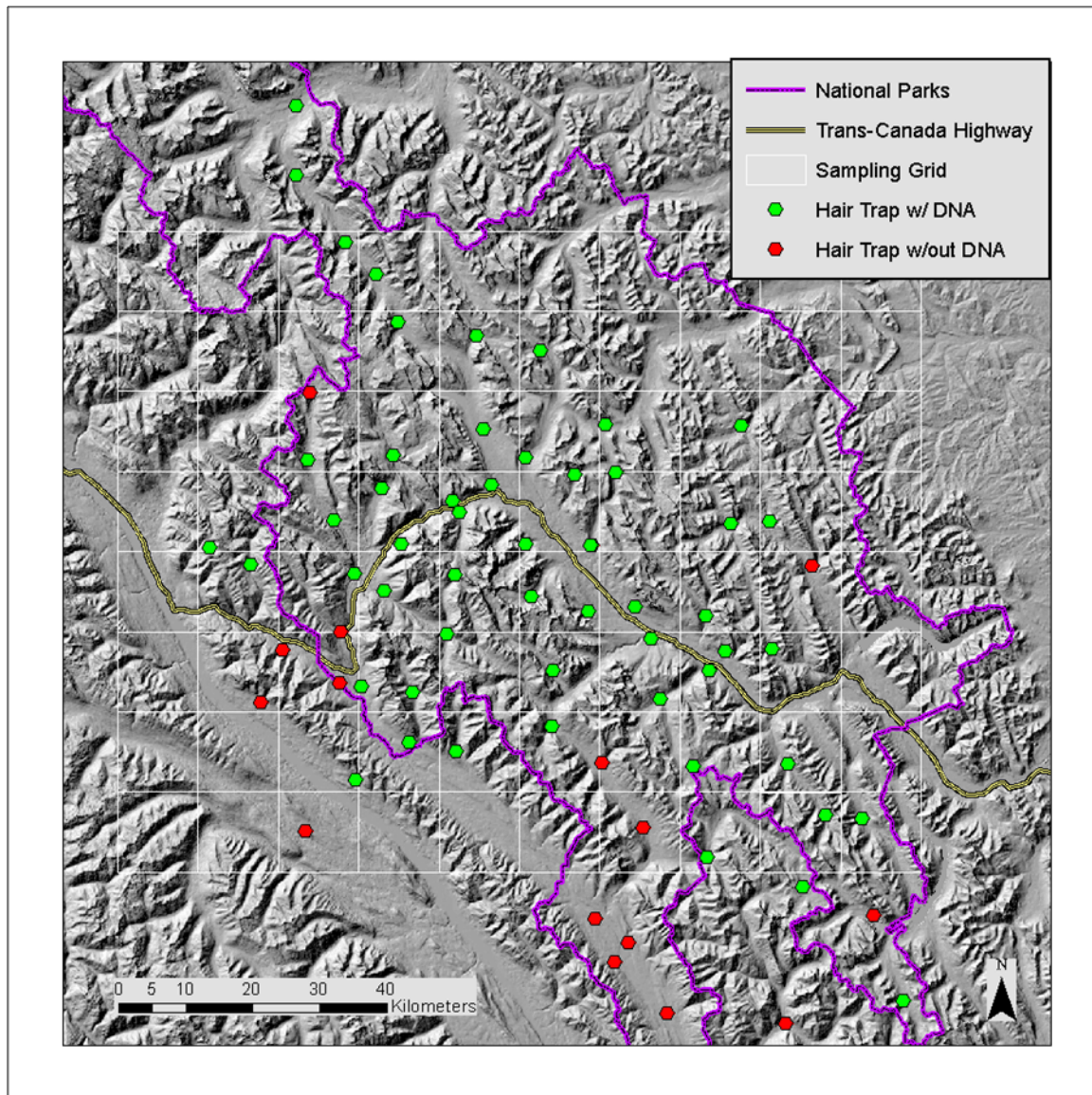


Figure 1: Wolverine hair trap success in parks complex between 2011 and 2013.

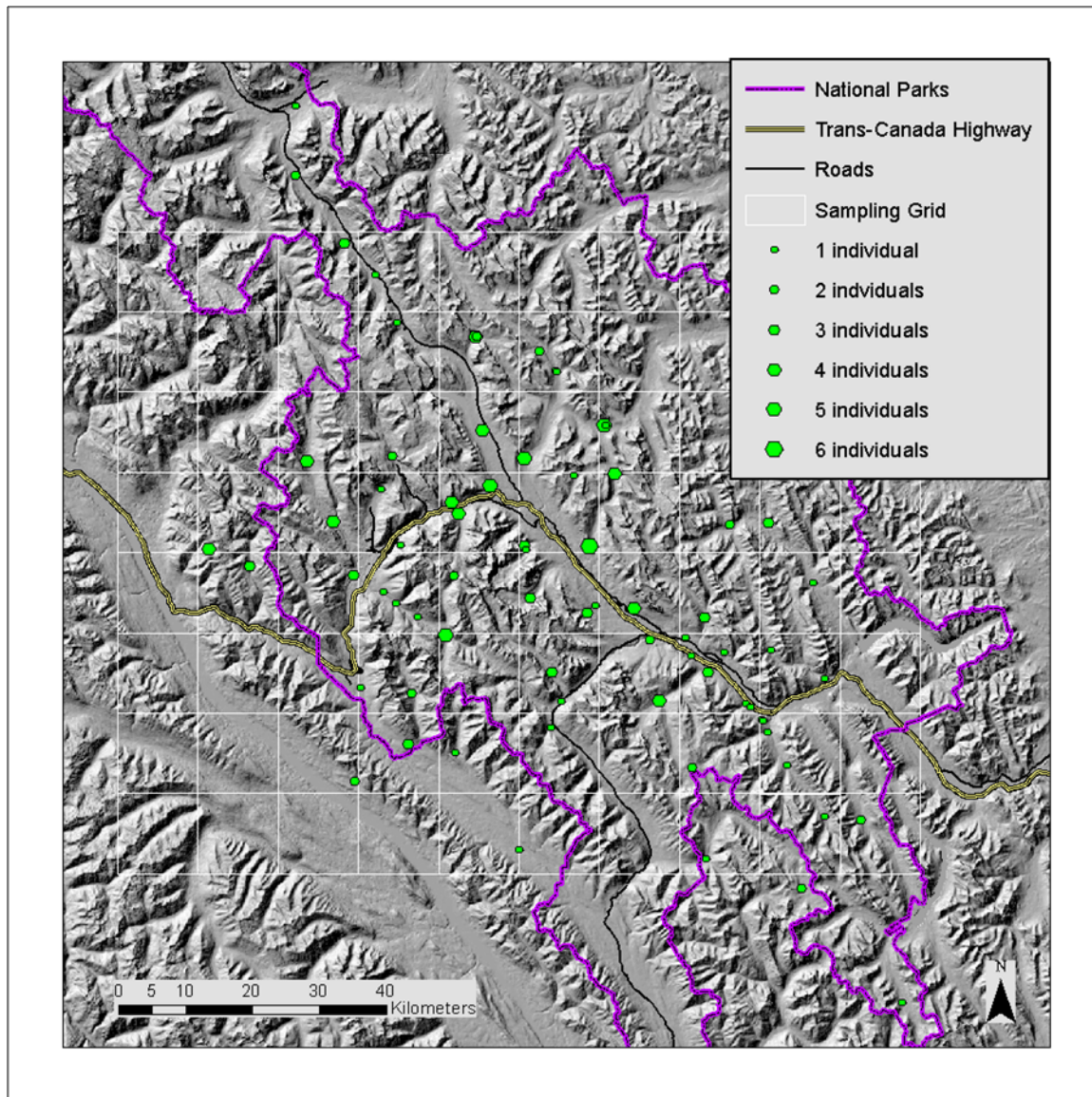


Figure 2: Number of unique wolverines detected at each sampling site in parks complex between 2011 and 2013.

