

**Mapping the Wolverine Way:
Identifying Conservation Corridors and Transboundary Linkages
in the Canadian Crown of the Continent Region**



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<p>ABSTRACT:</p> <p>The Canadian Crown of the Continent (CCoC) is one of three zones where wolverines can move between Canada and the US, providing the last links for recruitment and ultimately gene flow to the highly fragmented population in the US Rocky Mountains. However, a combination of rapidly expanding logging, energy development and motorized recreation, along with a growing road network, threatens to fragment and diminish connections in this critical transboundary linkage between the US and Canada. This report summarizes a project to complete a 3-year sampling effort in the CCoC, which in turn completed a larger 6-year effort over a vast area of the central and southern Canadian Rockies. In 2016, the research team surveyed the last unsampled portion of the Alberta Rockies (south of Kananaskis Country to Highway 3) in addition to a substantial portion of the East Kootenay region of the British Columbia Rockies (BC; >9000 km²). This follow-up effort allowed the team to complete an entire ecoregion-wide wolverine survey in the Canadian Rockies ecoregion, from the US-Canadian border north to Banff and Yoho National Parks. From this data, researchers created density estimates and occupancy models of wolverine distribution and its multiple landscape stressors across an extensive and complex region of the Great Northern Landscape. The report summarizes research findings and makes recommendations regarding management strategies.</p>		
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Table of Contents

Disclaimer	i
Acknowledgments.....	iv
List of Figures	viii
List of Tables	x
Executive Summary	1
CHAPTER 1.0 Introduction.....	4
CHAPTER 2.0 Conduct survey of wolverine occurrence	6
2.1 Methods	6
2.2 Results	9
CHAPTER 3.0 Develop occupancy models of wolverine distribution	14
3.1 Occupancy Estimation Methods (camera-based)	14
3.2 Results	16
3.3 Discussion	26
CHAPTER 4.0 Estimate wolverine density in Canadian Rocky and Columbia Mountains	30
4.1 Introduction	30
4.2 Study Area	35
4.3 Methods	37
4.4 Results	46
4.5 Discussion	55
4.6 Management Implications	64
CHAPTER 5.0 Assess wolverine gene flow and fine-scale genetic structure.....	66
5.1 Introduction	66
5.2 Methods	68
5.3 Results	71
5.4 Discussion and Management Implications	77
CHAPTER 6.0 References.....	81

List of Figures

Figure 1: Three study area grids (12 x 12 km) and location of 162 sampling sites for wolverine occurrence in the Canadian Crown of the Continent, 2014-2016.....	8
Figure 2: Location of 70 sampling sites and frequency of wolverine detections in the Elk and Flathead Valley study area, Southern Canadian Rockies, 2016.....	10
Figure 3: Location of 162 sampling sites and frequency of wolverine detections in the Canadian Crown of the Continent, 2014-2016.	12
Figure 4. Wolverine winter sampling areas showing trap locations and secr mask boundaries for each area in matching colors. Mask boundaries were created by assuming large lakes were hard population boundaries and, where boundaries did not exist, the mask was extended approximately 40 km beyond the outer sample sites. The year of sampling is given with the study area name and is the year during late winter.	36
Figure 5. The relationship between spring snow cover, road density and wolverine density based on our best fit model (model 2 in Table 9). We built our spring snow map using 17 years of snow cover data following methods outlined in Copeland et al (2010). The upper figure is for the combined sex model and the lower figure is for separate sex models.....	51
Figure 6. Wolverine density in southeast BC and southwest Alberta estimated from spatial capture-recapture analysis of genetically identified wolverine sampled during winter 2011-2016. There was no trapping in national parks but trapping was permitted in some provincial parks.....	53
Figure 7. The harvest rate of wolverine based on population estimates extrapolated from spatial capture-recapture analysis of genetically identified wolverine sampled during winter 2011-2016 in southeast BC and southwest Alberta, Canada. Horizontal error bars are 95% confidence intervals of population estimates. Vertical error bars are our best guess of the likely error in the recording of wolverine trapping kill. Pink shading denotes harvest above recommended levels, red shading denotes harvest rates that are likely not sustainable.....	54
Figure 8. Wolverine hair trap success in parks complex between 2011 and 2013; number of unique wolverines detected at each sampling site in parks complex between 2011 and 2013. Locations of 229 wolverine detections in parks complex between 2011 and 2013.....	70
Figure 9. Individual detection centers of 64 wolverines (color-coded by haplotype) 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.	74
Figure 10. Individual detection centers of A) 25 female and B) 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 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.	75
Figure 11. Graphical plots showing Factorial Correspondence Analysis [A) 25 female and B) 39 male], Principle Coordinates Analysis [C) 25 female and D) 39 male] and Assignment Test [E) 25 female and F) 39 male] wolverines detected to the north (red) or	

south (green) of the Trans-Canada Highway in the parks complex between 2011 and 2013.
.....76

List of Tables

Table 1. Selection of occupancy models for wolverines detected by cameras in the combined Alberta study area, combined 2014 and 2015. Detectability (p) could be constant (\cdot), vary independently among SURVEYs, or as a TREND among surveys. Occupancy (ψ) could be constant (\cdot), vary north-south (UTMN), east-west (UTME), or between YEARS.....	19
Table 2. Selection of occupancy models for wolverines detected by cameras in the combined BC study area, 2015/2016. Detectability (p) could be constant (\cdot), vary independently among SURVEYs, or as a TREND among surveys. Occupancy (ψ) could be constant (\cdot), vary north-south (UTMN), east-west (UTME), or between YEARS.....	21
Table 3. Selection of occupancy models for wolverines detected by cameras in the 2016 BC study area. Detectability (p) could be constant (\cdot), vary independently among SURVEYs, or as a TREND among surveys. Occupancy (ψ) could be constant (\cdot), vary north-south (U UTMN), or vary east-west (UTME).	22
Table 4. Selection of occupancy models for wolverines detected by cameras in the combined Alberta and BC study areas (2014 - 2016). Detectability (p) could be constant (\cdot), vary independently among SURVEYs, vary as a TREND among surveys, vary across YEARS or between PROVinces. . Occupancy (ψ) could be constant (\cdot), vary north-south (UTMN), vary east-west (UTME), across YEARS, or between PROVinces.	24
Table 5. Evidence ratios (ER) of the covariates used in models of combined AB - BC occupancy analysis.....	25
Table 6. Wolverine sampling effort and detection success in southeast British Columbia and southwest Alberta, 2011-2016. Year is the year at the end of the sampling winter and the area sampled is the mask area for each study area (Fig. 4). BYK_NP stands for Banff, Kootenay and Yoho National Parks. MRG_NP stands for Mount Revelstoke and Glacier National Parks. There were 153 individuals among the sampling areas and years which equaled 126 individuals because some animals were detected in multiple sampling areas or years.	47
Table 7. Model selection table to evaluate possible variation in detection success for wolverine sampled in southeast British Columbia and southwest Alberta, 2011-2016. D = density, g_0 = detection probability, σ = movement parameter, bk = trap specific behavior, $snwdepth$ = snow depth at trap site at last check, DNA = separate g_0 for each genetic lab, $Bait$ = separate g_0 for ungulate versus beaver bait, t = separate g_0 for each trapping occasion. k = the number of model parameters, $logLik$ = model log likelihood value, $AICc$ = Akaike Information Criteria corrected for small sample size, $\Delta AICc$ = the difference in $AICc$ values, $weight$ = relative model weight based on $\Delta AICc$ values.	48
Table 8. Mean annual home range size for wolverine in the montane mountains of western North America (see SM for data). σ is the movement parameter estimated via secr and was calculated as $\sigma = r/2.45$ where r is the radius of the 95% home range (Sun et al. 2014).	49
Table 9. A comparison of the fit of a selected group of models to estimate density of wolverine in southeast BC and southwest Alberta. All models include trap specific behavior (g_0 ~ bk) and no covariation for spatial parameter (σ ~1). Roadden = road	

density, Snow17 = the number of years with spring snow cover between 2000-2016, TrapHarvest = area weighted measure of the number wolverine killed in the trapping season previous to sampling, Alpine = the proportion of alpine habitat, ESSF = the proportion of upper elevation forest, Hii = human impact index which is a cumulative measure based on road density, human habitation and other human footprints.50

Table 10. Wolverine densities from selected studies in North American. Confidence Intervals assume $\alpha=0.05$ unless stated. Study area size was taken from each publication and in some cases was the area trapped and in other cases included a buffer around the traps to account for the detection of animals living across the study area boundary.59

Table 11. DNA sample collection and genotyping success for wolverine hair and scat* samples collected in parks complex with barbed wire hair traps and snow tracking.72

Executive Summary

The Canadian Crown of the Continent (CCoC) is one of three zones where wolverines can move between Canada and the US, providing the last links for recruitment and ultimately gene flow to the highly fragmented population in the US Rocky Mountains. A combination of rapidly expanding logging, energy development and motorized recreation, along with a growing road network, threatens to fragment and diminish connections in this critical transboundary linkage between the US and Canada.

The province of Alberta recently created two parks in the CCoC expanding protection in the Castle Wilderness north of Waterton Lakes National Park and along the British Columbia (BC)-Alberta border. The western boundary of the Castle is the biologically rich Flathead Valley of BC. The Castle expansion highlighted the need to manage the Flathead to maintain viable wolverine populations and the corridors that keep them connected and transborder connections with the northern US Rockies. However, there is limited baseline data on wolverine density, distribution, or gene flow in this critical transboundary area.

In August 2014, the US Fish and Wildlife Service (FWS) withdrew its Proposed Rule to list the distinct population segment (DPS) of the North American wolverine as threatened “due to uncertainty in the science and effects of climate change on their population.” Stated in their withdrawal was recognition that there is good evidence that genetic diversity is lower in wolverines in the DPS than it is in the contiguous habitat in Canada and Alaska. Further, the effect of small population sizes and low genetic diversity may become more significant if populations become smaller and more isolated.

Wolverines are a conservation priority both provincially and nationally. Wolverines are a species of management focus for BC Ministry of Forests, Lands and

Natural Resource Operations (FLNRO) due to uncertainty about sustainability of legal trapping and hunting harvest, particularly in the Kootenay Boundary Region. Our work addresses information needs by providing a science-based assessment to inform the management and conservation of wolverines in the CCOC and Columbia Basin.

In 2016 with Wilburforce funding, we completed a 3-year non-invasive sampling effort in the CCoC, which was a key part of a larger 6-year effort that surveyed the central and southern Canadian Rockies. This final year we surveyed the wolverine population in the Elk and Flathead Valleys.

Key outcomes from the project are as follows:

(1) Deployed 70 sampling sites in 2016, completing a 3-year survey of wolverine populations in the Canadian Crown of the Continent ecosystem (CCoC). The project sampled 153 sites from 2014-2016.

(2) 460 hair samples sent to Wildlife Genetics International for analysis, assigning 12 individuals (8FM: 4M).

(3) Wolverines occupied 40% of the grid cells within our 2016 study area. We found a clear pattern of decreasing occupancy from north to south.

(4) Population density estimates are low compared to adjacent national parks and population estimates from a harvest sustainability analysis conducted in 2007. Density estimates confirm occupancy modeling results that densities are highest in the northern part of study area (Elk/Cadorna Lakes) and decrease moving south towards the Highway 3 transportation corridor and the US/Canadian border.

(5) In our study area, the number of trap lines currently outnumber the estimated resident wolverine population by a factor of four. The study area intersects with 21 trap

lines on the Alberta side, and with at least 62 trap lines on the BC side. On the BC side, each trap line provides for unlimited harvest. In Alberta, trappers are limited to one harvested animal per year. Given the low resident wolverine population, we recommend careful evaluation of this management strategy by both BC and Alberta provincial governments. Our forthcoming harvest sustainability assessment will provide further recommendations on this topic.

(6) The low wolverine density in this critical transboundary linkage area is of concern given the status of wolverines in the contiguous US and reliance on immigration from Canadian populations.

(7) Understanding the limits of trapper harvest on the long-term persistence of wolverines in the BC Rockies and effectively managing their habitat and the landscape corridors that link them need to be key conservation priorities for both BC and Alberta governments and coordinated in a transboundary, international framework.

CHAPTER 1.0 INTRODUCTION

Wolverines naturally occur in low numbers and have extensive home ranges. Accordingly, the scale of research should be appropriately large and defined by ecological boundaries, instead of political jurisdictions. We designed our research to be at the metapopulation scale and transboundary. This “wolverine-scale” approach enables us to make strong inferences regarding the effects of land use change and human disturbance on wolverine occurrence and genetic connectivity.

The project enabled us to complete a 3-year sampling effort in the CCoC and complete a 6-year effort over a vast area of the central and southern Canadian Rockies. In 2016 we surveyed the last unsampled portion of the Alberta Rockies (south of Kananaskis Country to Highway 3) in addition to a substantial portion of the East Kootenay region of the British Columbia Rockies (BC; >9000 km²). The follow-up effort allowed us to complete an entire ecoregion-wide wolverine survey in the Canadian Rockies ecoregion, from the US-Canadian border north to Banff and Yoho National Parks. We created density estimates and occupancy models of wolverine distribution and its multiple landscape stressors across an extensive and complex region of the Great Northern Landscape.

We began to expand our collaboration, data sharing and coordination south of the US-Canadian border to a multi-state sponsored wolverine-monitoring program starting in late 2016. We merged occupancy and genetic datasets on both sides of the international border in order to strengthen dispersal models and identify linkages throughout the transboundary Crown of the Continent. Our multi-partner effort in Canada alone has resulted in amassing camera and NGS data over an area greater than the size of the entire

Crown of the Continent ecosystem (>51,000 km² [>19,000 mi²]. The multi-partner project invested over \$1M in data collection.

The project helped to fill an urgent need for critical information, given current Alberta land-use planning initiatives in the South Saskatchewan watershed, the Flathead (BC) wildlife management area, and highway mitigation planning along Highway 3 in Alberta and BC. We also used this data to assess the sustainability of trapper harvest in BC and communicated these results to regional wildlife managers via one of the PIs (GM). Like our previous research in the Banff park complex, we have engaged citizen scientists to assist researchers conducting field sampling. Our outreach and education efforts will ensure that new research on a 'sentinel' species will inform ongoing and future land management and transportation planning with the Alberta and BC Governments, Glacier National Park, USDA Forest Service and the Ktunaxa Nation in Canada and the US and educate and inform communities.

This research had the following objectives:

1. Conduct survey of wolverine occurrence in the Canadian Crown of the Continent (CCoC) using noninvasive methods.
2. Develop occupancy models of wolverine distribution and identify core habitats, dispersal corridors and highway mitigation.
3. Estimate wolverine density in Canadian Rocky and Columbia Mountains. Conduct population estimates in order to assess the sustainability of recent trapper harvest levels.
4. Assess wolverine gene flow and fine-scale genetic structure in the Crown of the Continent region.

CHAPTER 2.0 CONDUCT SURVEY OF WOLVERINE OCCURRENCE

2.1 Methods

Our study area was located in the Canadian Crown of the Continent (CCoC) ecosystem in southeastern British Columbia (BC) and focused in two main areas: the Elk and Flathead Valleys (Figure 1). The 2016 study area was the last of a 3-year sampling grid to survey, situated between two important national parks complexes: Banff-Yoho-Kootenay to the north and Waterton-Glacier to the south. The southern extent of the 2016 grid was positioned on the Canadian-US border. Study sites in 2014 were situated in the Alberta Rockies from the US-Canadian border (Waterton Lakes National Park) to the south boundary of Kananaskis Country (Figure 1). In 2015, sampling took place in BC north of Highway 3, west of the Elk Valley to the Columbia Trench and south boundary of Kootenay National Park. Study areas and sites sampled during all three years represented a wide range of biophysical attributes, landscape conditions and levels of human disturbance.

We surveyed wolverine occurrence using a systematic sampling design consistent with our previous wolverine research to enable data pooling and large-scale analyses. We overlaid a 12 x 12 km grid on the study area. In each grid cell we placed a sampling site consisting of a hair trap and remote camera aimed at the hair trap. Hair traps consisted of a skinned beaver carcass nailed to a tree and secured with baling wire (Fisher and Bradbury 2014). Barbed wire was wrapped from the carcass to ca. 1 m above ground level. Sites were set up during the first month (January 2016) and revisited three times at monthly intervals to rebait, collect hair samples and service cameras. Three replicate

monthly surveys were conducted within each survey year to incorporate detectability into occupancy estimates.