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).

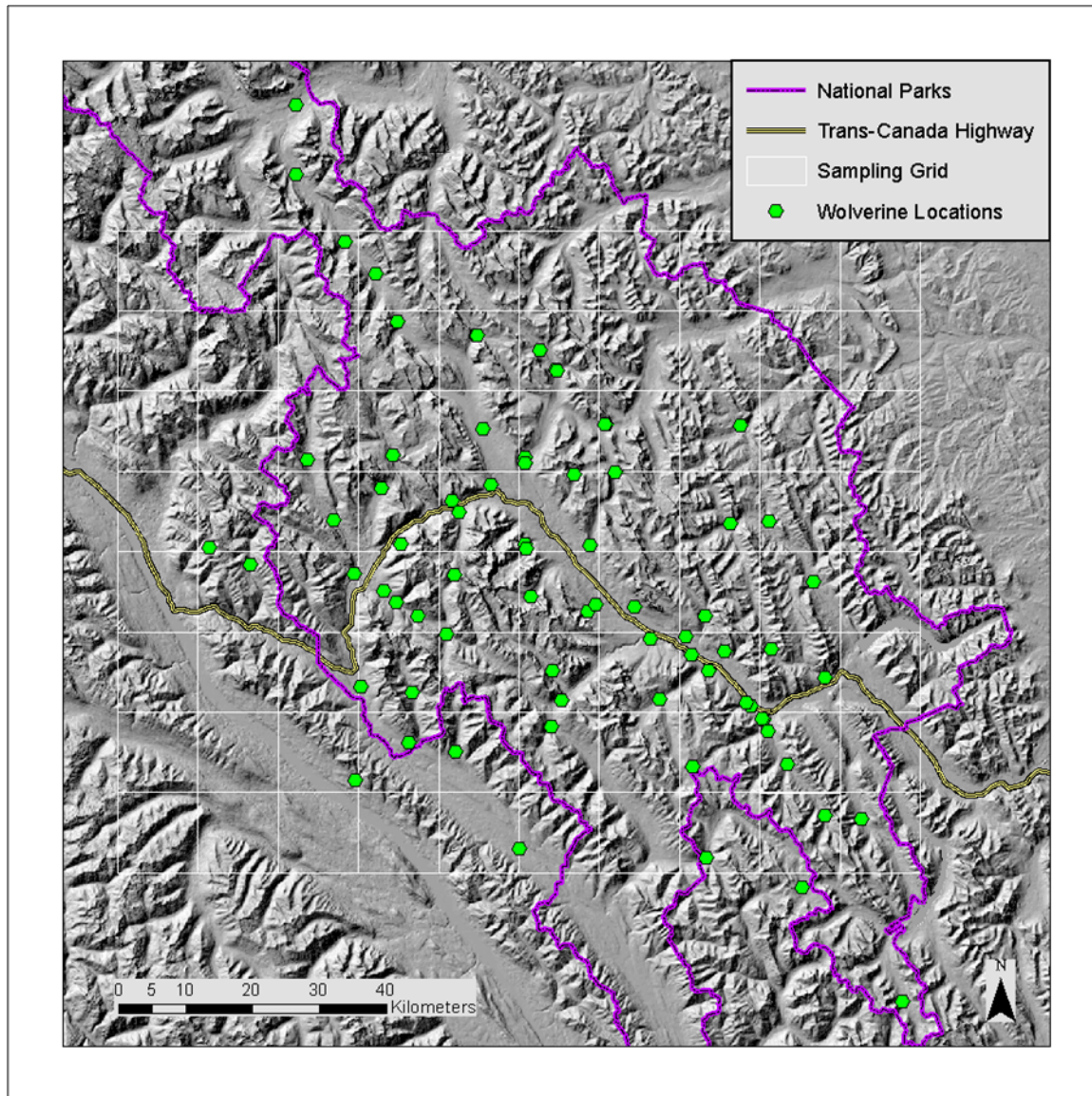


Figure 3: Locations of 229 wolverine detections in parks complex between 2011 and 2013.

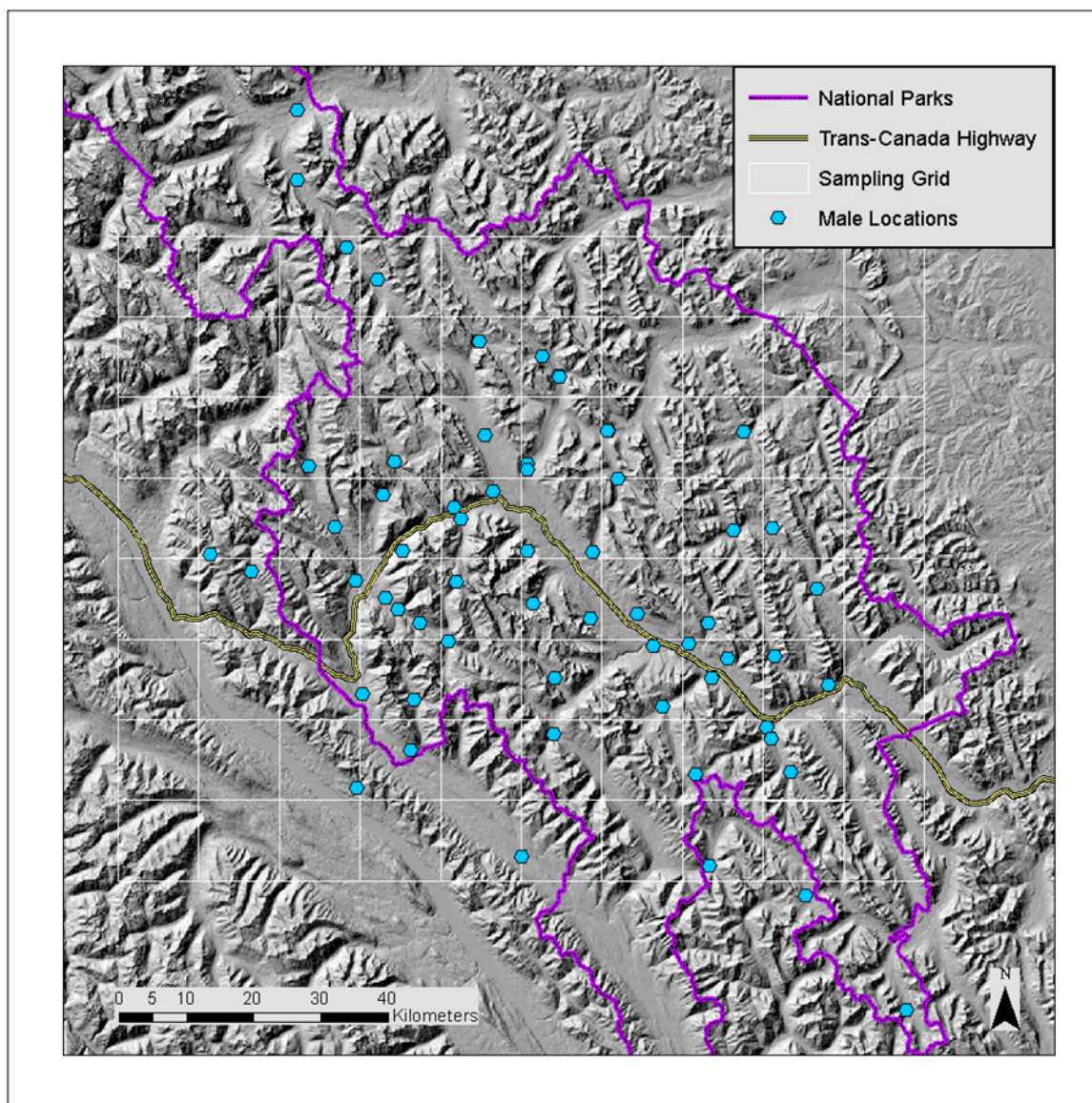


Figure 4: Locations of 155 male wolverine detections in parks complex between 2011 and 2013.

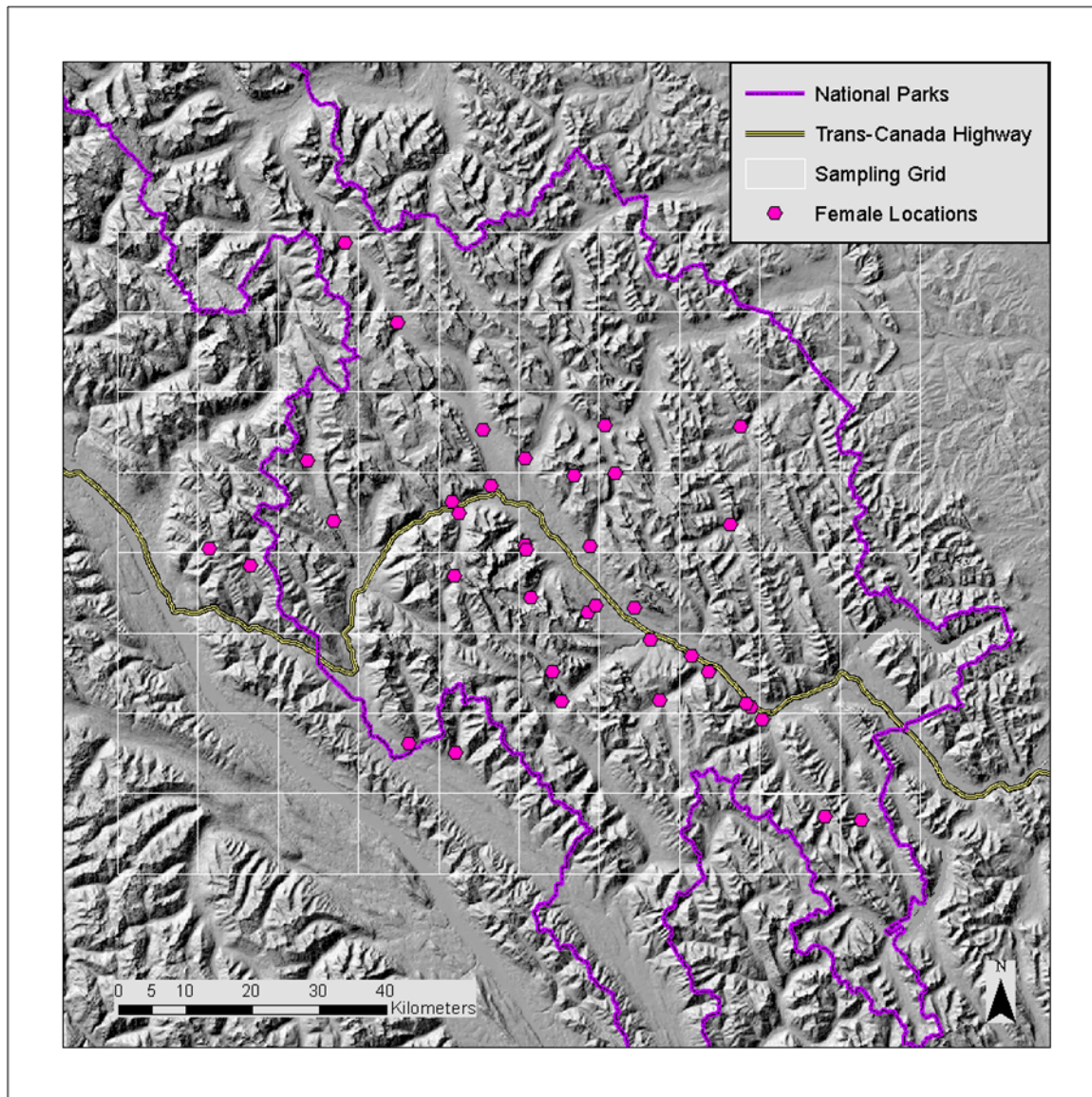


Figure 5: Locations of 74 female wolverine detections in parks complex between 2011 and 2013.

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 F_{st} for the total population of 64 individuals ($F_{st}=0.32$) and for each sex separately (female $F_{st}=0.70$, male $F_{st}=0.25$). 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 Mo36 had an unusual genotype within the dataset (Figure 6 and 8).