Given the small sample sizes inherent to wolverine population sampling, and the fact the sexes will likely need to be modeled separately for spatial capture-recapture (SCR) models to estimate wolverine abundance, an “extra” sampling site was placed in some grid cells.

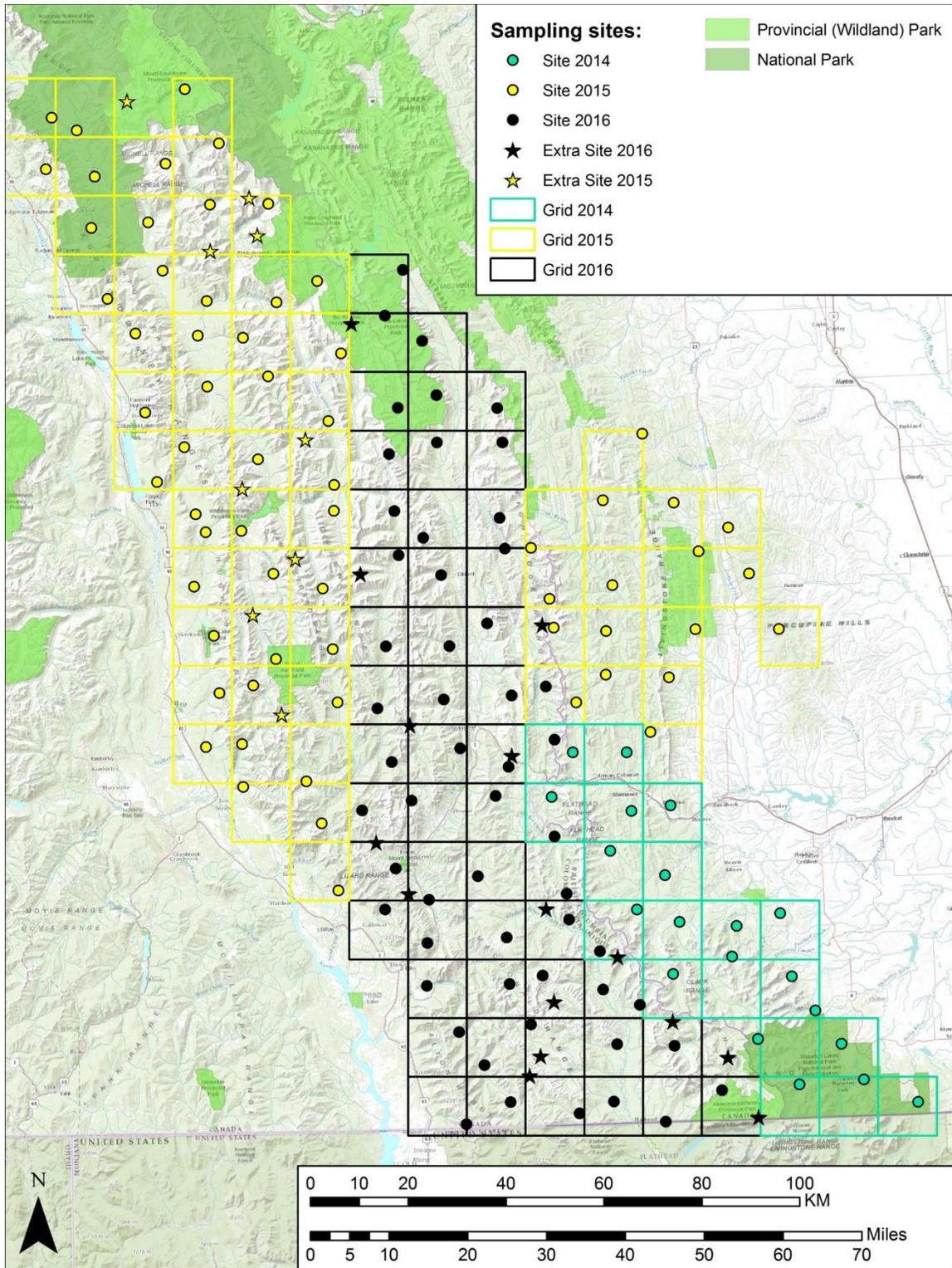


Figure 1: Three study area grids (12 x 12 km) and location of 162 sampling sites for wolverine occurrence in the Canadian Crown of the Continent, 2014-2016.

2.2 Results

2.2.1 Camera-based sampling: 2016 season

During 2016, we deployed 57 sampling sites over an area of 8208 km² that were checked on average at monthly intervals for three months. We set an additional 13 sites in the study area to increase the number of individual detections for modeling wolverine abundance and sampled them during two monthly survey sessions. Eight of the 13 “extra” sites were just outside our study grid within areas sampled in 2014 or 2015. These sites were typically near the Continental Divide and set in attempts to detect wolverines moving across the Divide between Alberta and BC. Overall, 70 sites were set within the 2016 study area.

Of the 70 sampling sites, 26 sites (37%) had confirmed wolverine photo-detections and 51 confirmed visits by wolverines (Figure 2). More than one individual may have visited some sites; however, without the genetic analysis of hair samples collected, we only report the confirmed presence of wolverine visiting a sampling site.

Of 194 monthly sampling sessions during 2016, wolverines visited the sampling sites 26 times (13%). Wolverines were never detected at 63% (n=44) of the sites. At 13% of the sites, wolverines were detected during one or two sessions only (n=9), while at 11% of the sites they were detected during all three sessions. Note that 13 of the 70 sites (18%) were only sampled during two sessions and herein we report on the absolute numbers and do not correct for the 13 sites only sampled twice.

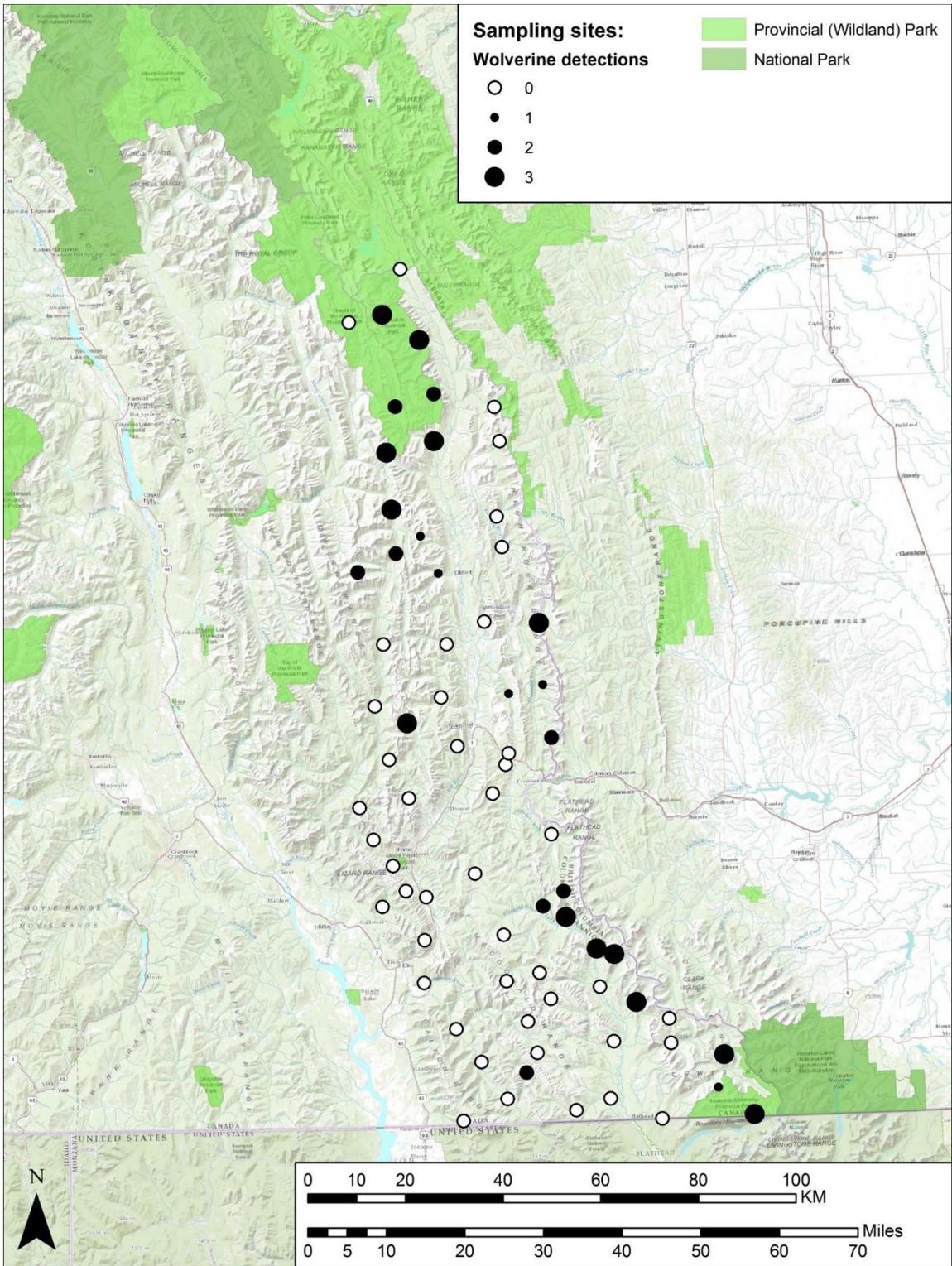


Figure 2: Location of 70 sampling sites and frequency of wolverine detections in the Elk and Flathead Valley study area, Southern Canadian Rockies, 2016.

2.2.2 Canadian Crown of the Continent, 2014-2016

The following summary covers sampling conducted during the last three years, including 2016 (Figure 3). From January to April 2014, 2015 and 2016, our surveys encompassed an area of 20,288 km², more than twice the area of Yellowstone National Park. During this time, we deployed 162 sampling sites (153 sites with cameras, 9 without cameras). One hundred twenty-five sites were set in BC, while 37 were set in Alberta.

To increase the number of individual detections and generate more precise estimates of abundance, we set an additional 22 sites within the sampling grid in 2015 (n=9) and 2016 (n=13). These extra sites did not have cameras in 2015, while in 2016 all extra sites had cameras. The extra sites in both years were only sampled during two monthly sessions and all were in BC.

During the 3-year period, 45 sites (29%) had confirmed wolverine photo-detections (Figure 3). Wolverines were never detected at 71% (n=108) of the sampling sites. They were detected at 11% (n=18) of the sites once, 9% (n=14) twice, and 8% (n=13) all three times. Note that 22 of the 162 sites (13%) were only sampled during two sessions. Of 441 monthly sampling sessions during the three years, wolverines were detected during 13% (n=60) of sessions.

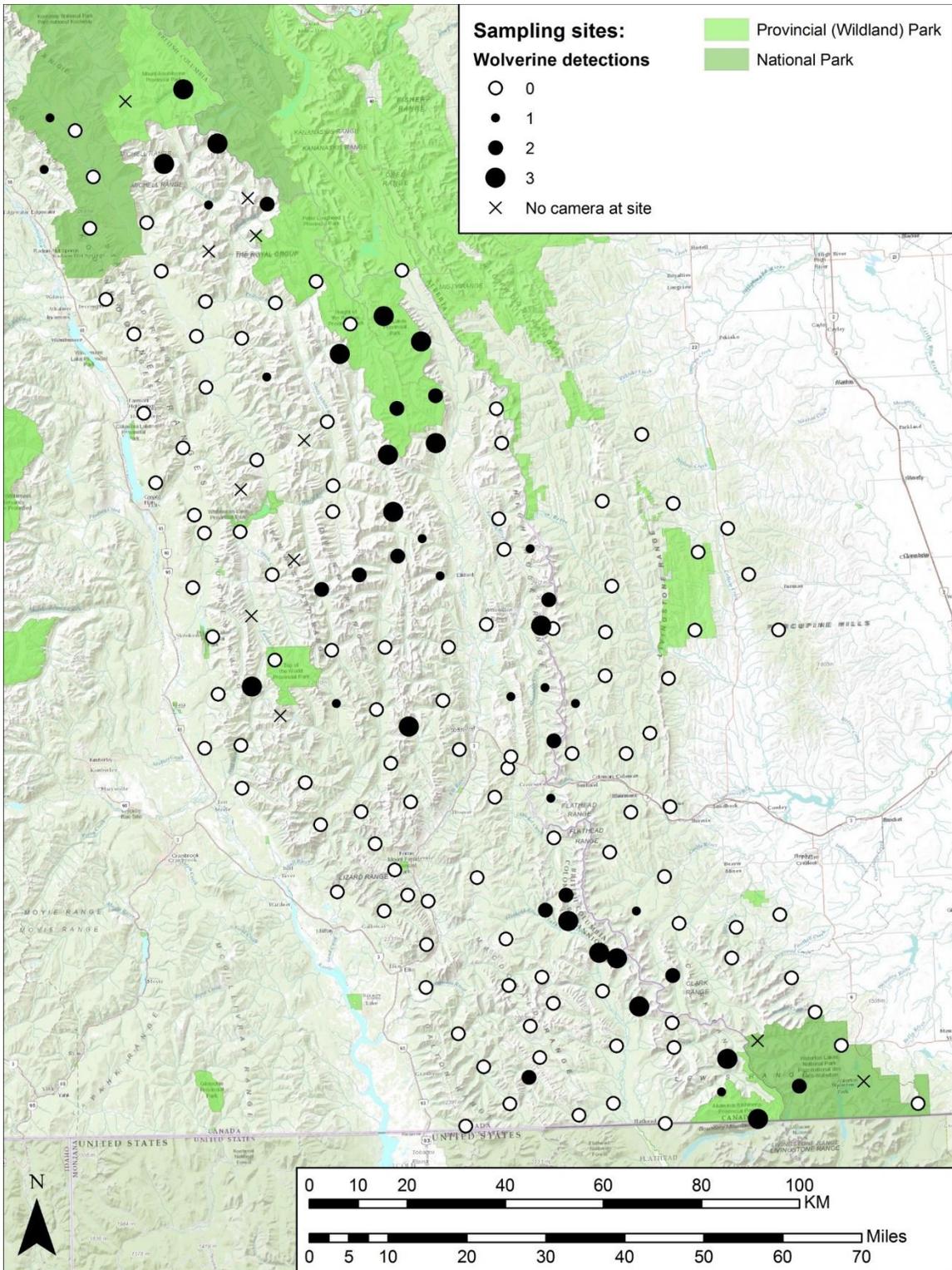


Figure 3: Location of 162 sampling sites and frequency of wolverine detections in the Canadian Crown of the Continent, 2014-2016.

2.2.3 Tree-climbing behaviour

A reluctance of wolverines to climb bait trees may affect detectability using noninvasive genetic sampling and result in fewer individuals identified in the study area using microsatellite genotyping. At 67% of the visits (35 of 52) wolverines climbed the bait tree at least once, while at 33% (n=17) of the site visits wolverines were not observed climbing. In contrast, over 90% of the sites-sessions during the 3-year Canadian Rockies national parks survey detected wolverines climbing bait trees, while in Kananaskis Country climbing occurred at 57% (4 of 7 sites) of the sites.

2.2.4 Non-target species

In 2016, we detected 19 vertebrate species at the hair traps. Snowshoe hares were most frequent followed by American marten, lynx and wolverine. In 2015, we detected 18 vertebrate species at the hair traps. American marten were most frequent followed by wolves, snowshoe hares, coyotes and wolverines. Fishers were not detected at any sampling sites in 2015 or 2016.

CHAPTER 3.0 DEVELOP OCCUPANCY MODELS OF WOLVERINE DISTRIBUTION

3.1 Occupancy Estimation Methods (camera-based)

Occupancy estimation methods strive to estimate the proportion of the survey area that is occupied (or used) by the species of interest (MacKenzie et al. 2006). While the presence of a wolverine at a sampling site can be confirmed through remote cameras, it is generally impossible to confirm their absence. Highly mobile and elusive, wolverines can have low detectability, but sampling for three winter months using this double method has been shown to greatly increase detectability and provide confidence in our estimates of occupancy, and conversely, of absence (Fisher and Bradbury 2014). After three months, the probability of missing a wolverine given it was present using this method is <10% for hair traps, and approaching zero for camera traps, making it highly reliable (Fisher and Bradbury 2014).

For this report we estimated the proportion of sampling sites occupied by wolverines with single season models, using the occupancy modeling program *Presence* v.1.10). *Presence* uses generalized linear models and maximum likelihood estimation to estimate the probability of missing a species when it is present at the site (p =detectability) and the probability that a site is occupied (Ψ). To estimate these parameters, repeat observations (survey or sampling sessions) need to be conducted over a period of time during which site occupancy is assumed to be constant.

We analyzed several subsets of the data: Alberta sites (sampled in 2014 and 2015), BC sites (sampled in 2015 and 2016), 2016 BC sites only, and finally the

combined Alberta and BC data sets (2014-16). For both the Alberta and BC sites, each site was only sampled in one year. Therefore, multi-season models that estimate changes in occupancy among years (MacKenzie et al. 2003) were not appropriate. Occupancy analysis makes the assumption that movement of animals in and out of sites is random (Burton et al. 2015), and also assumes demographic closure at the species level within a season – which for wolverines is likely appropriate for a three-month period in winter (Fisher and Bradbury 2014).

We pooled sites sampled in different years into a single analysis. Doing so assumes that there is no bias among sampling and among years, e.g., all our "bad" sites were sampled together in 1 year, and our "good" in another year, and our design aimed to achieve this goal. Including sites sampled in different years does not violate the closure assumption, as each site needs only be closed to changes in occupancy for the 3-month season it was sampled (Fisher et al. 2014) but not necessarily for a 16-month period. We investigated if this assumption of closure for site occupancy across years was justified by including models with Ψ varying by year.

We ran several competing single-season models, each with different assumptions about how detectability and site occupancy varied through time and space. For all data sets we tested whether the probability of detection was constant, varied among monthly surveys, or varied as a trend through time. We likewise tested whether site occupancy was either constant, varied by year, varied east-west (UTME), or varied north-south (UTMN). For the complete dataset, we also tested whether detectability and occupancy varied by Province.

For this preliminary analysis, we did not yet investigate the impact of biophysical variables such as remoteness, elevation, persistent spring snow or land cover on occupancy probability; our objective was a study area-wide estimate of occupancy.

We ranked competing models using Akaike's Information Criterion (AIC) scores, which provide a balance between the variance in the wolverine data explained by the model, and the number of variables needed to explain that variance to identify the best-supported model of wolverine occupancy (Burnham and Anderson 2002). Lower AIC scores indicate a parsimonious model that explains more variance than other models. From AIC_w we calculated evidence ratios for each variable (ER). This is the ratio of the sum of all AIC_w of all models that included a given covariate, vs. those models that did not include that covariate. For example, $ER=2$ suggests there is twice as much evidence supporting the inclusion of a covariate, than evidence supporting omitting that variable.

3.2 Results

3.2.1 Alberta sampling sites – 2014 and 2015

The Alberta portion of our study area was sampled in two consecutive years. In 2014, 20 sampling sites were set from the US-Canada border north to the Highway 3 corridor in the Crowsnest Pass and including Waterton National Park. In 2015, we continued north in the Alberta Rockies sampling 17 sites between the Highway 3 Crowsnest Highway corridor and the southern extent of Kananaskis Country. Kananaskis was surveyed with 43 sites in 2010-11 and 2011-12 (Fisher and Heim 2012) and forms part of our greater study area in the central and southern Canadian Rockies.

As outlined in our 2015 summary report (Clevenger et al. 2015), there were few wolverine detections both in the 2014 Crowsnest Pass-Waterton study area and the area sampled to the north of Crowsnest Pass in 2015.

In 2014, of 20 sampling sites, two sites (Snowshoe and Sofa Creek) had non-functional cameras during the entire season and were dropped from this analysis. Of the 18 remaining sites, 4 sites (22%) (Tent Ridge, Gardiner Creek, W Castle and Rowe Creek) had camera detections of wolverines, during six sampling sessions (visits during two sessions at W Castle and Rowe Creek).

All sites with wolverine detections had a detection during the third sampling session, while there were no detections during the second session. Despite the few detections, there was a strong geographic pattern, with all sites with detections being located within or in close proximity to the Continental Divide.

The Alberta portion of the 2015 study area consisted of 17 sampling sites (including Beehive and Tornado Pass); only 3 sites (17%) (Beehive, Tornado Pass, Racehorse Pass) had confirmed wolverine camera detections and 4 visits (two visits occurred at Tornado Pass).

Detection probability p varied by sampling session (hereafter referred to as “survey” in the occupancy analysis; SURVEY; ER=2.02). P of the top model ($\text{psi}(\text{UTME})$, $\text{p}(\text{SURVEY})$) was low for the first two sessions, estimated at 0.28 (s.e. = 0.17) for both surveys. Detection probability for the third survey was 1.00 (s.e. = 0.00); however, such border estimates can be unreliable especially in light of the small sample size. There was no evidence for a temporal trend among surveys (TREND; ER = 0.44).

The east-west gradient in wolverine detections were reflected in estimates of occupancy probability ψ (UTME; ER = 1.36), and the top model (ψ (UTME), p (SURVEY)) estimated ψ as a gradient along UTME: the westernmost site had an estimate of 0.51 (s.e. = 0.12), and the easternmost site had an estimate of 0.01 (s.e. = 0.01; Table 1). There was no evidence for a north-south gradient (UTMN; ER = 0.13). Year had no impact on ψ (YEAR; ER = 0.10), which suggests that there were not issues with pooling data among years. We estimated an area-wide occupancy probability (as opposed to site-specific based on UTMs) to allow comparison with other study areas. This ψ estimate comes from the third highest ranking model (ψ (.), p (SURVEY)), which had a Δ AIC of 1.93 and was therefore not markedly less supported than the top model (Burnham and Anderson, 2002). Ψ for this model was 0.21 (s.e.=0.07). The naive estimate of ψ for the combined Alberta study areas was 0.20. The corrected estimate is close to the naïve uncorrected estimate, due to high probabilities of detection yielded by this method (Fisher and Bradbury 2014). This gives us a great deal of confidence that wolverine are indeed absent from places in which we did not detect them.

Table 1. Selection of occupancy models for wolverines detected by cameras in the combined Alberta study area, combined 2014 and 2015. Detectability (p) could be constant (.), vary independently among SURVEYs, or as a TREND among surveys. Occupancy (ψ) could be constant (.), vary north-south (UTMN), east-west (UTME), or between YEARS.

Model	AIC	ΔAIC	AIC weight	Model Likelihood	K	- 2*LogLike
psi(UTME),p(SURVEY)	57.35	0.00	0.38	1.00	5	47.35
psi(UTME),p(TREND)	58.91	1.56	0.18	0.46	4	50.91
psi(.),p(SURVEY)	59.28	1.93	0.15	0.38	4	51.28
psi(UTMN),p(SURVEY)	60.50	3.15	0.08	0.21	5	50.50
psi(.),p(TREND)	60.85	3.50	0.07	0.17	3	54.85
psi(YEAR),p(SURVEY)	61.09	3.74	0.06	0.15	5	51.09
psi(UTMN),p(TREND)	62.14	4.79	0.04	0.09	4	54.14
psi(YEAR),p(TREND)	62.67	5.32	0.03	0.07	4	54.67
psi(UTME),p(.)	63.80	6.45	0.02	0.04	3	57.80
psi(.),p(.)	65.80	8.45	0.01	0.01	2	61.80
psi(UTMN),p(.)	67.23	9.88	0.00	0.01	3	61.23
psi(YEAR),p(.)	67.66	10.31	0.00	0.01	3	61.66

3.2.2 British Columbia sampling sites – 2015 and 2016

The combined BC datasets for 2015 and 2016 had 116 sites, with 15 of 46 sites (33%) visited at least once in 2015, and 26 of 70 sites (37%) visited at least once in 2016. Thirteen sites (11%) had one visit, 11 sites (9%) had two visits, 13 sites (11%) had three visits, and 79 sites (68%) had no visits. Naive occupancy in BC for both years combined was 35%.

Similar to the Alberta surveys, there was a distinct geographical pattern; sampling detected wolverines mostly along the Continental Divide, albeit not as closely to it as on the Alberta side. In addition, there was a potential influence of proximity to protected areas. It is unclear whether this may be an effect of less trapping pressure and/or the relative inaccessibility of human and potential disturbance. The only sites with wolverine detections far from the Divide and close to the western edge of the study area were situated close to protected areas (Height of the Rockies Provincial Park, BC; Glacier National Park, MT).

In the BC dataset, detection probability p did not vary by survey (SURVEY; ER = 0.71) or over time (TREND; ER = 0.34). Unlike the Alberta data, occupancy probability ψ did not vary with either position along an east-west gradient (UTME; ER = 0.66), along a north-south gradient (UTMN; ER = 0.24) or with sampling year (YEAR; ER = 0.27). Accordingly, the ΔAIC - values of all models were <2 , meaning that of the models considered, none had significantly more support by the data over all other models (Table 2). To examine an area-wide occupancy estimate consistent with other regions, we report the estimates for p and ψ of the last-ranked, but simplest model ($\psi(\cdot), p(\cdot)$): The estimate of ψ was 0.35 (s.e. = 0.05, CI: 0.26 – 0.52), and the estimate for p was 0.67 (s.e. = 0.05). In comparison, naive occupancy for this dataset was 0.35.

Table 2. Selection of occupancy models for wolverines detected by cameras in the combined BC study area, 2015/2016. Detectability (p) could be constant (\cdot), vary independently among SURVEYs, or as a TREND among surveys. Occupancy (ψ) could be constant (\cdot), vary north-south (UTMN), east-west (UTME), or between YEARS.

Model	AIC	Δ AIC	AIC weight	Model Likelihood	K	- 2*LogLike
psi(UTME), p(SURVEY)	279.29	0	0.16	1.00	5	269.29
psi(UTME),p(\cdot)	279.72	0.43	0.13	0.81	3	273.72
psi(UTME),p(TREND)	280.27	0.98	0.10	0.61	4	272.27
psi(YEAR),p(SURVEY)	280.53	1.24	0.09	0.54	5	270.53
psi(UTMN), p(SURVEY)	280.66	1.37	0.08	0.50	5	270.66
psi(\cdot),p(SESSION)	280.70	1.41	0.08	0.49	4	272.7
psi(YEAR),p(\cdot)	280.96	1.67	0.07	0.43	3	274.96
psi(UTMN),p(\cdot)	281.15	1.86	0.06	0.39	3	275.15
psi(\cdot),p(\cdot)	281.17	1.88	0.06	0.39	2	277.17
psi(YEAR),p(TREND)	281.51	2.22	0.05	0.33	4	273.51
psi(UTMN),p(TREND)	281.73	2.44	0.05	0.30	4	273.73
psi(\cdot),p(TREND)	281.74	2.45	0.05	0.29	3	275.74

3.2.3 British Columbia study area – 2016

Although the previous model did not suggest there were fundamental differences in occupancy probability by sampling year (which in this case equaled region as well as time), we were still interested in estimating occupancy probability for the 2016 survey independently. In the 2016 BC dataset, detection probability p did not vary with survey (SURVEY, ER = 0.60) or time (TREND; ER = 0.41; Table 3), although the top model indicated variation by survey, it was not well supported. Occupancy probability ψ did not

vary by an east-west gradient (UTME; ER = 0.2). However, there was evidence for a north-south gradient in occupancy probability, with higher ψ at more northern sites (UTMN; ER = 1.80).

Estimated p for the top model ($\psi(\text{UTMN}), p(\text{SURVEY})$) for the first survey was 0.56 (s.e. = 0.10). The estimate for the second survey was highest, at 0.82 (s.e. = 0.08). The third survey had an estimated p of 0.72 (s.e. = 0.11). Occupancy probability estimates for the top model ranged between 0.70 (s.e. = 0.06) for the northern most site to 0.23 (s.e. = 0.05) for the southernmost site. The estimate of ψ was 0.40 (s.e. = 0.06, CI: 0.29 – 0.52) and naive occupancy for this dataset was 0.39.

Table 3. Selection of occupancy models for wolverines detected by cameras in the 2016 BC study area. Detectability (p) could be constant (\cdot), vary independently among SURVEYS, or as a TREND among surveys. Occupancy (ψ) could be constant (\cdot), vary north-south (U UTMN), or vary east-west (UTME).

Model	AIC	ΔAIC	AIC weight	Model Likelihood	K	- 2*LogLike
$\psi(\text{UTMN}), p(\text{SESSION})$	177.71	0.00	0.24	1.00	5	167.71
$\psi(\text{UTMN}), p(\cdot)$	177.99	0.28	0.21	0.87	3	171.99
$\psi(\text{UTMN}), p(\text{TREND})$	178.24	0.53	0.19	0.77	4	170.24
$\psi(\cdot), p(\text{SESSION})$	180.20	2.49	0.07	0.29	4	172.20
$\psi(\cdot), p(\cdot)$	180.30	2.59	0.07	0.27	2	176.30
$\psi(\text{UTME}), p(\text{SESSION})$	180.51	2.80	0.06	0.25	5	170.51
$\psi(\text{UTME}), p(\cdot)$	180.58	2.87	0.06	0.24	3	174.58
$\psi(\cdot), p(\text{TREND})$	180.70	2.99	0.05	0.22	3	174.70
$\psi(\text{UTME}), p(\text{TREND})$	180.99	3.28	0.05	0.19	4	172.99

3.2.4 Canadian Crown of the Continent, 2014-2016

Although data collected among different years can be pooled for analysis as long as no biases in sampling are expected (MacKenzie et al. 2006), we still wished to perform due diligence by examining evidence for a potential time (and space) effect in occupancy probability by using a year covariate for ψ . One potential issue with this is that year of study may reflect the quality of wolverine habitat sampled among years. This is likely the case in our study with 2014 appearing to be the lowest quality habitat, 2016 the highest quality, and 2015 of moderate quality.

Because our methodology was consistent during all three years, we were not as concerned with a year effect in detectability. Climate and related environmental factors may affect p differently each year, but we expect that effect to be relatively small compared to other variability.

The simplest possible model, ($\psi(\cdot), p(\cdot)$), returned an estimate of detectability p of 0.64 (s.e. = 0.05; CI: 0.25 - 0.40), and of occupancy probability ψ of 0.32 (s.e. = 0.04; CI: 0.54 - 0.73). As expected, however, year had an effect on ψ (YEAR; ER = 1.43; Table 4 and 5). There was evidence for a north-south gradient in ψ , with more northern sites having a higher occupancy probability (UTMN; ER = 2.06). There was no evidence for a strong effect of any other covariates on either p or ψ .

The highest ranking model ($\psi(\text{UTMN}+\text{YEAR}), p(\text{TREND})$) estimated p for survey one at 0.54 (s.e. = 0.07), for survey two at 0.66 (s.e. at 0.05), and survey three at 0.76 (s.e. = 0.07; Table 4). The estimates for ψ varied by year and UTMN, with 2016 having highest, and 2014 having lowest estimates for ψ . The site with the highest estimate, BC E1 (Elk Lakes), was one of the northernmost sites and sampled in 2016. Coincidentally it did not have any wolverine visits. Its estimate was 0.52 (s.e. = 0.06; CI:

0.40 - 0.64). The site with the lowest estimate of ψ , ABS 20 (Beebe Flats), was one of the southernmost sites and sampled in 2014 (ψ : 0.10; s.e. = 0.04; CI: 0.04 - 0.20).

Table 4. Selection of occupancy models for wolverines detected by cameras in the combined Alberta and BC study areas (2014 - 2016). Detectability (p) could be constant (.), vary independently among SURVEYs, vary as a TREND among surveys, vary across YEARS or between PROVINces. . Occupancy (ψ) could be constant (.), vary north-south (UTMN), vary east-west (UTME), across YEARS, or between PROVINces.