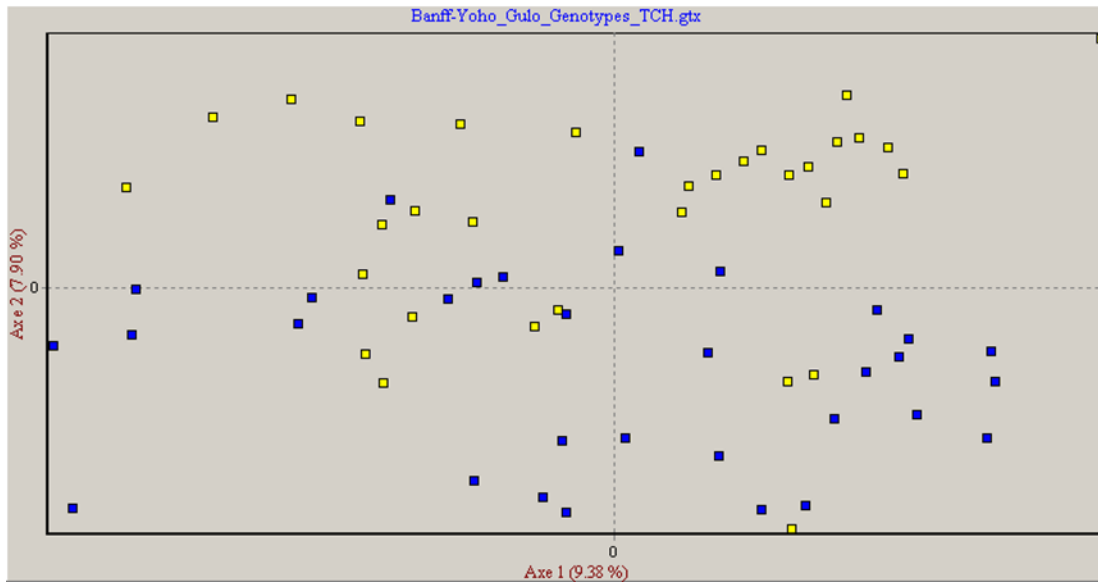


Figure 6: Factorial Correspondence Analysis plot showing 64 wolverines detected to the north (yellow) or south (blue) of the Trans-Canada Highway in the parks complex between 2011 and 2013. Mo36 is located in far lower left portion of graph.

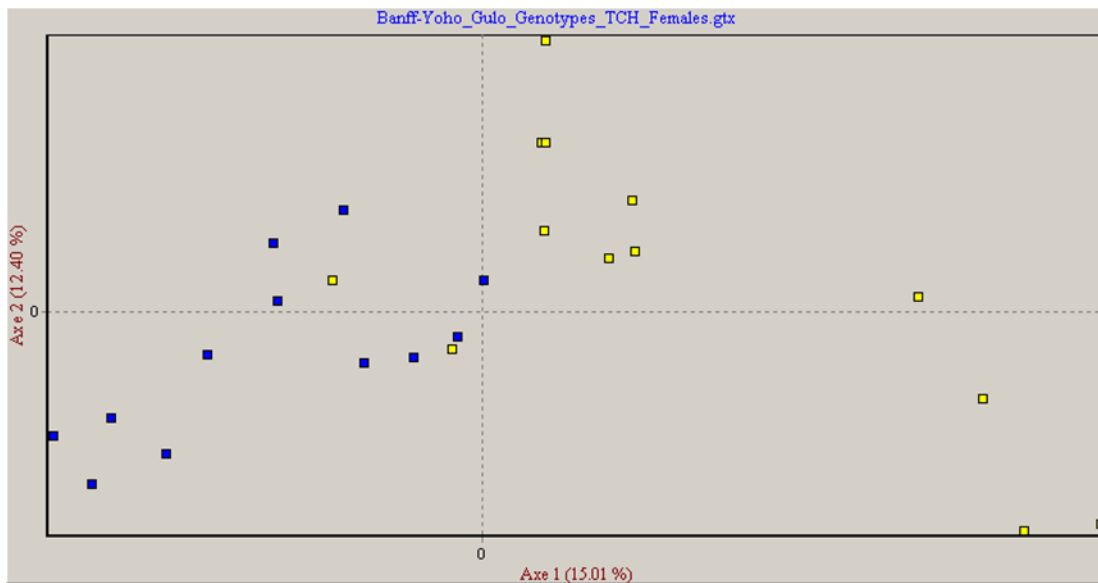


Figure 7: Factorial Correspondence Analysis plot showing 25 female wolverines detected to the north (yellow) or south (blue) of the Trans-Canada Highway in the parks complex between 2011 and 2013.

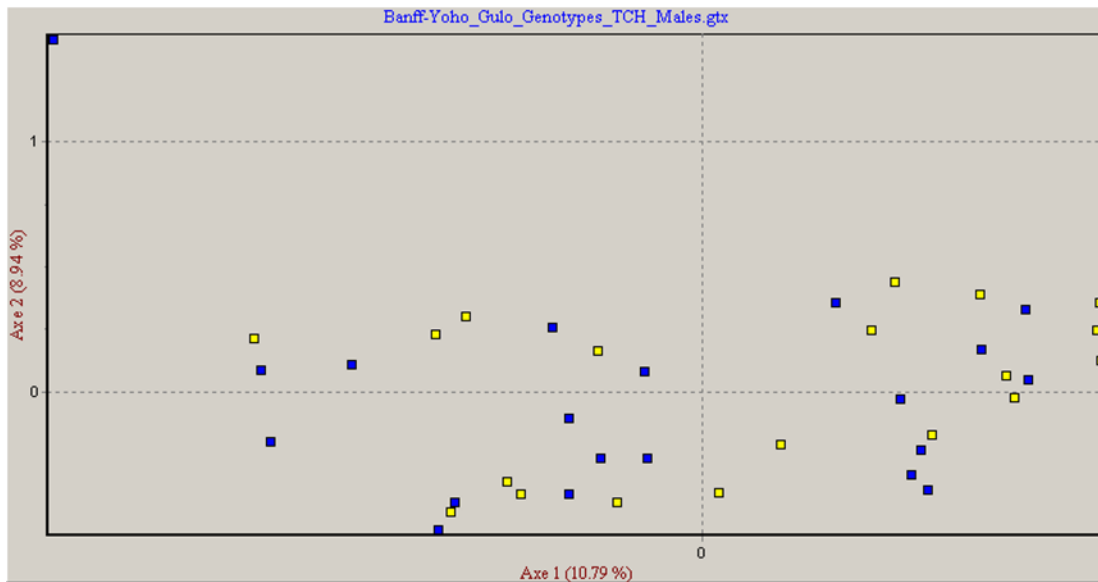


Figure 8: Factorial Correspondence Analysis plot showing 39 male wolverines detected to the north (yellow) or south (blue) of the Trans-Canada Highway in the parks complex between 2011 and 2013. Mo36 is located in far upper left portion of graph.

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).

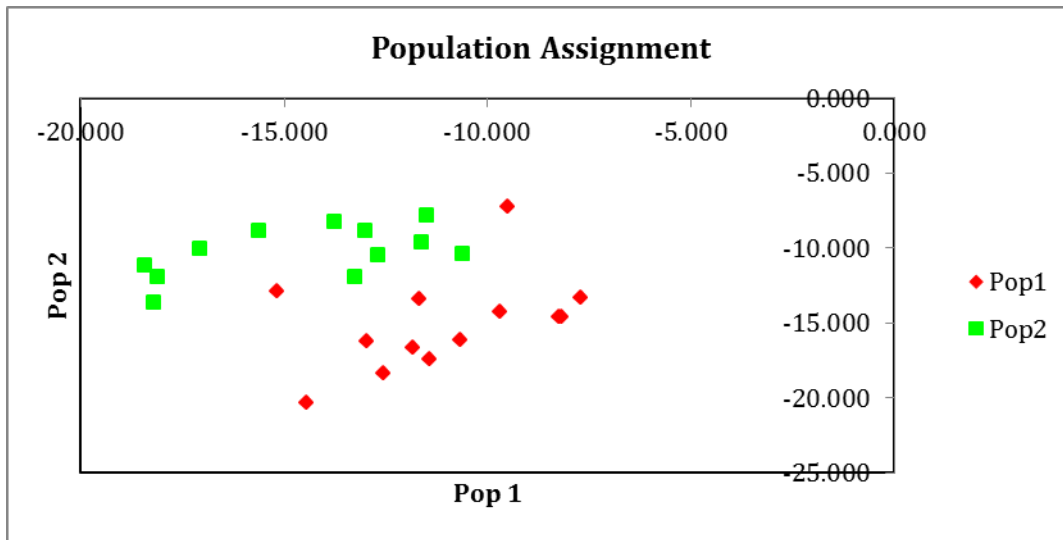


Figure 9 Population assignment graph showing 25 female wolverines detected to the north (red) or south (green) of the Trans-Canada Highway in the parks complex between 2011 and 2013.