Model	AIC	ΔAIC	AIC weight	Model Likelihood	K	$-2 * \text{LogLike}$
psi(UTMN+YEAR),p(TREND)	341.17	0.00	0.24	1.00	5	331.17
psi(UTMN+YEAR),p(SURVEY+YEAR)	341.37	0.20	0.21	0.90	7	327.37
psi(YEAR),p(TREND)	344.28	3.11	0.05	0.21	4	336.28
psi(UTMN),p(PROV)	344.34	3.17	0.05	0.20	4	336.34
psi(UTMN),p(TREND)	344.39	3.22	0.05	0.20	4	336.39
psi(UTMN+PROV),p(SURVEY+PROV)	344.40	3.23	0.05	0.20	7	330.4
psi(UTMN),p(YEAR)	344.69	3.52	0.04	0.17	4	336.69
psi(YEAR),p(PROV)	345.54	4.37	0.03	0.11	4	337.54
psi(PROV),p(TREND)	345.57	4.40	0.03	0.11	4	337.57
psi(.),p(PROV)	345.61	4.44	0.03	0.11	3	339.61
psi(YEAR),p(SURVEY)	345.66	4.49	0.03	0.11	5	335.66
psi(UTMN),p(SURVEY)	345.74	4.57	0.02	0.10	5	335.74
psi(.),p(TREND)	346.02	4.85	0.02	0.09	3	340.02
psi(YEAR),p(YEAR)	346.07	4.90	0.02	0.09	4	338.07
psi(.),p(YEAR)	346.25	5.08	0.02	0.08	3	340.25
psi(PROV),p(YEAR)	346.80	5.63	0.01	0.06	4	338.8
psi(UTME),p(PROV)	346.81	5.64	0.01	0.06	4	338.81
psi(YEAR),p(.)	346.86	5.69	0.01	0.06	3	340.86

Model	AIC	ΔAIC	AIC weight	Model Likelihood	K	-2*LogLike
psi(PROV),p(SURVEY)	346.93	5.76	0.01	0.06	5	336.93
psi(UTMN),p(.)	346.94	5.77	0.01	0.06	3	340.94
psi(PROV),p(PROV)	346.97	5.80	0.01	0.06	4	338.97
psi(.),p(SURVEY)	347.39	6.22	0.01	0.04	4	339.39
psi(UTME),p(TREND)	348.02	6.85	0.01	0.03	4	340.02
psi(PROV),p(.)	348.14	6.97	0.01	0.03	3	342.14
psi(UTME),p(YEAR)	348.18	7.01	0.01	0.03	4	340.18
psi(.),p(.)	348.58	7.41	0.01	0.02	2	344.58
psi(UTME),p(SURVEY)	349.38	8.21	0.00	0.02	5	339.38
psi(UTME),p(.)	350.58	9.41	0.00	0.01	3	344.58

Table 5. Evidence ratios (ER) of the covariates used in models of combined AB - BC occupancy analysis.

Parameter	Covariate	ER
<i>P</i>	SURVEY	0.51
<i>P</i>	TREND	0.64
<i>P</i>	YEAR	0.46
<i>P</i>	PROV	0.21
ψ	UTMN	2.06
ψ	UTME	0.04
ψ	YEAR	1.43
ψ	PROV	0.14

3.3 Discussion

3.3.1 British Columbia study area - 2016

Estimates of occupancy can act as a surrogate for abundance for territorial species such as wolverine when the sites sampled approximate territory sizes (MacKenzie et al. 2006). The last three years our annual surveys covered on average 6700 km² and were designed around a 12 x 12 km sampling grid, which is based on the average home range size for female wolverines (Banci and Harestad 1990, Inman et al. 2012b). The estimate of wolverine occupancy in our 2016 BC Rockies study area was 0.40 (s.e. = 0.04;). Previous estimates of occupancy in the Canadian Rockies were 0.88 (s.e. = 0.05) in the Banff-Yoho-Kootenay park complex (Clevenger and Barreto 2014) and 0.36 (s.e. = 0.11) in Kananaskis Country (Heim 2015). Our 2014 survey in the Waterton-Crowsnest Pass area had one of the lowest estimates of occupancy in the Canadian Rockies to date ($\psi=0.17$, s.e. = 0.09), rivaling the highly impacted west-central Foothills ($\psi = 0.14$, s.e. = 0.07).

Noninvasive surveys conducted in the Columbia Mountains had occupancy estimates ranging from 0.38 (s.e. = 0.10) in the southern Purcells to 0.71 in the main Purcell Range (s.e. = 0.10) (Kortello and Hausleitner 2012, 2013; Hausleitner and Kortello 2014). When viewed in context of these two mountain systems, our 2016 survey area in British Columbia had moderate wolverine abundance relative to other areas sampled thus far in the Canadian Rockies and Columbia Mountains.

3.3.2 Canadian Crown of the Continent

We found that wolverine occupancy in the CCoC differed markedly between years and study areas; however, this is likely a result of habitat quality among areas sampled each year. The lowest occupancy estimates were from the southern Alberta

Rockies in 2014, where wolverines occupied roughly 20% of the landscape. This occupancy estimate is lower than estimates from Kananaskis Country, Alberta (Heim 2015), and rivaled the industrially developed Alberta foothills further north (Fisher et al. 2013). Occupancy increased east to west in the Alberta survey area, with higher occupancy close to the Continental Divide. The probability of detection varied monthly in all study areas and in the combined data set, but was relatively high by the last session, lending confidence that where wolverines were not detected, they did not occur. The probability of false absence was low, meaning there was high chance that we detected a wolverine given it was present at a camera site each year, very strongly supporting our results: wolverines did not occur where we did not detect them.

Wolverine occupancy was greatest in the 2016 BC study area, but varied markedly through space. Similar to our summary results in 2015 (Clevenger et al. 2015), we found a clear pattern of decreasing occupancy from north to south. The results from our 2016 survey reinforce the pattern of occupancy we observed in the CCoC last year. This north-south gradient in occupancy mirrors reported wolverine occurrence in the Columbia Mountains (Kortello and Hausleitner 2013, 2015; Hausleitner and Kortello 2014), the next major north-south range west of the Canadian Rockies. Here a notable decline in wolverine detections occurred from north to south in both the Selkirk and Purcell Mountains in addition to evidence of low genetic connectivity between the south Purcell population and other populations in southeastern British Columbia (Hausleitner and Kortello 2014). These findings are noteworthy given the Columbia and Rocky Mountains are two of the three remaining areas where wolverines and other wide-ranging carnivores can move between Canada and the U.S.

The north-south pattern from our CCoC study area differs from occupancy patterns observed in our 2014-2015 Alberta sampling, and in the Banff-Yoho park complex – Kananaskis Country and the Willmore Wilderness – Foothills where a decreasing west-east pattern of wolverine occurrence was reported (Fisher et al. 2013, Heim 2015). Wolverine occupancy in the CCoC study area decreased significantly moving south and the mechanisms for this variability have yet to be explained, but will be the focus of our future analysis (see below).

At first glance, wolverine camera-detections in our CCoC study area appear to be associated with proximity to the Continental Divide, and areas with low levels of landscape disturbance. Previous surveys in the Canadian Rockies revealed wolverines are more abundant in rugged and remote areas protected from human activity and landscape disturbance (Fisher et al. 2013, Clevenger and Barreto 2014, Heim 2015). Hausleitner and Kortello (2014) found similar patterns of wolverine occurrence in the Columbia Mountains where the majority of wolverine detections were within or immediately adjacent to large protected areas: provincial parks, nature and wilderness conservancies. The geographic location of these relatively protected areas, or their proximity to source populations, may account for the north to south gradient in distribution.

The Canadian Rockies have been identified as a potential corridor for wolverine movement into the US (Schwartz et al. 2009) and the most likely long-term prospect for transboundary wolverine habitat connectivity given climate change scenarios (Copeland et al. 2010). The results we present are preliminary; nonetheless, our data summary suggests lower populations than expected and lower connectivity between the US-Canada border and populations to the north. Lower wolverine occupancy estimates in the

southern/transboundary regions compared to those in the central Columbia and Rocky Mountains may be a result of habitat quality and/or human disturbance on wolverine distribution and abundance.

Several wolverine researchers have recommended the creation of refugia (such as those created by protected areas like the Banff-Yoho-Kootenay and Waterton-Glacier national park complexes) or restricting or eliminating trapping quotas – as a crucial element in the overall conservation of wolverine (Weaver et al. 1996, Krebs et al. 2004). Due to the large home ranges of wolverines and their low density, an effective conservation strategy will require large areas managed at both regional and transboundary metapopulation scale. Similar transboundary management schemes have been developed for other wide-ranging carnivores in the past (Proctor et al. 2012).

Our next steps are to use the data collected the last three years in the CCoC to create spatially explicit capture-recapture (SCR) models to produce the first density estimates of wolverines in this area. As part of this analysis, our wolverine density estimates will inform management of wolverine harvest to ensure long-term persistence and viability of wolverines in one of the last remaining linkage zones with populations in the Northern Continental Divide Ecosystem. Further, we will apply the SCR method across a gradient of human land-uses and landscape characteristics in the CCoC to assess potential impacts on wolverine spatial distribution, abundance and landscape connectivity (Royle et al. 2013, Graves et al. 2014).

CHAPTER 4.0 ESTIMATE WOLVERINE DENSITY IN CANADIAN ROCKY AND COLUMBIA MOUNTAINS

4.1 Introduction

There is considerable conservation concern for wolverines (*Gulo gulo*) throughout their range in North America (Ruggiero et al. 2007, COSEWIC 2014). Wolverines were extirpated in much of their southern and eastern range post-European contact and many populations along the current southern range are still partly or entirely isolated from the continuous population in northwest North America (Aubry et al. 2007, COSEWIC 2014, IDFG 2014). One conservation risk to wolverine populations in some parts of their range is the demographic impact of fur trapping (Krebs et al. 2004, Lofroth and Ott 2007). Western and northern Canada and Alaska allow trapping. Portions of southwest British Columbia (BC) and most of the lower 48 states closed trapping several decades ago.

Wolverine are described as facultative scavengers and the amount of food they scavenge is related to prey abundance, the proximity of the prey to carrying capacity, and the presence of other large carnivores that kill large prey that wolverine could not kill themselves (van Dijk et al. 2008, Mattisson et al. 2016). In Scandinavia, the more food-limited reindeer (*Rangifer tarandus*) there were, the more reindeer calves wolverine killed in spring (Mattisson et al. 2016). Wolverine reproduction appears to be contingent on adequate female body condition (Persson 2005) and even adult females regularly fail to reproduce. Survival of wolverine may also be influenced by food limitation (Saether et al. 2005). Researchers in southern Sweden have shown strong density-dependence in survival of wolverine (Broseth et al. 2010). Food availability, moderated by variation in ungulate abundance, vulnerability and kills by other predators— including people—

across space and time limits wolverine growth. The large potential variation in wolverine vital rates suggests that population growth and density of wolverine could be quite variable across its range.

Wolverine also hunt smaller prey such as snowshoe hares (*Lepus americanus*), marmots (*Marmota caligata*) and ground squirrels (*Spermophilus columbianus*; Lofroth et al. 2007, Inman et al. 2015) and they confine their use of the landscape to higher elevation ecosystems in montane environments in North America (Inman et al. 2012b) where these species are often most common. Caribou (*Rangifer tarandus*) and mountain goats (*Oreamnos americanus*) are the most common ungulates found in these environments in winter.

The distribution of wolverine and the location of their dens has been linked to the presence of continuous snow cover during the spring denning period (Copeland et al. 2010, Magoun et al. 2017). These authors also found that radio telemetry locations and home ranges in spring were mostly in areas of continuous spring snow. The functional link is not clear but there are three working hypotheses to explain the link between spring snow and wolverine distribution. The first hypothesis proposes the need for snow to protect the safety and thermoneutrality of the young in the den. The second hypothesis is based on the observation that wolverine cache food for winter. Inman et al. (2012a) suggested that wolverine require continuous snow during late-fall to spring to preserve food during winter because food is particularly scarce during this season. Third, wolverine may be physically adapted to snow covered temperate environments and these adaptations may exclude them from moderate environments (Lofroth et al. 2007, Schwartz et al. 2009).

Wolverine density has been studied in one area of southern Canada, but see Barrueto et al. (submitted) for an earlier analysis of a portion of the data included here. Using live-capture data and open capture-recapture models during 4 years of study, these researchers calculated a mean density across years, and they used camera sightings and a closed model to obtain a single estimate of abundance during one winter of study (Lofroth and Krebs 2007). Both these estimates were likely biased low because the substantive food baits placed at the capture sites meant previously captured animals were more likely to be captured in subsequent trapping sessions than animals that had never been captured. However, density estimates were not corrected for the partial residency of those animals living near the study area boundary, which probably caused a positive bias in the density estimates. Wolverine density was also estimated in a sister study that used very similar methods in the northern limit of the montane mountains in central BC. These two studies yielded density estimates of about three individuals per 1000 km². Other estimates of wolverine density, in similar ecosystems, were similar (Lofroth and Krebs 2007), except for one study in Idaho (Hornocker and Hash 1981) which observed much higher density. We suspected that biases influenced previous estimates of wolverine density though the combined effect on the density estimates is unclear.

Natural mortality of wolverines has been observed to vary greatly from 4-20% per year (Krebs et al. 2004, Squires et al. 2007, Persson et al. 2009) and reproduction is very low for an animal of this size. Females produce <0.5 female young per year (Persson et al. 2006). Previous researchers used simple population models and observed estimates of survival and reproduction to estimate the influence of trapping mortality on population growth. They concluded that wolverine demographics are sensitive to adult mortality and

that current harvest rates in North America may limit population growth, except perhaps in parts of northern Canada and Alaska where mortality rates appear to be lowest (Krebs et al. 2004, Squires et al. 2004, Lofroth and Ott 2007). None of these models incorporated density dependence or accommodated differential sex and age-based trapping vulnerabilities and hence they may have under-estimated sustainable harvest rates.

A specific analysis of harvest sustainability in BC by Lofroth and Ott (2007) suggested recent levels of wolverine kill were sustainable at the provincial scale but harvest in some areas may not have been sustainable. They found that uncertainty in the harvest data was an important part of the conservation risk and recommended improved data collection and evaluation. A different probabilistic modeling approach also concluded that adult mortality was the population parameter of greatest sensitivity (Dalerum et al. 2007). These authors gamed their model with various realistic harvest scenarios and immigration levels and found that the model population was sensitive to adult female harvest and that immigration was necessary to ensure long-term viability and avoid extirpation. Saether et al. (2005) examined conservation risk in the Scandinavian wolverine population using a population viability approach and found that harvest posed the largest conservation risk to the population. In summary, previous studies of wolverine demography suggest that the species can support small, male-dominated harvests and that harvesting isolated populations presents considerable risk of population decline or extirpation.

We used baits to sample wolverines across large areas, genotypes from hair samples to identify individuals, and spatial mark-recapture analysis to estimate population density. Juvenile and yearling dispersal begins in January, when we began our

trapping, and males probably disperse more commonly than females (Magoun and Copeland 1998, Morten Vangen et al. 2001, Gervasi et al. 2015). Sub-adults have larger home ranges than adults while they are searching for a permanent range; sub-adult males cover particularly large areas (Inman et al. 2012b). In addition, pregnant female wolverines begin looking for dens in January and their young are born in February or March (Magoun 1985, Banci 1994, Magoun and Copeland 1998). Hence, breeding females had restricted home ranges during our sampling period. The variation in home range size among sex and age cohorts is enormous in wolverine and likely greater during our sampling period in late winter than any other time of year. Resident females with young may have home ranges $<100 \text{ km}^2$ while dispersing sub-adult males may have home ranges $>2000 \text{ km}^2$. Hence, we may expect considerable bias in all density estimators that do not specifically account for space and individual variation in detection probability due to these space use patterns (Royle et al. 2011).

We used institutional harvest data to estimate the range of recent wolverine trapping kills. We then calculated observed wolverine harvest rates using our estimates of population size and compared these to sustainable harvest rates as predicted from population models to evaluate conservation risk. We also built a population model using a meta-analysis of vital rates, the age and sex ratios of trapped animals and our observed density estimates, to calculate putative sustainable harvest rates.

The main objective of this study was to evaluate the demographic risk of trapping to wolverine populations in southeast BC and the adjacent Rocky Mountains of southern Alberta. Second, we tested the hypothesis that spring snow was related to the density of wolverine. Lastly, we investigated habitat factors that were related to the density of

wolverine to gain insights into their habitat needs and to predict density in areas that we did not sample.

4.2 Study Area

Our study area included the Kootenay-Boundary region in southeast BC and the southern Rocky Mountains and foothills of southwest Alberta (Figure 4). This area is mountainous and included parts of the Monashee, Selkirk, Purcell, and Rocky Mountains. Many large lakes, highways and human settlements occur in low elevation valleys and may create resistance to movement. Extensive forest harvest has occurred throughout the area and mining was widespread historically but is much less active currently. Both industries built and continue to build many roads. Winter recreation (snow machine use, ski resorts, helicopter or snowcat-access skiing, ski lodges and backcountry skiing) was common. Provincial and national parks and protected areas occur throughout the area.

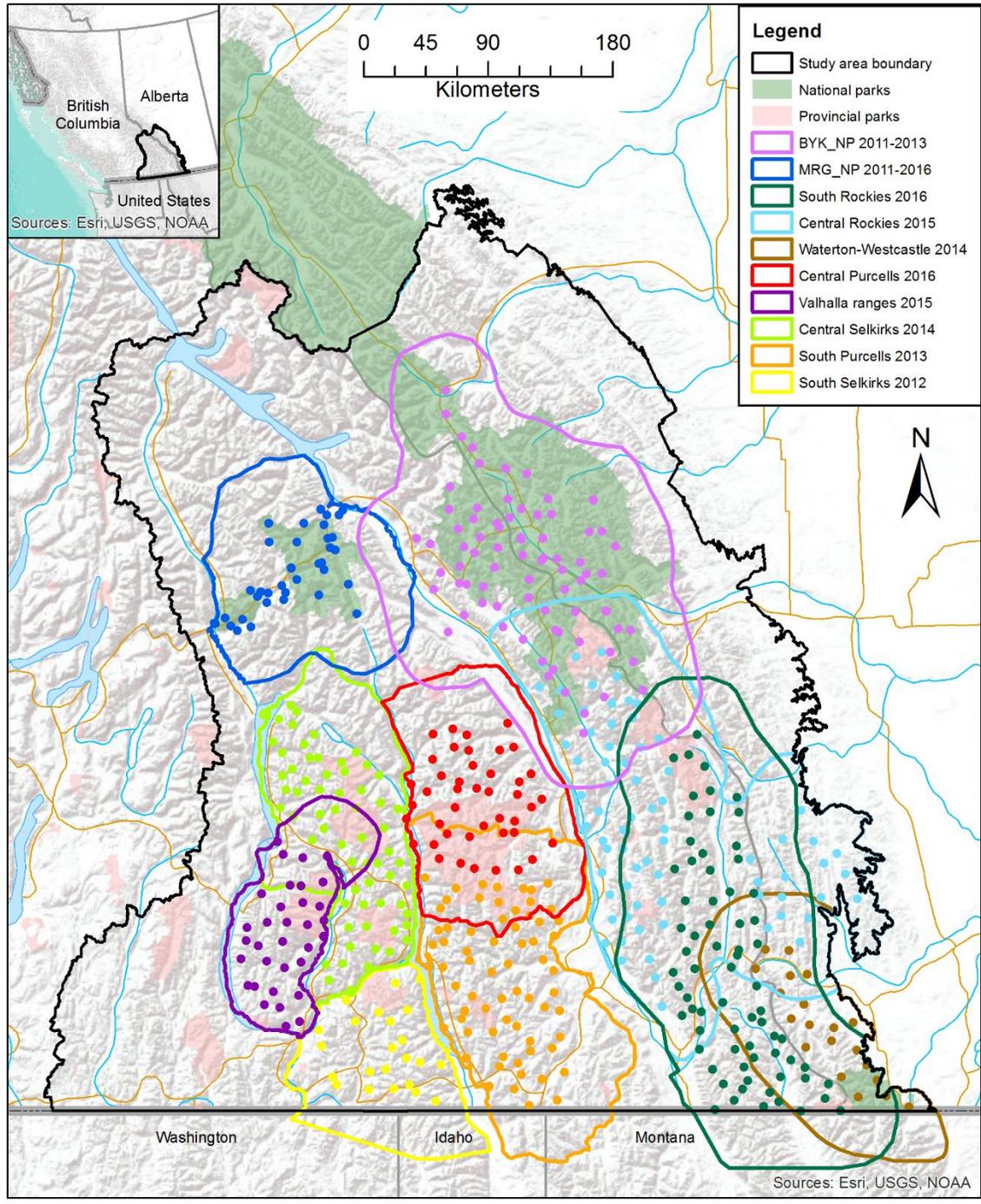


Figure 4. Wolverine winter sampling areas showing trap locations and secr mask boundaries for each area in matching colors. Mask boundaries were created by assuming large lakes were hard population boundaries and, where boundaries did not exist, the mask was extended approximately 40 km beyond the outer sample sites. The year of sampling is given with the study area name and is the year during late winter.

Elevations range from 400 m to >3000 m with major variation in summer and winter precipitation. In general, the mountains become less rugged from north to south, which leads to lower precipitation as well, though precipitation also roughly declines from west to east. Low elevation forests are composed of western redcedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), Douglas fir (*Pseudotsuga menziesii*), Ponderosa pine (*Pinus ponderosa*), lodgepole pine (*Pinus contorta*), trembling aspen (*Populus tremuloides*), and western larch (*Larix occidentalis*). At higher elevations, Englemann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) forests transition to treeless alpine meadows, rock and ice (MacKillop and Ehman 2016).

Potential wolverine ungulate prey included mountain goats, mountain caribou, mountain sheep (*Ovis canadensis*), moose (*Alces alces*), elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*O. virginianus*). Only mountain goats and caribou were found at high elevations consistently during winter; goats were irregular in their distribution and rarely abundant (Poole 2006). Caribou have declined to <200 individuals as of 2018 (Aaron Reid, BC Ministry of FLNRORD, pers. comm.) and were confined to four areas with large expanses of the study area without caribou. Small mammal prey included; hoary marmots, Columbian ground squirrels, snowshoe hares, American pika (*Ochotona princeps*) and porcupine (*Erithizon dorsatum*; Lofroth et al. 2007).

4.3 Methods

We collected samples from wolverines during late winter by remotely removing hair and occasionally collecting scat samples. We sampled five study areas in the West Kootenays during 2012- 2016 and three study areas in the East Kootenays during 2014-

2016 in southeast BC and southwest Alberta. The project partitioned each study area into 10 by 10 km cells that approximate the minimum size of a female home range. We set one or two bait sites in each cell and checked them twice in the West Kootenays and three times in the East Kootenays at roughly monthly intervals. Because of the rugged nature of the terrain, we selected sites for ease of access and used local knowledge of wildlife movements when available. Hair traps were made by wrapping barbed wire around a baited tree to capture hair from an animal that climbed the tree after the bait, similar to Mulders et al. (2007). We used a deer or elk head as bait in the West Kootenays and a skinned beaver carcass in the East Kootenays and Alberta. We attached bait to the tree approximately two meters from the ground or snow surface. Each time we re-visited the site, the barbed wire was examined for hairs and the bait replenished if necessary. Each barb was burned after hair was collected to clean the wire of any remaining hair. We collected and stored hair in paper envelopes in a dry environment. In the East Kootenays a camera was attached to a nearby tree to photograph animals that visited the site. During each visit to the bait site we looked for wolverine tracks and scat. We also included data from five different sites in 2015 and 2016 in the East Kootenays sampled contemporarily for two different environmental impact assessments using similar methods.

Additionally, we collected data using similar methods in two areas centered around national parks. The primary objective of these studies was to examine movement across the highways that crossed the parks (Sawaya et al. submitted). We collected data for 5 years near Revelstoke in Mt. Revelstoke and Glacier National Parks and for 3 years in Banff, Kootenay and Yoho National Parks. These studies used three sampling sessions

and beaver as bait like our East Kootenay study areas. See Barrueto et al (submitted) for more detail on sampling methods in the East Kootenay National Parks. Hair samples were sent to Wildlife Genetics International (WGI) in Nelson B.C. for microsatellite genotyping. Only samples that had >1 guard hair with a root or >5 underfur were selected for analysis and we used up to 10 guard hairs or approximately 30 underfur in an extraction. The project extracted DNA using QIAGEN DNeasy Tissue kits following the manufacturer's instructions (Qiagen Inc., Toronto, ON). Species identification was based on a sequence-based analysis of a segment of the mitochondrial 16S rRNA gene (Johnson and O'Brien 1997). For samples that yielded wolverine DNA, WGI utilized multilocus genotyping, consisting of a ZFX/ZFY sex marker, and 7 additional microsatellite markers for individual identification. Error checking followed established rules (Paetkau 2003), which have been exhaustively tested using grizzly bear hair and found to deliver very low error rates (Kendall et al. 2009). The studies in the national parks were first analyzed at the Rocky Mountain Research station laboratory in Missoula, Montana using nearly identical methods. One sample from each individual was later reanalyzed at WGI in order to verify that individual identities were comparable between the labs and studies in order to combine the datasets.

We estimated wolverine trapping harvest rates using government collected kill data. In British Columbia (BC) and Alberta, trapping is regulated by a registered trapline system where licensed trappers must either own a registered trapline, or have permission to trap on private land or someone else's trapline. Very few areas are trapped by more than one person so trapping effort tends to be well dispersed in Canada (Slough et al. 1987). In southeast BC and southwest Alberta, trappers may trap wolverine between 1

November and 31 January and each trapper may catch one wolverine per year in Alberta while there is no limit in BC. Most public land not classed as a park is included in a registered trapline and traplines even occur in some recent provincial parks. Trapper kill is recorded by mandatory reporting in southern BC and Alberta and by the fur sales recording system throughout BC. Hunters must submit all wolverines they kill to a government inspector, though few wolverines are killed by hunters. Occasional wolverines kills occur in highway collisions, but few of these are recorded. See Lofroth and Ott (2007), Hatler and Beal (2003) and Webb et al. (2013) for more details on wolverine trapping and management in BC and Alberta.

4.3.1 Spatial capture-recapture analysis

We used spatial capture-recapture analysis (secr) to estimate wolverine density (Efford 2004, Efford 2018). This method is fast becoming the standard method for estimating animal density (Royle et al. 2013). Spatial capture-recapture methods estimate three parameters: detection, a spatial parameter and density. The detection parameter can be likened to the detection probability in non-spatial capture-recapture; although in this case, detection probability declines with distance from the animal's putative home range center. The spatial parameter is an index of the range size during sampling, and along with the trap and animal location data, is used in estimating residency of individuals in and near the sampling area. The final parameter is density, which is the response variable and commonly the parameter of interest.

Covariates can be fit to all estimated parameters in order to remove bias, improve model fit or better predict density within or beyond the study area. Covariates can also be fit to trap sites and individuals to accommodate heterogeneity in detection or space, or

among individuals, but there is a limit to the number and type of covariates that can be fit simultaneously (Efford 2018). We accommodated variation in sampling effort by coding the number of days each trap was set directly into the trap data. Detection success commonly increases from mid to late winter in wolverine (Broseth et al. 2010, Royle et al. 2011,) and so we allowed the detection parameter to vary among trapping sessions, expecting increased detection in latter sessions. We expected female ranges to be smaller than males, but we did not run separate analyses for each sex to estimate density because we had small sample sizes, and smaller range size is often compensated for by higher detection success (Efford and Mowat 2014). In this case combined models often yield nearly identical density estimates to separate models for each sex.

Our hair traps were far apart and included a substantive meat reward. Many individuals had few traps in their home range and were more likely to pass by a site they had already visited than a different site, especially given the food reward. Hence, we expected repeated detections of an individual wolverine would be more likely at sites they were detected at previously, and we allowed for this explicitly in our model structure. This trap-based behavior response has been detected in wolverine (Mulders et al. 2007, Royle et al. 2011) and many other carnivore species where baited sites were used.

Additionally, we hypothesized that wolverine winter movements may be influenced by current snow cover, which varied considerably among years during our study. We measured snow depth on the final visit to each detection site and entered this as a trap covariate for detection on the idea that current snow conditions may influence movement and hence detection. We tested to see if the difference in baits used in the East

and West Kootenay measurably influenced detection success. In addition, we included a parameter (DNA) that allowed for different detection success based on which lab originally analyzed the genetic data.

We calculated mean annual home range sizes for all wolverine studies done in the montane region of western North America. Where possible we chose extensive estimates such as 95% minimum convex polygon estimates and did not use core estimates. We weighted the mean from each study by the sample size of individual animals and used this mean to calculate a priori sigma values, which is the spatial parameter that scales for density in secr models. Sigma can be calculated as $\sigma = r/2.45$ where r is the radius of the 95% home range (Sun et al. 2014). We compared these independently calculated spatial values to those estimated by secr analysis of our detection data.

Wolverine density is affected by human-caused mortality, principally trapping in BC and Alberta (Krebs et al. 2004). We tested for this effect within our study areas by coding all pixels in each trapline with the number of wolverine killed the winter we worked. Trapping kills were assigned to a trapline because exact mortality locations were rarely collected. By assigning the number of trapped wolverine to a trapline, we had a spatial depiction of recent trapping mortality that could be incorporated into the secr analysis as a spatial mask. We corrected for the variation in trapline sizes by dividing the number of wolverine killed by area of the trapline.

We hypothesized that wolverine density would be higher in higher elevation ecosystems. Wolverines appear to use higher elevations at all times of year and especially in winter (Krebs et al. 2007, Inman et al. 2012b). We assumed that wolverine were not choosing elevation itself but preferred plant associations and climate envelopes typical of

higher elevation or latitudes (Copeland et al. 2010). Additionally, females are known to den at higher elevations in montane areas (Krebs et al. 2007). We used ecological mapping (MacKillop and Ehman 2016) to divide each study area into three broad zonal ecosystems:

- i) Low elevation forests which were wetter in our western study areas than our eastern study areas.
- ii) Subalpine forest of Englemann spruce-subalpine fir (ESSF) typical of upper elevations in North American montane forests.
- iii) Alpine, which included all high elevation communities such as alpine tundra and grassland, parkland and woodland forests and rock.

Because precipitation increases with elevation, both the latter ecosystems were wetter, snow affected ecosystems. Permanent ice was excluded. Alpine and ESSF were included as masks to test the idea that habitat type was related to density while low elevation forest was excluded to contrast the other two habitats.

Snow cover varied considerably across our study area. We calculated the average spring snow cover for each year from 2000-2016 using MODIS data (after Copeland et al. 2010) and included the score for the presence of snow (0-17) in our secr analysis as a mask to test the relationship between spring snow cover and local wolverine density.

We calculated road density using up to date road data acquired from both provincial governments. We used open source data for roads in the USA. We also acquired Human Influence Index mapping as an alternative and more generalized measure of disturbance (<http://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-influence-index-geographic>).

The spatial data for all variables were re-scaled using a moving window analysis with a radius of 10 km, which is roughly the radius of a female home range. We did this because secr uses the habitat value at the putative home range center, but we felt wolverine density would be more strongly related to the amount of each spatial variable in the entire home range and not at a specific site.

4.3.2 Population model

We built an annual discrete-time population model to better understand sustainable harvest rates of wolverine. A number of previous efforts have used population modelling to examine the sustainability of harvest (Krebs et al. 2004, Lofroth and Ott 2007, Squires et al. 2007, Dalerum et al. 2007) or population viability (Saether et al. 2005). In particular, we wanted to understand how sex and age-biased harvest affected harvest sustainability, and how environmental stochasticity and density dependence might further influence harvest rates. We used field data from radiotelemetry studies to parameterize reproduction and survival and we used carcass studies to estimate potential reproduction based on in-utero measures of pregnancy rate and the proportions of each age and sex cohort in the trapped sample. Vulnerabilities to harvest of each sex and age class were estimated by solving the system of equations that aligned the model output with the sex and age structure of observed harvested samples. We added environmental stochasticity to the reproduction component of the model because successful reproduction appears to be closely linked to late winter food abundance, which can be as random an event as the discovery of a single ungulate carcass by an individual female (Mattisson et al. 2016). For each reproductive parameter, a beta distribution was used to generate

random realizations that fell within a set expected value (tol) of the parameter approximately 95% of the time.

Our model was structured into 5 cohorts: juveniles, yearling females and males, and adult females and males. Annual survival was split into an initial pre-harvest rate and a second post-harvest rate that modestly reduced the initial rate as a function of harvest rate. Density dependence was incorporated into reproduction using a theta power function. Only one study has estimated theta for wolverine (Saether et al. 2005) and it found evidence for very strong density-dependence near carrying capacity (K; theta = 12.5). We set K at roughly 50% higher than our observed population estimate because much of the study area appeared to be unoccupied though this was often the poorer habitat. Density-dependence was trivial when K was 50% higher than the starting population size. We used survival rates from Krebs et al. (2004) for yearlings and adults and juvenile survival as measured by Persson et al. (2006). We used the mean reproduction observed by 3 field studies (Magoun 1985, Copeland 1996, and Persson et al. 2006). This value (0.77 young/year/female) was for adult females only as yearling females have not been observed to reproduce. The sex ratio of litters at birth was assumed to be equal. Age ratios of trapper killed carcasses were 36% juveniles, 20.2% yearling males, 12.6% yearling females, 20.4% adult males, and 10.8% adult females and were derived by taking the mean ratio from five mid to long-term carcass collection studies from northern Canada (Banci and Harestad 1988, Mulders 2000, Awan and Szor 2012, Lee 2016 and Kukka et al. 2017). We first ran a model to solve for harvest vulnerabilities which were then used as parameters in the subsequent population modelling process. We ran the model for 60 years and focused attention on its long-term steady state behaviour.