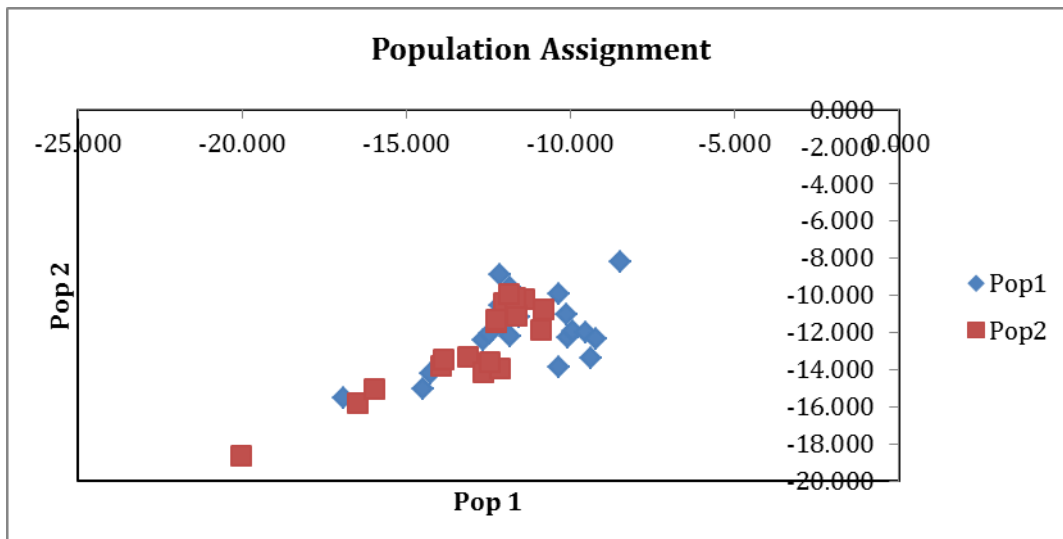


Figure 10: Population assignment graph showing 39 male wolverines detected to the north (blue) or south (red) of the Trans-Canada Highway in the parks complex between 2011 and 2013.

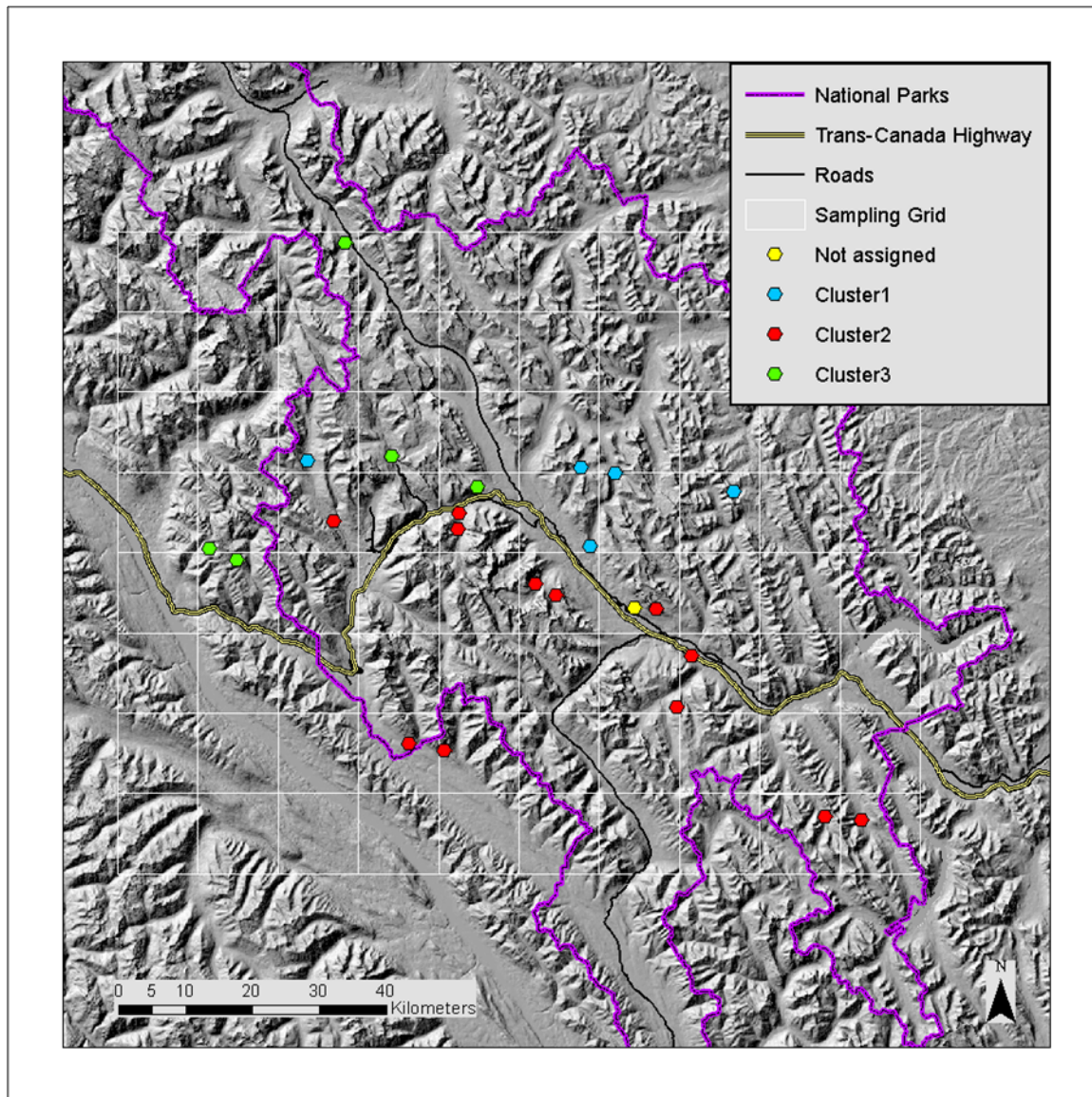


Figure 11: Individual detection centers of 25 female wolverines color-coded by their assignment to one of three population clusters identified in program STRUcTURE to examine the effect of the Trans-Canada Highway on fine-scale genetic differentiation in the parks complex between 2011 and 2013. Individuals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