Initial cohort sizes were based on observed age and sex ratios, which totaled to our estimate of the population size for the study area. It took about 10 years for the age structure to stabilize for each new model run. All data and models were built in R (R Core Team 2016).

4.4 Results

4.4.1 Density and harvest rate

We sampled wolverine during 6 winters between December 2010 and April 2016 throughout southeast BC and southwest Alberta (Figure 4). We identified 126 individual wolverine that were detected 326 different times across years, study areas, trapping occasions and sites (Table 6). Only the two study areas in the national parks were sampled more than one year and these study areas generated much of the recapture data in the dataset (Table 6).

We found that wolverine were more commonly detected at traps where they had previously been detected, which is expected when food rewards are provided at trap sites. We also expected detection success to increase as the winter progressed, but variation among capture occasions was not supported (Table 7). The best fitting detection model included separate detection parameters for each sampling area and year, but this model had 19 parameters and was unstable. This model was unrealistic given the small sample sizes in some studies (Table 6) and we did not consider it further. The binary variables representing the two genetic labs, snow depth at the trap site, and bait type were all weakly related to detection probability, so we did not include these variables in further analyses. Trap-effort and trap-specific behavior were included in all future model fitting to account for the variation in detection probability among traps and individuals.

Table 6. Wolverine sampling effort and detection success in southeast British Columbia and southwest Alberta, 2011-2016. Year is the year at the end of the sampling winter and the area sampled is the mask area for each study area (Fig. 4). BYK_NP stands for Banff, Kootenay and Yoho National Parks. MRG_NP stands for Mount Revelstoke and Glacier National Parks. There were 153 individuals among the sampling areas and years which equaled 126 individuals because some animals were detected in multiple sampling areas or years.

Study Area	Year	Area sampled (km²)	Sites sampled	Detection occasions	Individuals detected	Detections (spatial detections)	Mean trap spacing (km)
Rocky Mountains							
BYK_NP	2011	19,617	48	3	23	46 (46)	8.5
BYK_NP	2012	19,617	10	3	8	14 (14)	12.9
BYK_NP	2013	19,617	64	3	26	62 (63)	7.6
Waterton-Westcastle	2014	7347	20	3	1	1 (1)	9.3
Central Rockies	2015	18,785	78	3	11	21 (28)	8.7
South Rockies	2016	18,714	75	3	11	22 (37)	7.1
Purcell Mountains							
South Purcells	2013	10,833	66	2	8	9 (12)	7.0
Central Purcells	2016	7910	43	2	8	11 (23)	7.1
Selkirk Mountains							
MRG_NP	2011	7150	6	3	3	4 (4)	9.7
MRG_NP	2012	7150	7	3	9	11 (11)	6.1
MRG_NP	2014	7150	12	3	3	3 (6)	4.4
MRG_NP	2015	7150	6	3	10	15 (20)	12.4
MRG_NP	2016	7150	6	3	10	13 (13)	8.9
South Selkirks	2012	5452	23	2	4	5 (6)	7.8
Central Selkirks	2014	7863	63	2	16	22 (40)	7.0
Valhalla ranges	2015	4445	33	2	2	2 (2)	7.5
Total			560		153	261 (326)	7.75

Table 7. Model selection table to evaluate possible variation in detection success for wolverine sampled in southeast British Columbia and southwest Alberta, 2011-2016. D = density, g0 = detection probability, sigma = movement parameter, bk = trap specific behavior, snowdepth = snow depth at trap site at last check, DNA = separate g0 for each genetic lab, Bait = separate g0 for ungulate versus beaver bait, t= separate g0 for each trapping occasion. k = the number of model parameters, logLik = model log likelihood value, AICc = Akaike Information Criteria corrected for small sample size, Δ AICc = the difference in AICc values, weight = relative model weight based on Δ AICc values.

model	k	logLik	AICc	ΔAICc	weight
D~1 g0~bk sigma~1	4	-1078.2	2164.676	0	0.2487
D~1 g0~DNA + bk sigma~1	5	-1077.14	2164.695	0.019	0.2463
D~1 g0~bk + snowdepth sigma~1	5	-1077.19	2164.797	0.121	0.2341
D~1 g0~Bait + bk sigma~1	5	-1077.42	2165.24	0.564	0.1876
D~1 g0~t + bk sigma~1	6	-1077.14	2166.861	2.185	0.0834
D~1 g0~t sigma~1	5	-1101.78	2213.969	49.293	0
D~1 g0~1 sigma~1	3	-1107.33	2220.828	56.152	0
D~1 g0~snowdepth sigma~1	4	-1107.08	2222.43	57.754	0

Detection probability was 0.006 (SE 0.001) for wolverines that were detected at a trap for the first time and 0.023 (SE 0.003) for individuals that had already been detected at the same trap. Previously detected animals had 4 times the chance of being detected again at the same trap, which is a very strong behavior response. Sigma, the spatial parameter, was 9.8 km (SE 0.54 km) for both sexes combined and 11.2 km (SE 0.95 km) for males and 8.4 km (SE 0.61 km) for females. Sigma values, as calculated from home range data for wolverines living in montane areas, varied from 4.4 km for adult females to 11.4 km for sub-adult males (Table 8). Sub-adults may make such large movements while exploring for a permanent home range that they may effectively emigrate from many study areas (Inman et al. 2012b). Our mean sigma value, which was pooled across age-classes, was closer to the size expected for males than females and the sex-based values were closer to those expected for sub-adults than adults (Table 8).

Table 8. Mean annual home range size for wolverine in the montane mountains of western North America (see SM for data). Sigma is the movement parameter estimated via secr and was calculated as $\sigma = r/2.45$ where r is the radius of the 95% home range (Sun et al. 2014).

Sex	Age	Mean home range size (km²)	Home range radius	sigma	n
Female	Adult	339	10.4	4.2	28
Female	Sub-adult	787	15.8	6.5	22
Male	Adult	1097	18.7	7.6	25
Male	Sub-adult	2333	27.3	11.1	16

After testing the influence of covariates on detection probability, we tested variables we hypothesized would be related to density. We did not compare spring snow with alpine or ESSF (high elevation forest) in the same model because these variables were strongly correlated. Spring snow and road density were most strongly related to estimated density (Table 9); all other variables generated only minor improvements in fit. Surprisingly the trapping mortality variable was not related to density (Table 9). Density varied from 0.9 to 4.4 wolverine/1000 km² among our sampling areas and averaged 2.0 (CI 1.70-2.47) across the study area. We also ran the top model separately for each sex, and summed male and female densities were nearly identical to the mean density as estimated by the model that did not accommodate sex. Females were 62% of the estimated population. Density was positively related to the annual consistency presence of spring snow cover and negatively related to road density (Figure 5).

Table 9. A comparison of the fit of a selected group of models to estimate density of wolverine in southeast BC and southwest Alberta. All models include trap specific behavior ($g_0 \sim bk$) and no covariation for spatial parameter ($\sigma \sim 1$). Roaddden = road density, Snow17 = the number of years with spring snow cover between 2000-2016, TrapHarvest = area weighted measure of the number wolverine killed in the trapping season previous to sampling, Alpine = the proportion of alpine habitat, ESSF = the proportion of upper elevation forest, Hii = human impact index which is a cumulative measure based on road density, human habitation and other human footprints.

model	k	logLik	AICc	ΔAICc	weight
D~roaddden + Snow17	6	-1037.6	2087.7	0.0	0.52
D~roaddden + Snow17 + TrapHarvest	7	-1037.4	2089.6	1.9	0.20
D~Snow17	5	-1039.9	2090.2	2.5	0.15
D~hii + Snow17	6	-1038.9	2090.4	2.7	0.13
D~roaddden + Alpine	6	-1042.5	2097.5	9.8	0.00
D~roaddden + ESSF + Alpine	7	-1042.3	2099.4	11.7	0.00
D~roaddden + ESSF + Alpine + TrapHarvest	8	-1041.9	2100.8	13.1	0.00
D~roaddden	5	-1045.7	2101.7	14.0	0.00
D~Alpine	5	-1048.2	2106.8	19.1	0.00
D~hii	5	-1063.9	2138.3	50.5	0.00
D~ESSF	5	-1076.4	2163.2	75.5	0.00
D~1 (null)	4	-1078.2	2164.7	77.0	0.00
D~TrapHarvest	5	-1077.8	2166.0	78.2	0.00

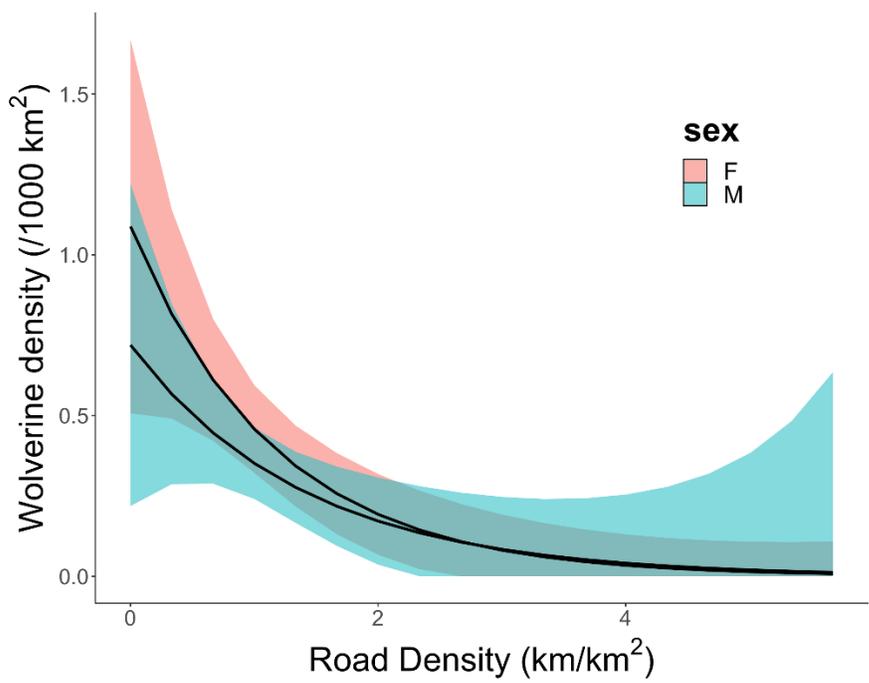
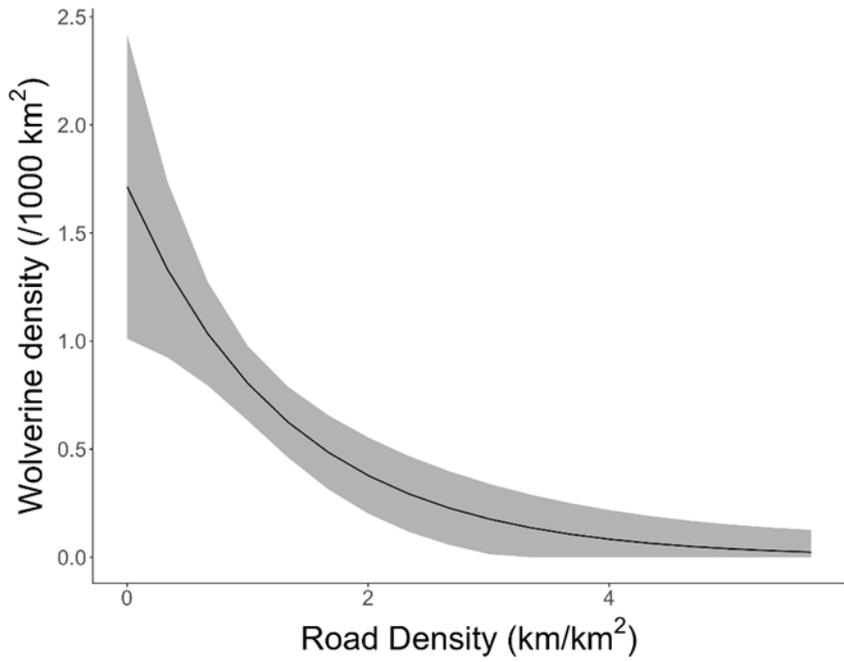


Figure 5. The relationship between spring snow cover, road density and wolverine density based on our best fit model (model 2 in Table 9). We built our spring snow map using 17 years of snow cover data following methods outlined in Copeland et al (2010). The upper figure is for the combined sex model and the lower figure is for separate sex models.

Our data are the first to observe a positive relationship between wolverine abundance and spring snow cover. This observation supports the earlier hypothesis that the distribution of wolverine relates to the probability that an area has complete snow cover during the late denning period. The slope of the relationship between spring snow and density was steeper for female than male wolverines (Figure 5), which suggests snow cover affected their habitat choice or survival more than males.

We used this model to extrapolate wolverine density to our entire study area; estimated density generally declined from north to south (Figure 6). We derived population estimates for the Kootenay Region of BC, the Alberta portion of our greater study area, and for the two areas combined. The wolverine kill during the 6 years of our field sampling and the 3 years previous averaged 19 animals/year for the greater study, and 16.6 animals in the BC portion and 2.3 animals in the Alberta portion of our study area. Our estimate of the kill rate for the entire study area was 8.4%. The kill rate in BC was higher than the kill rate in Alberta (Figure 7) because much of the wolverine distribution in southern Alberta was in national parks (Figure 6). We also set road density to zero and predicted wolverine abundance without the depressing effect of the road covariate; abundance increased 44% from 226 (SE = 21.5) to 326 (SE = 66.2).

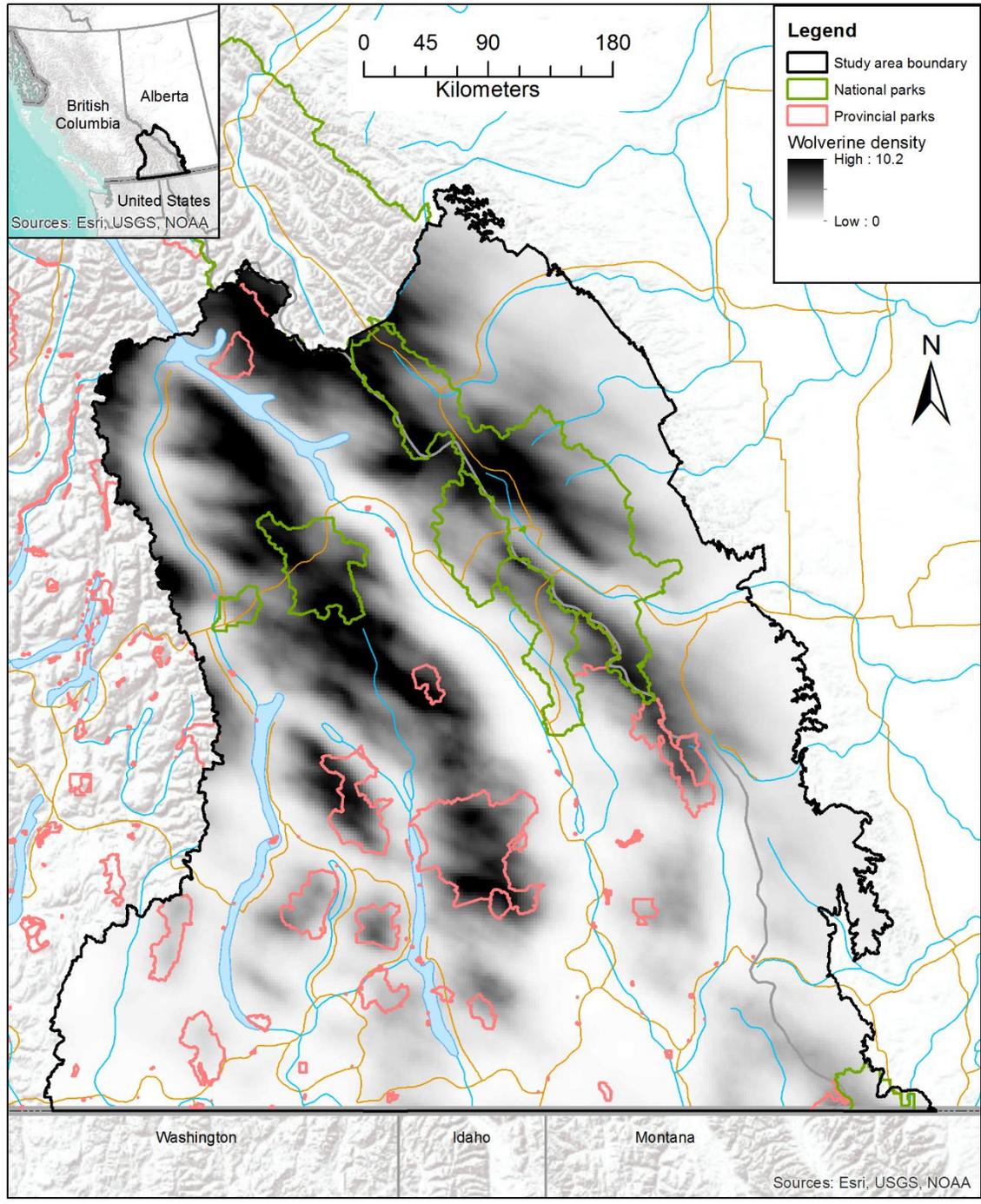


Figure 6. Wolverine density in southeast BC and southwest Alberta estimated from spatial capture-recapture analysis of genetically identified wolverine sampled during winter 2011-2016. There was no trapping in national parks but trapping was permitted in some provincial parks.

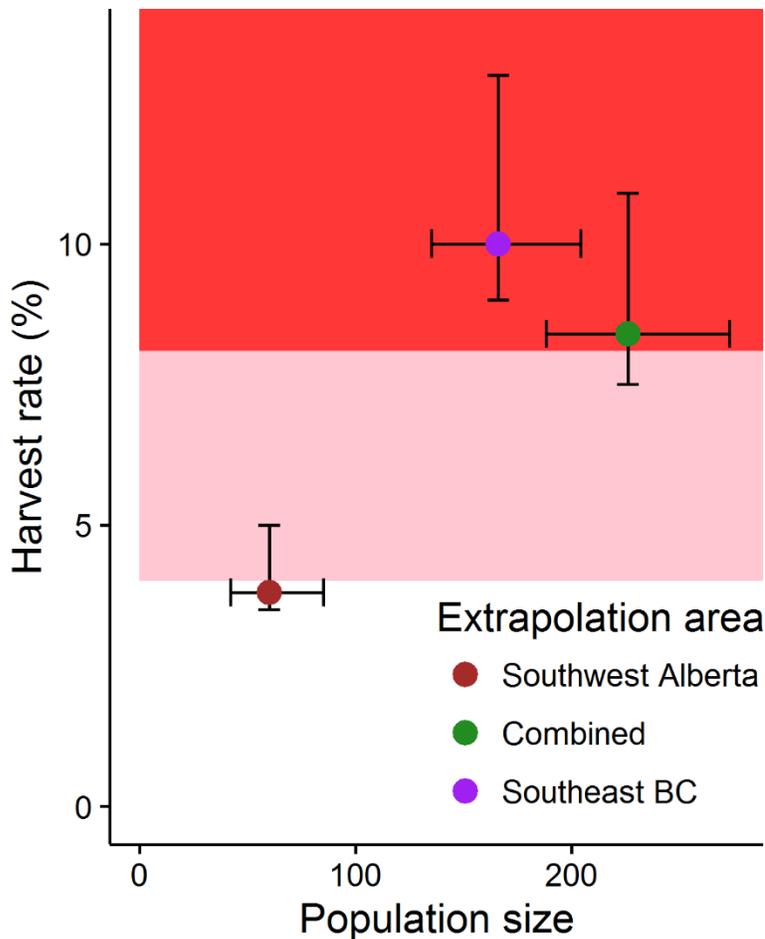


Figure 7. The harvest rate of wolverine based on population estimates extrapolated from spatial capture-recapture analysis of genetically identified wolverine sampled during winter 2011-2016 in southeast BC and southwest Alberta, Canada. Horizontal error bars are 95% confidence intervals of population estimates. Vertical error bars are our best guess of the likely error in the recording of wolverine trapping kill. Pink shading denotes harvest above recommended levels, red shading denotes harvest rates that are likely not sustainable.

4.4.2 Population modeling

Our population model suggested maximum sustainable mortality rates were 6.2%/year when harvest was drawn at random among sex and age classes. This result is similar to all other modelling efforts that also assumed a random harvest. We then used the mean age structure from published carcass studies to calculate harvest vulnerabilities by age and sex cohorts and found that young age classes were 6-10 times more vulnerable to harvest than adult females. When these vulnerabilities were incorporated in

our model, the average maximum sustainable harvest increased to 8.3%. Stochasticity in reproduction caused rapid declines in the sustainable harvest rate from 8.1% at $\text{tol} = 0.05$ to 7.2% at $\text{tol} = 0.1$ to zero when tol was 0.4.

The above models used reproduction and survival values measured in the field and maximum sustainable harvest was quite sensitive to variation in reproduction. When we varied adult reproduction from 0.6-1 young/female/year (yearling reproduction was zero), the maximum sustainable harvest rate varied from 5-12%.

Potential reproduction in wolverine is much higher than what has been observed in the field post-partum because many more females are pregnant than give birth, including some yearlings. When we used in-utero pregnancy rates in our model the maximum harvest rate increased to between 18-23%.

4.5 Discussion

Wolverine trapping harvest is likely not sustainable in southeast BC and southwest Alberta, and the current level of mortality presents considerable conservation risk to this population. While the observed harvest rate equaled the theoretical maximum we calculated in our population modelling exercise, the study area includes many parks and protected areas, so the harvest rate in the portion of the study where trapping was allowed far exceeded sustainable levels. The uncertainty in the recording of the wolverine harvest largely leads to under-reporting which created a substantive portion of the conservation risk (Figure 7). Several other North American researchers have concluded that wolverine harvest in their study populations was not sustainable or was being sustained by immigration (Krebs et al. 2004, Squires et al. 2007, Dalerum et al. 2008).

So what is the sustainable harvest rate for wolverine in this area? Harvest rates can be considered the policy portion of the harvest regime because the selection of an allowable harvest rate involves both social and biological considerations (Mowat et al. 2013). The scientific part of the regime is often described by data and we collected data on population size and used various sources of data to build our population model. The social component involves the trade-off between the value to society and the perceived risk to the population. Wolverine generate relatively little value to the trapping industry compared to other important furbearers like marten or lynx, but moderate value to the few trappers that catch them. About 15 trappers catch wolverine in our study area each year. Conservation risk from harvest is high because wolverine occur in a discontinuous fashion at low densities, have few young, and harvest sustainability was strongly affected by environmental stochasticity which could greatly affect reproduction (Persson 2005). Because of the low monetary value and high conservation risk we suggest that the target harvest rate should be conservative and less than half the theoretical maximum; we suggest a target harvest rate of $\leq 4\%$ of the population per year.

Pregnancy rates and litter sizes observed before birth suggest a potential birth rate that is double that observed in the field. All field studies of wolverine reproduction suggest that females do not reproduce every year (Rauset et al. 2015). The only observations of wild wolverine breeding every year were during an experimental study for a select few females fed all winter (Persson 2005). No field studies have recorded litter sizes above 3, which is commonly observed in-vitro. Many recent field studies were done on populations that were harvested, some heavily, and none of these studies suggested a density-dependent response in reproduction that approached levels seen in-

vitro (Copeland 1996, Krebs et al. 2007). Potential reproduction in wolverine is much higher than observed in the wild. We conclude that any analysis of wolverine population dynamics should use reproductive rates measured in wild populations of wolverine, not those measured in-vitro.

We found that sub-adult males and females were much more vulnerable to trapping (10x and 6x respectively) than adult females. Adult males were 3x more vulnerable than adult females to trapping. In a meta-analysis of survival of North American wolverine, Krebs et al. (2004) also found sub-adult males were most vulnerable to trapping. Our population model suggested that the maximum sustainable harvest rate increased by 2% due to the greater vulnerability of sub-adults. This resulted because adult females had lower mortality per capita and so reproduction did not decline with harvest rate as rapidly as with random mortality. Greater vulnerability of young animals to trapping moderates the conservation risk of trapping.

Why was the spatial trapping mortality variable not negatively related to density if trapping was limiting wolverine abundance in our study area? This may be due to the fact that wolverine mortality can only happen in areas that support wolverine, and large portions of our study area appear to support few or no wolverines. This creates a positive relationship between density and trapping kill, at least at low to medium abundance. At higher abundance, this relationship may switch, resulting in a non-linear relationship. Also, resident wolverine that are killed may be quickly replaced by juveniles given the large effort juveniles put into searching for a territory after dispersing from their natal range (Inman et al. 2012b). In the Rocky Mountain National Parks, in the northeast corner of our study area, density increased with distance from the park boundary

suggesting trapping outside the parks reduced density measurably (Barrueto et al. submitted).

Population density averaged two wolverine/1000 km² across the study area. Previous density estimates in the montane mountains of western North America were mostly higher than our estimate (range 4-15.4 wolverine/1000 km²; Table 10). This difference could be explained by the very high mortality rate observed in our study area. However, none of these earlier studies corrected for closure bias, which could lead to large over-estimates for an animal like wolverine that have large home ranges and who disperse during the period of study. Wolverine densities appear similar in montane and boreal forests although none of the boreal estimates were corrected for closure either (Table 10), so it is possible wolverine density in boreal environments is actually lower than in montane environments. Higher densities have been recorded in coastal Alaska and in several places in the arctic; however again, the highest observed densities were not corrected for closure. In one comparative study closure bias was 2.5 fold greater than the closure corrected density. Efford and Boulanger (2018) estimated wolverine density using the same data as Mulders et al. (2007), but they corrected for closure bias explicitly using spatial capture-recapture methods. Their estimate was 6.7 (CI 5.4-8.3), compared to 17.2 (CI 16.4-24.3) from the earlier work. It would appear imperative to correct for closure bias in all wolverine inventories given the possibility for large biases, especially if the inventory area is relatively small. In summary, the highest reliable wolverine densities (about 10 wolverine/1000 km²) were observed in coastal Alaska and the Yukon north slope, with moderate densities observed in the central arctic when caribou were

abundant (Table 10). Our work suggests that densities in montane environments are low compared to environments further north.

Table 10. Wolverine densities from selected studies in North American. Confidence Intervals assume $\alpha=0.05$ unless stated. Study area size was taken from each publication and in some cases was the area trapped and in other cases included a buffer around the traps to account for the detection of animals living across the study area boundary.

Density (animals/1000 km ²)	Precision (95 % CI)	Study Area Size (km ²)	Location	Methods	Closure correction	Authors
Coastal rainforest						
9.7	5.9-15	2140	Alaska Panhandle	Camera trapping at baited sites	yes	Royle et al. 2011
3.0	2.6-3.4 (80% CI)	4340	Coastal Alaska	Aerial track counts & probability estimator	yes	Golden et al. 2007
Montane forest						
15.4		1300	Northwest Montana	live-capture/radiotelemetry & track counts	no	Hornocker and Hash 1981
4-11.1		8000	Northern Idaho	as above	no	Copeland (1995)
5.8		4000	SE British Columbia	live capture/photo traplines	no	Lofroth and Krebs 2007
3.5	2.8-9.6	4381	Yellowstone-southwest Montana	Live capture & genetic sampling	no	Inman et al. 2012b
1.8 & 3.0		2260 & 2334	Westcentral Alberta	DNA capture & mark-recapture	partial	Fisher et al. 2013
6.8		4140	Willmore-westcentral Alberta	DNA capture & mark-recapture	partial	Fisher et al. 2013

Density (animals/100 0 km ²)	Precisio n (95 % CI)	Study Area Size (km ²)	Location	Methods	Closure correctio n	Authors
3.1	2.3-4.2	9000	Rocky Mountain National Parks	DNA hair capture & mark- recapture	yes	Barrueto et al. submitted
0.9-4.4 $\bar{x}=2.0$	1.70- 2.47	110,700	Southeast BC- southwest Alberta	DNA hair capture & mark- recapture	yes	This study
Boreal sub-boreal forest						
4.8		51,200	Northeast BC	snow tracking and harvests	no	Quick 1953
5.2	4.2-6.2	1870	Central Alaska	tracking and probability estimator	no	Becker 1991
10.8		1800	Southern Yukon	live-capture and telemetry assuming exclusive home ranges	no	Banci and Harestad 1990
6.4		8900	NE British Columbia	live capture/photo traps	no	Lofroth and Krebs 2007
6.6	5.5-7.7	13,500	Southern Norway	DNA hair capture & mark- recapture	no	Flagstad et al. 2004
2.8-3.6		≈13,000	Central Norway	Extrapolation s from den surveys	no	Landa et al. (1998)
Arctic plains						
20.8		2400	Alaska- foothills	as above	no	Magoun 1985
7.2		≈ 5000	Alaska- foothills and coastal plain	as above	no	Magoun 1985
9.7	9.1-10.3 (80% CI)	3375	Northern Yukon	Aerial track counts & probability estimator	yes	Golden et al. 2007

Density (animals/1000 km ²)	Precision (95 % CI)	Study Area Size (km ²)	Location	Methods	Closure correction	Authors
17.2	16.4-24.3	2556	Daring Lake-Central arctic	DNA capture mark-recapture	hair &	partly Mulders et al. 2007
2-7	over multiple years	2000-3000	multiple areas-Central arctic	DNA capture mark-recapture	hair &	yes Efford and Boulanger 2018
4.8	3.22-6.38	unknown	Izok-Central Arctic	DNA capture mark-recapture	hair &	yes EDI & AWR 2013
6.9	5.85-7.95	unknown	High lake-Central Arctic	DNA capture mark-recapture	hair &	yes EDI & AWR 2013
2.4	2.09-3.33	3344	Aberdeen Lake-Eastern Arctic	DNA capture mark-recapture	hair &	yes Awan and Boulanger 2016
3.3-4.4	2.89-5.93	4550	Henik Lake-Eastern Arctic	DNA capture mark-recapture	hair &	yes Awan et al. 2018

We suggest that most, if not all, previous studies that did not use spatial capture-recapture methods to analyze their sampling data have substantively over-estimated wolverine abundance. All studies that presented densities >10 wolverine/1000 km² had study areas <3000 km² (Table 10). For example, Lofroth and Ott (2007) used density estimates from two study areas in BC and extrapolated a population estimate for all of BC. They predicted the Kootenay region to have 324 wolverines, while our model predicted a population of 166. If this difference is a measure of bias in their population

estimates, then closure bias could lead to considerable under-estimates of the impact of trapping mortality throughout the wolverine range.

We found that continuous spring snow cover strongly correlated with density at the scale of our analysis. The circumpolar distribution of wolverine and the known den sites were also related to spring snow in a multi-continent scale analysis (Copeland et al. 2010). Other studies have examined the relationship between spring snow and habitat selection and most find some positive relationship (Copeland et al. 2010, Heim et al. 2017, Kortello et al. In Prep.), and these relationships appear to be stronger in more topographically complex environments (see Webb et al. 2016 for example). Our results demonstrate that spring snow relates to density in montane environments, which suggests a functional relationship with wolverine ecology.

Several reasons have been posited for this relationship including:

- i) A preference for snowier areas because wolverine are physically adapted to these environments (Copeland et al. 2010).
- ii) The need or preference for snow to cover dens for thermoneutrality of young (Copeland et al. 2010).
- iii) The need for snow to preserve cached meat (Inman et al. 2012a).

We cannot unequivocally test among these hypotheses with our data, but we did run our best-fit density model for each sex separately. Females selected for snow more strongly than males (Figure 5), which supports the denning hypothesis more than the two alternatives. However, this is a weak test among these hypotheses because the stronger selection for snow by females could simply be due to the smaller ranges of female wolverine, which allows them to locate their ranges in relatively better habitat. Clarifying

the functional relationship between wolverine ecology and spring snow will require detailed study of their autecology.