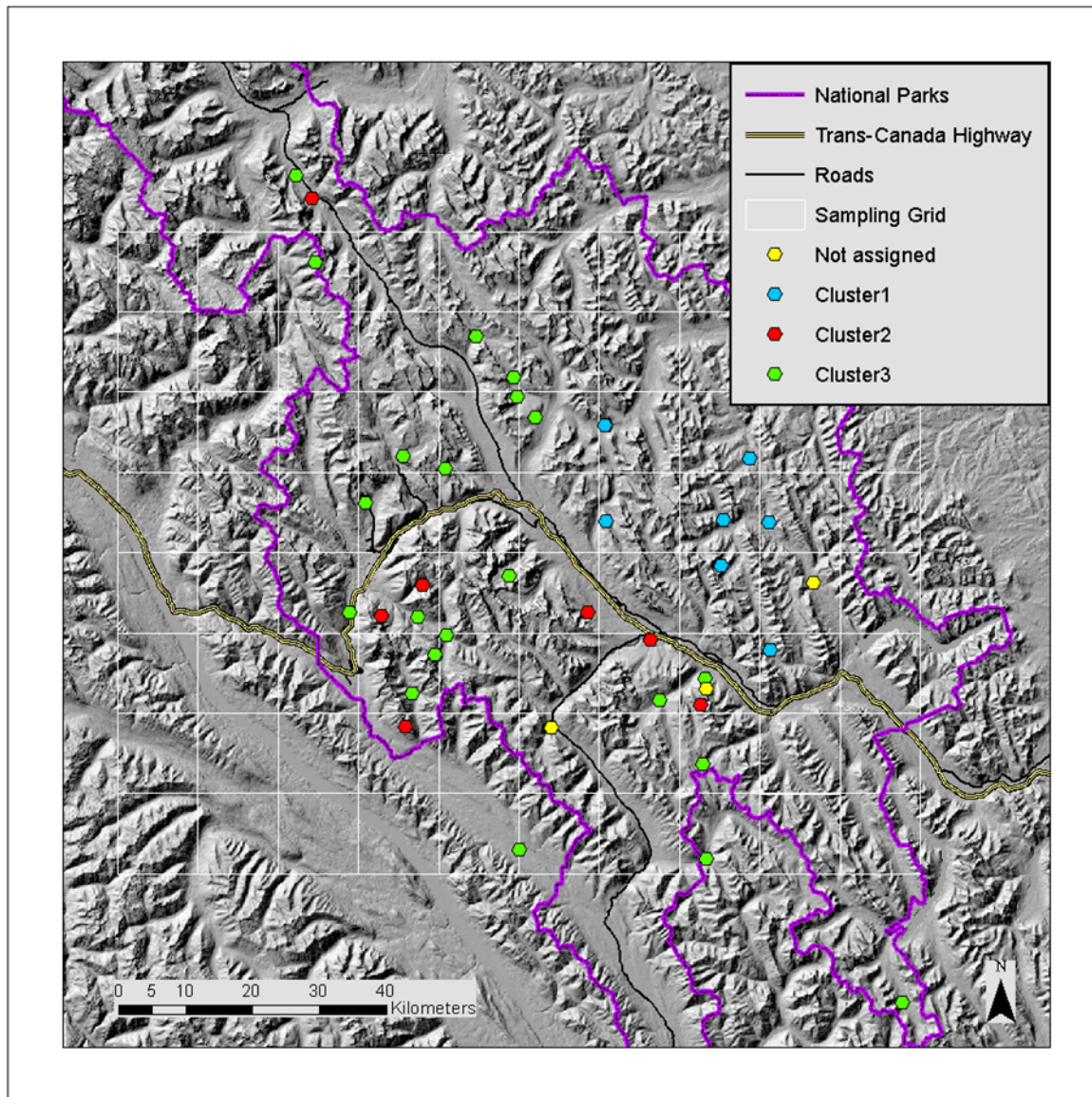


Figure12: Individual detection centers of 39 male wolverines color-coded by their assignment to one of three population clusters identified in program STRUCTURE to examine the effect of the Trans-Canada Highway on fine-scale genetic differentiation in the parks complex between 2011 and 2013. Individuals with $q\text{-value} < 0.7$, 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.

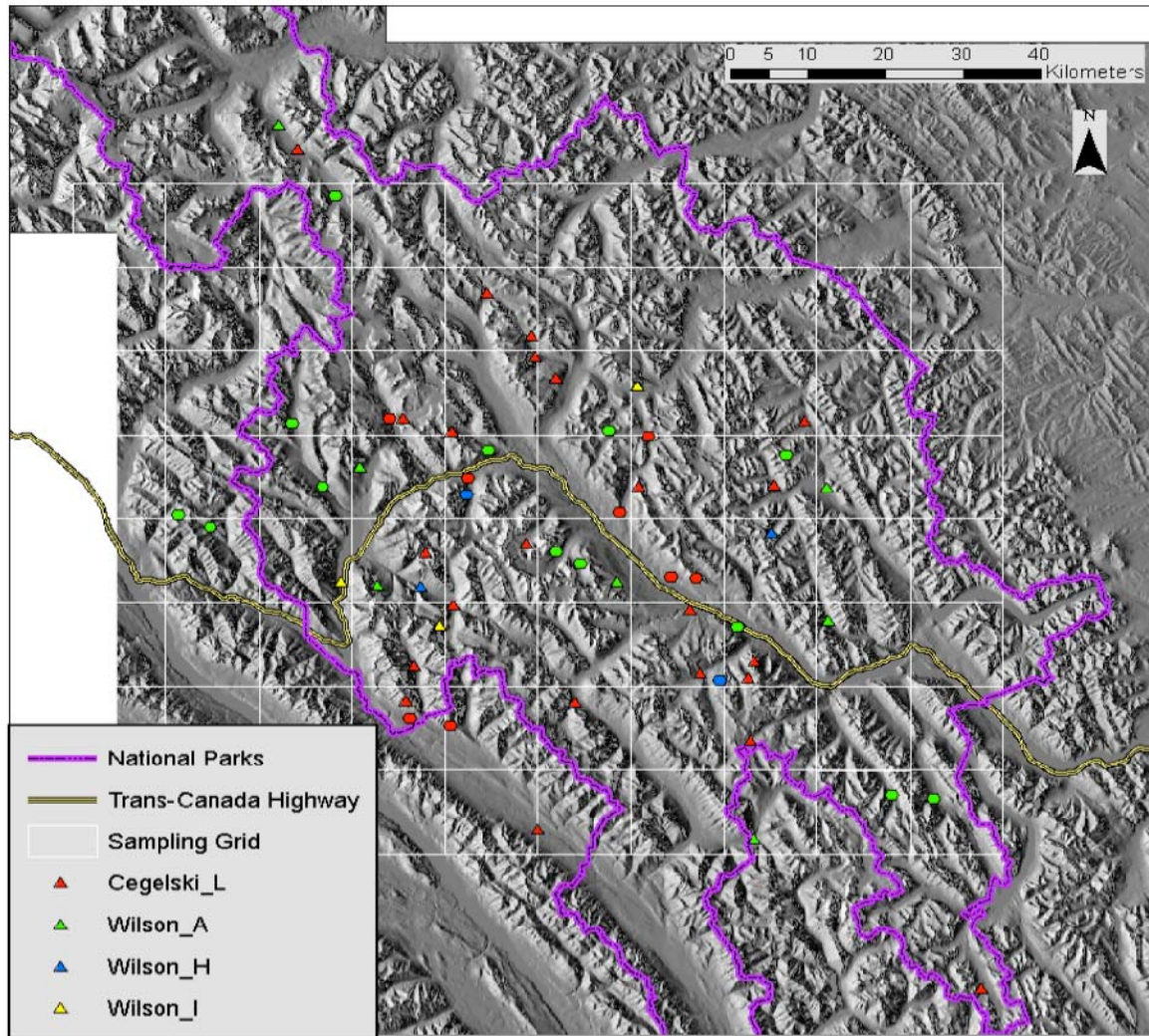


Figure 13: Individual detection centers of 64 wolverines with Mo36 color-coded blue to highlight his location in relation to other wolverines detected with noninvasive genetic sampling to examine the effect of the Trans-Canada Highway on fine-scale genetic differentiation in the parks complex between 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).

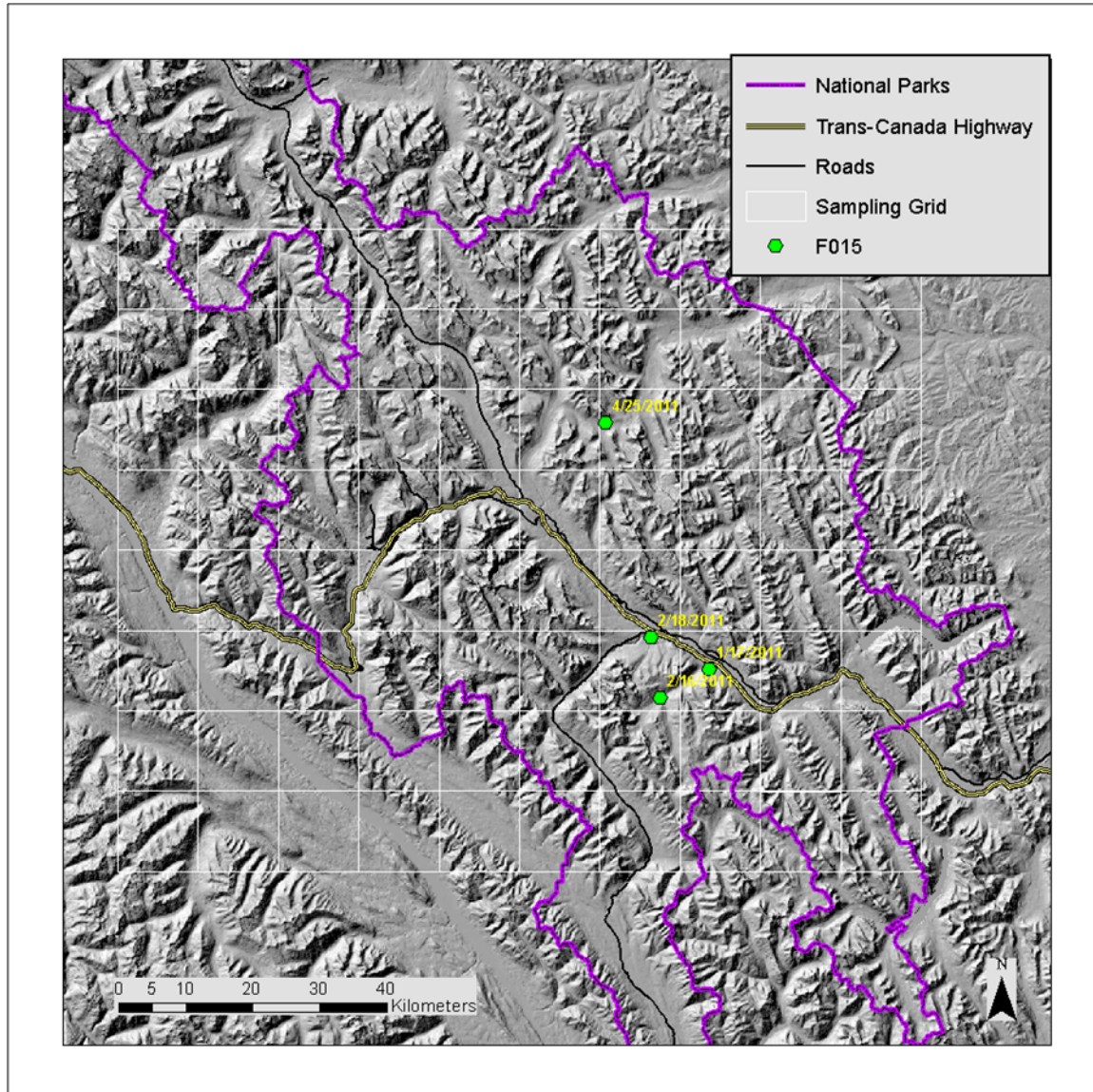


Figure 14: Pooled DNA-based detection locations with dates of sample collection for wolverine F015 that span the Trans-Canada Highway in the parks complex between 2011 and 2013.

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. F_{st}) 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 is 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 sample 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 km² 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).

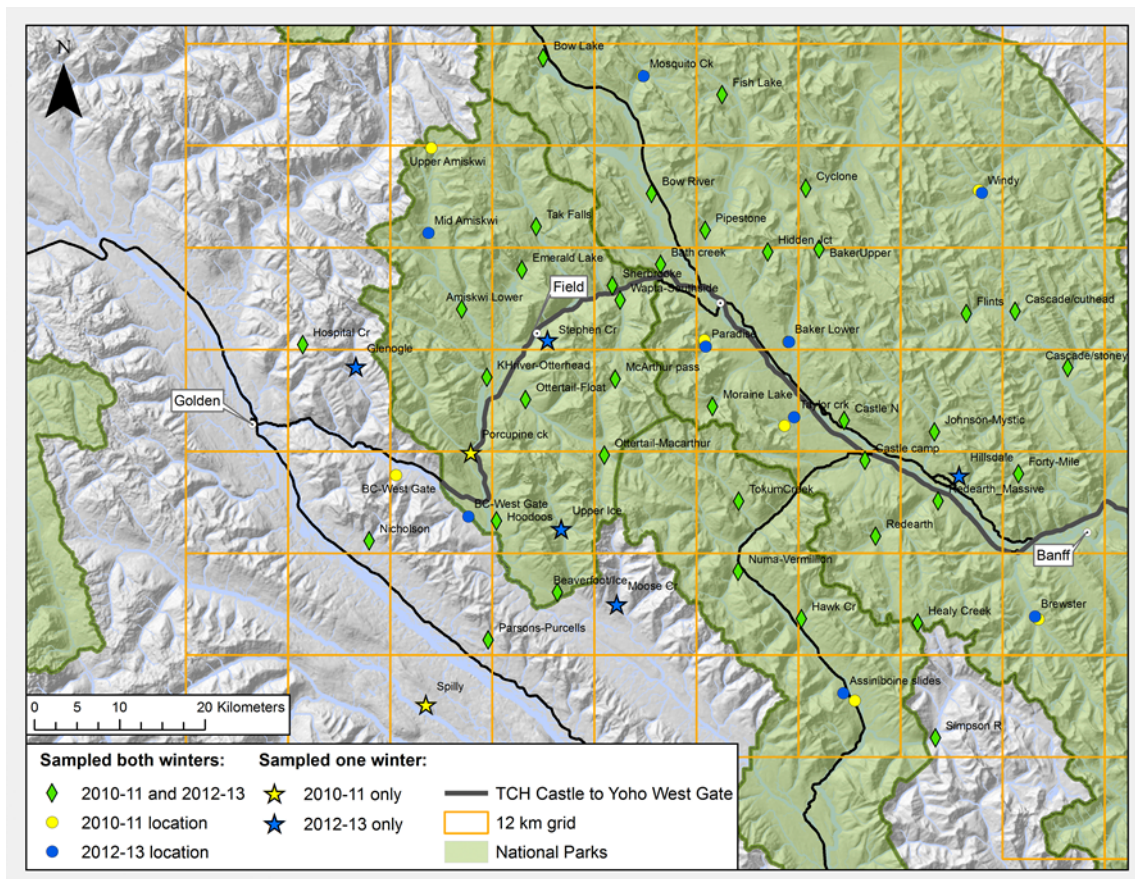


Figure 1. Map of study area in the Canadian Rocky Mountains centered on the Trans-Canada Highway with 12 x 12 km grid overlay. The area is bounded by Banff in the east, Bow Summit in the north, Golden, BC in the west, and Simpson River (Kootenay National Park) in the south. The study area encompasses 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 ($\cdot$). All other variables were held constant.

Model	AIC	Δ AIC	AIC weight	Model Likelihood	no.Par.*	$-2\ln$ **
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)

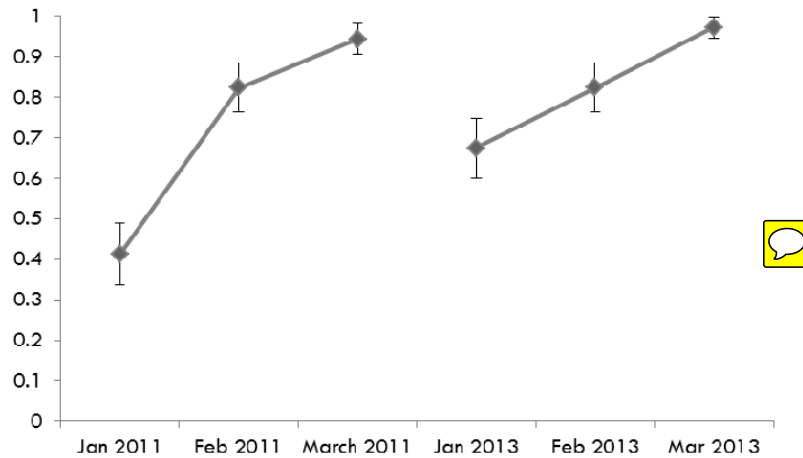


Figure 2. The probability of detecting a wolverine at a camera, given it was present at a site, increased from January through March in both years, and approached 1.0 at the end of surveying.

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 ($AIC_w = 0.65$), 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 (γ) or the probability of site extinction (ϵ) from Year 1 to Year 2.

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

Model	AIC	ΔAIC	AIC wgt	Model Likelihood	no.Par.*	-2LL**
$\psi(SNOWICE), \gamma(), \epsilon(), p(SURVEY)$	282.75	0.00	0.65	1.00	10.00	262.75
$\psi, \gamma(SHRUB), \epsilon(), p(SURVEY)$	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.

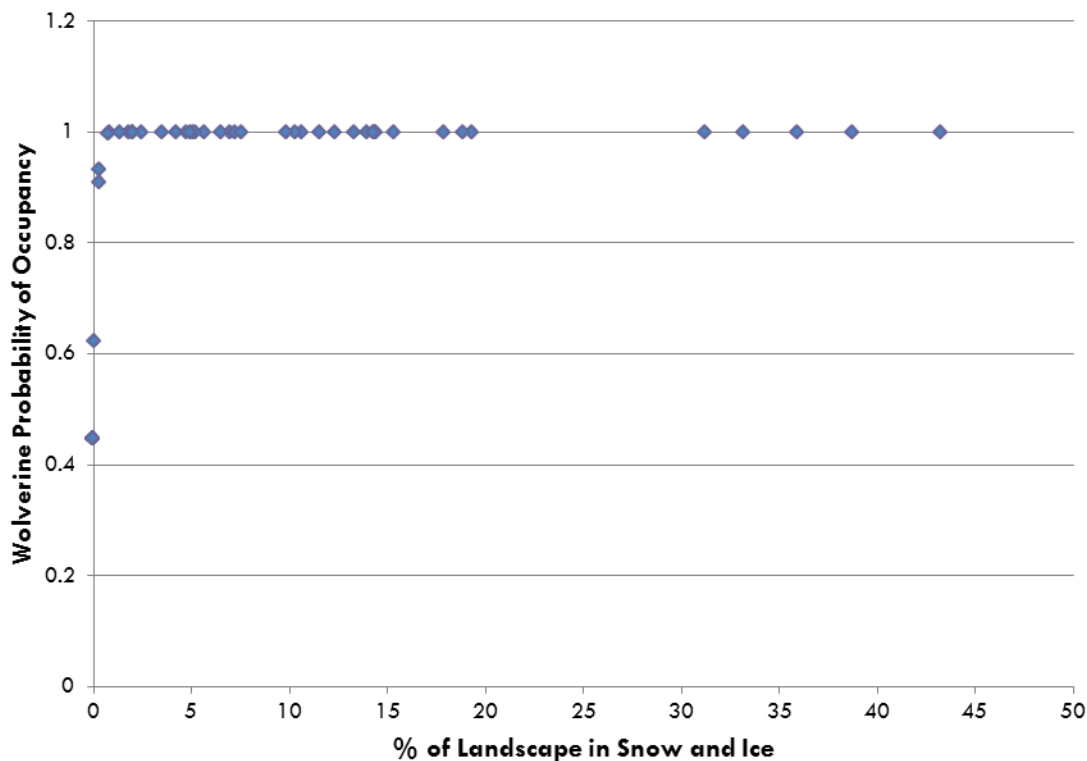


Figure 3. The probability of wolverine occupancy at a site increased markedly with the % of the landscape covered in ice and snow within a 5000-m radius of the camera site.

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	Δ AIC	AIC weight	Residual deviance*	Degrees of freedom
Landcover	% shrub cover	182.73	0	0.69	45.36	55
	% snow and ice cover					
Snow	years (0-12) of persistent spring snow through May 15 th	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	190.44	7.71	0.01	53.43	53
	density of linear industrial features					
	road density					
	recreational trail density					

*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 . 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.