Wolverine density was negatively related to roads and the functional nature of this relationship is perhaps even less well understood than spring snow. Other works have reported similar relationships for wolverine (Krebs et al. 2007, Fisher et al. 2013), including an occupancy-based analysis of our West Kootenay data (Kortello et al. In Press). The simplest explanation for this result is the tendency for wolverine to select high elevation habitats, which are mostly found above the road network (Inman et al. 2012b, Kortello et al. In press). However, trappers use roads to access their trapping areas so this relationship may be partly explained by the recent or historical effects of trapping. Only about 70% of the traplines in the Kootenay are trapped in any year (Aaron Reid, pers. comm.) and many fewer trappers try to catch wolverine, though some wolverine are caught as by-catch in traps set for other species. Further, only a small fraction of roads are travelled by trappers during winter so it seems likely that there are other negative effects of roads on wolverine density. Given other cases of human-caused mortality are rare, either food is less abundant near roads or, wolverine are avoiding roads to the point it influences density. Helicopter and backcountry skiing was negatively related to winter habitat selection in the north part of our study area (Krebs et al. 2007). In addition, female wolverines are known to abandon dens following human disturbance (Pulliainen 1968, Magoun and Copeland 1998) and choose not to place den sites near human infrastructure (May et al. 2012). These observations suggest disturbance can influence habitat use and perhaps density. Forestry roads are also travelled on snowmobile by recreationists and used during winter logging operations and perhaps wolverine avoid

these collective uses. The human influence variable measures human habitation, which is correlated with front-country all surface roads. The lack of fit of this variable compared to the strong fit when forestry roads were included suggests it is the back-country forestry roads that wolverine are most strongly avoiding. It is also possible, though perhaps least likely, that the impact of ungulate hunting near roads reduces large prey numbers or promotes increased body condition in the surviving animals, such that fewer individuals die of poor body condition so less winter food is created for wolverine (Mattisson et al. 2016). Efford and Boulanger (2018) documented a decline in wolverine numbers consistent with a decline in caribou numbers in the central arctic of Canada suggesting wolverine numbers link to ungulate numbers in at least part of their range. We conclude that the functional significance of the relationship between roads and wolverine density is unclear and requires further study.

Juvenile wolverine begin to disperse in late winter which presents a potential positive bias to density estimates, because recapture rates would be negatively biased if juveniles move out of a study area entirely. This is possible given the large movements that have been documented (Inman et al. 2012b). It is also possible that spatial models may largely correct for this bias and we note that the estimate of the spatial parameter in this study was higher than expected based on the estimate of home range size.

4.6 Management Implications

Based on our work we suggest wolverine trapping mortality should be reduced by at least half in our greater study, and perhaps more than that for an interim period of recovery. Negative human impacts to wolverine density could be mitigated by reducing road density but the uncertainty of the mechanism behind this relationship makes it

difficult to identify the best areas to implement closures or traffic restrictions. Many forest roads have little traffic in winter in BC, especially at higher elevation. Most winter traffic is by snow machines for recreation and to a lesser extent industry. Given the strong relationship we observed between wolverine density and spring snow, it may be best to select areas with consistent spring snow cover and roads with substantive winter use when planning access mitigation for wolverine conservation. Denning females are most vulnerable to disturbance and of greatest population importance, so further research to identify denning habitat would offer more area specific access recommendations and provide the greatest benefit to wolverines.

CHAPTER 5.0 ASSESS WOLVERINE GENE FLOW AND FINE-SCALE GENETIC STRUCTURE

5.1 Introduction

Wolverines are a rare-occurring species that move over vast areas and without recognizing political boundaries. They inhabit extreme alpine and subalpine environments and their populations have experienced considerable range reduction over the last 50 years (Laliberte and Ripple 2004, Brodie and Post 2010). Loss of habitat and barriers to movement, along with continuing warming climate, are threats that further diminish and fragment the critical landscapes they need for dispersal within their metapopulation (McKelvey et al. 2011, Inman et al. 2013).

Canada lists the wolverine as a species of *Special Concern*, while in Alberta lists it as Data Deficient (Alberta Fish and Wildlife 2008). Recently, in the United States the wolverine was a candidate species for federally listing as threatened under the Endangered Species Act (US Fish and Wildlife Service 2013). Wolverines used to be distributed across Alberta's Rocky Mountains, adjacent foothills, and boreal forests (Petersen 1997; Poole and Mowat 2001); however, their current distribution is poorly known and the landscape they occupy is increasingly fragmented.

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, Miistakis Institute 2009, Fisher et al. 2013).

Wolverines are known to be sensitive to human disturbance, including transportation infrastructure. A localized study in the Kicking Horse Pass (Yoho National Park, B.C.) found that wolverines rarely crossed the Trans-Canada Highway (TCH), while other studies showed anecdotally they were averse to crossing even two-lane highways. To our knowledge, there is no information regarding how wolverines respond to major transportation corridors, such as the US Interstate highway system or the east-west TCH corridor in southern Canada. Knowing how wolverine movements and their metapopulation are affected by high speed, high traffic highways will be critical for providing the necessary connectivity and designing effective metapopulation conservation strategies.

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. 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).

The current expansion (2 to 4 lanes) of the 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.

5.2 Methods

5.2.1 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, three ski areas, Canadian Pacific Railway (CPR), and a secondary highway. Neighboring 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.

5.2.2 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 (Figure 8a). 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 three, 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).

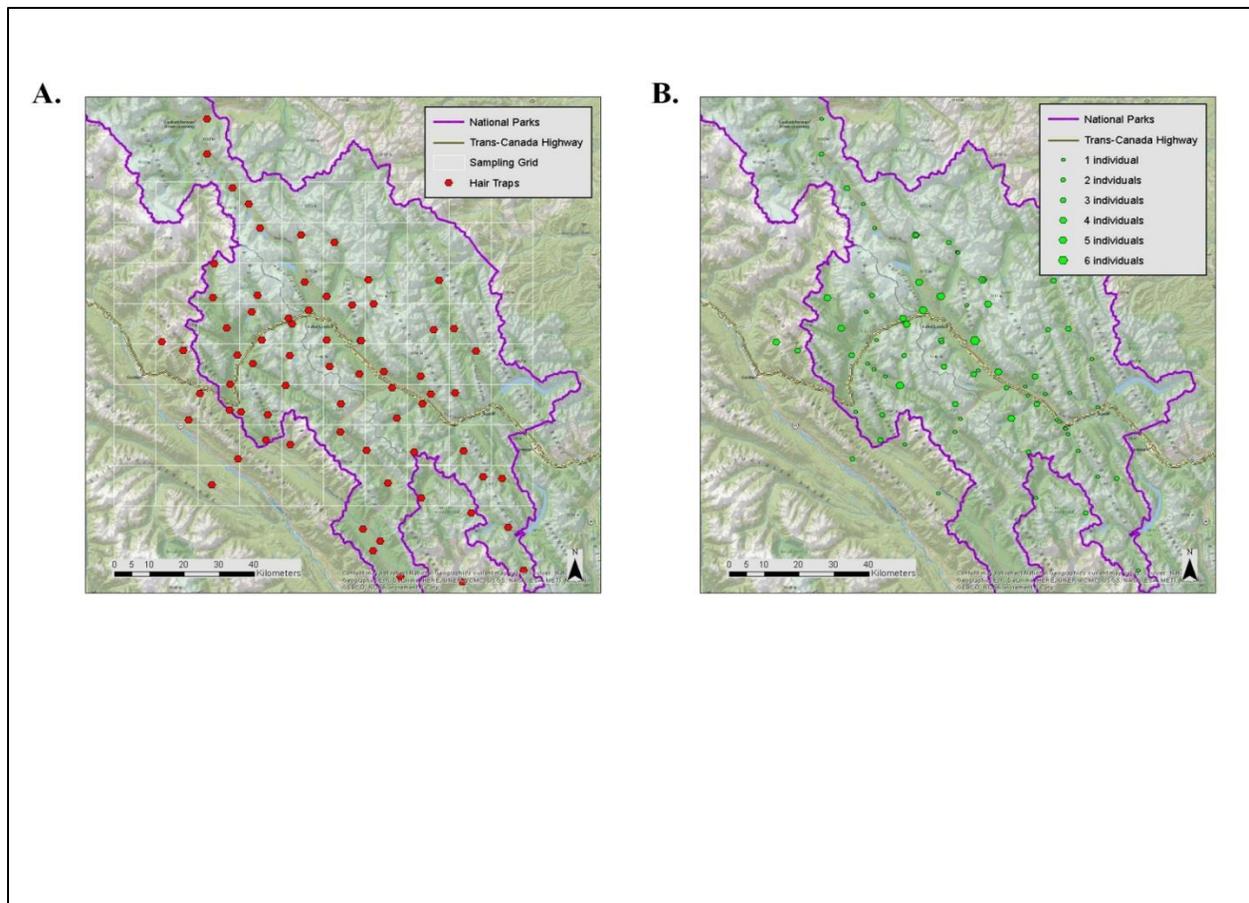


Figure 8. Wolverine hair trap success in parks complex between 2011 and 2013; number of unique wolverines detected at each sampling site in parks complex between 2011 and 2013. Locations of 229 wolverine detections in parks complex between 2011 and 2013.

5.2.3 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 three 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).

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 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.

5.3 Results

5.3.1 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 11). 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 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 8b). 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 8b).

Table 11. 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	# samples	# genotypes	# individual s	# 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	

5.3.2 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 8b). 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, whereas female detections were more

concentrated towards the center of the mountain park complex . 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).

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 9). However, FCA plots broken out by sex revealed structuring of females (Figure 10), but not males in relation to the highway (Figure 11). Interestingly, plots of the total population and males-only revealed that M036 had an unusual genotype within the dataset (Figure 9 and Figure 11).

We detected 7 wolverines that crossed the TCH, including two females and five males with DNA detections that spanned the roadway. Self-assignment probabilities (females=0.92, males=0.62) and population assignment graphs 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, 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 examining the individual spatial locations of population clusters, clustering appears related to the TCH for females, but unrelated to the TCH for males.

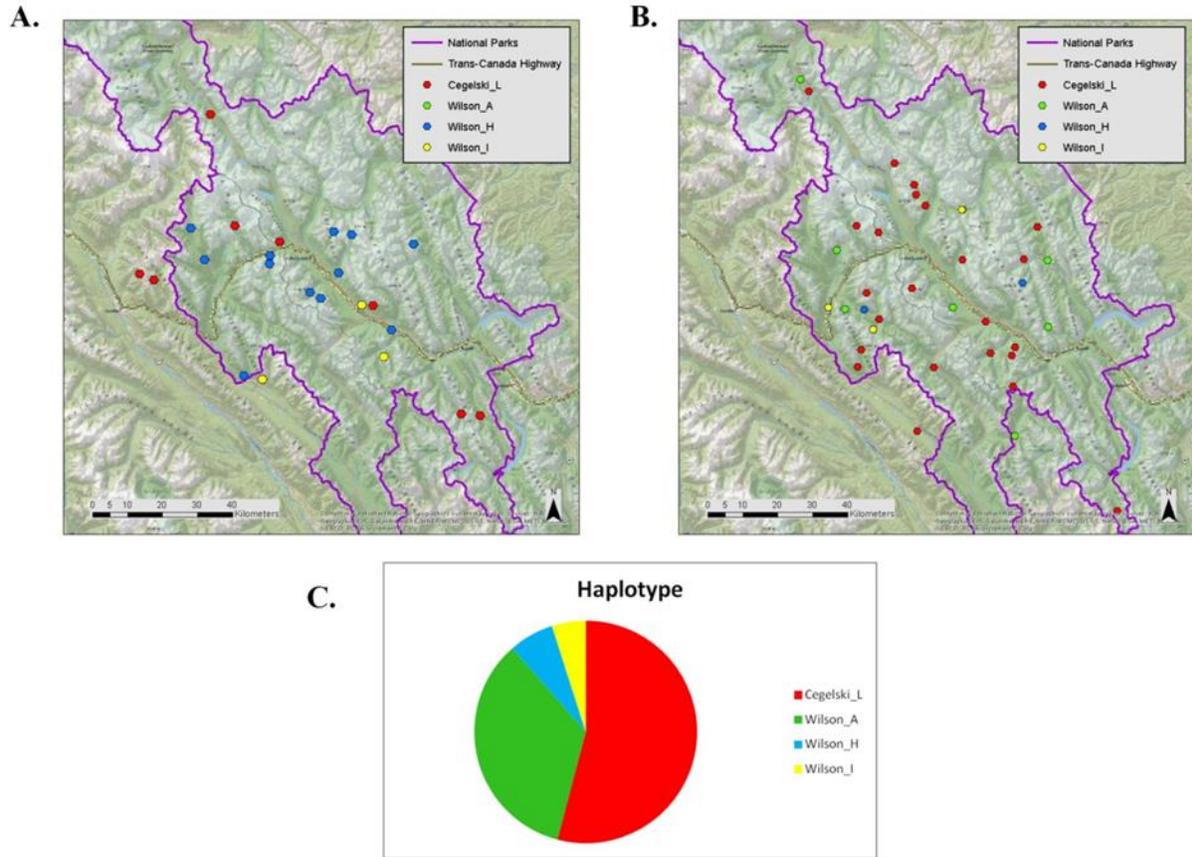


Figure 9. Individual detection centers of 64 wolverines (color-coded by haplotype) detected with noninvasive genetic sampling to examine the effect of the Trans-Canada Highway on fine-scale genetic differentiation in the parks complex between 2011 and 2013.

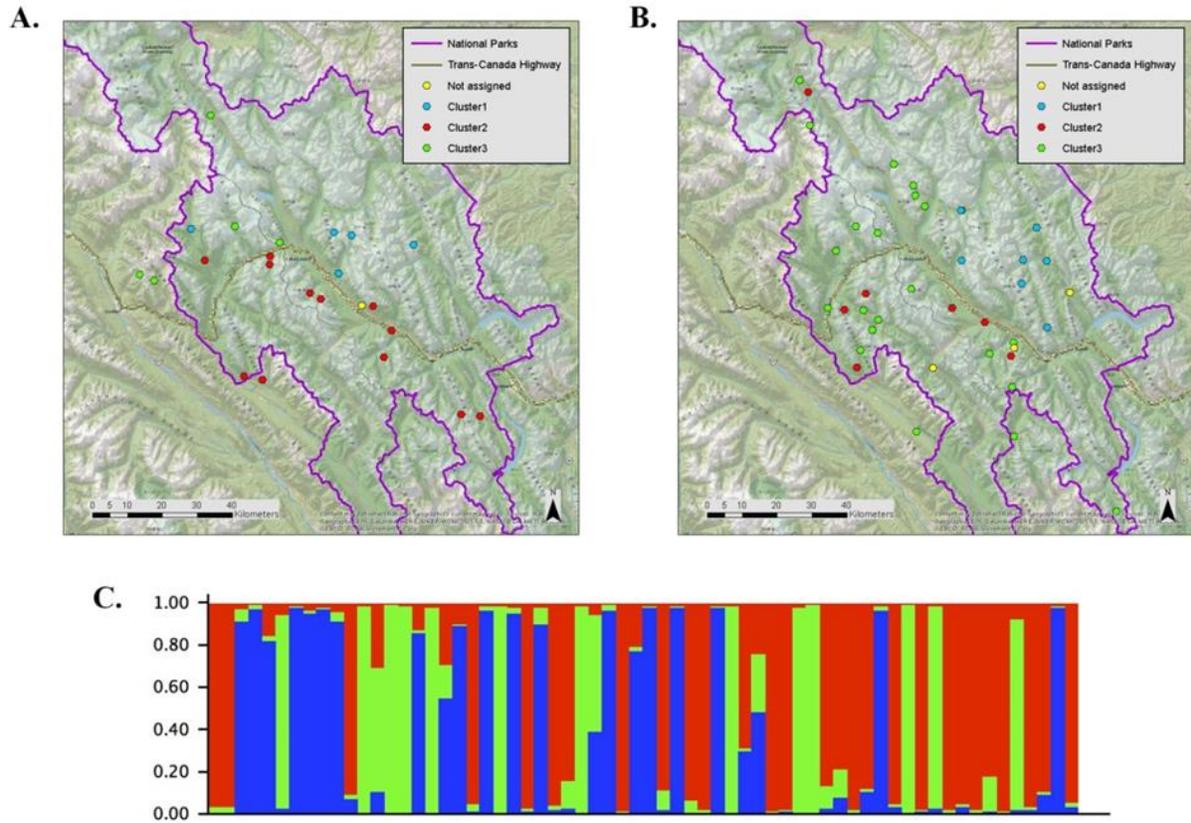


Figure 10. Individual detection centers of A) 25 female and B) 39 male wolverines color-coded by their assignment to one of three population clusters identified in program STRUCTURE to examine the effect of the Trans-Canada Highway on genetic differentiation in the parks complex between 2011 and 2013. Individuals with q -value < 0.7 , was not assigned to population cluster for this analysis.

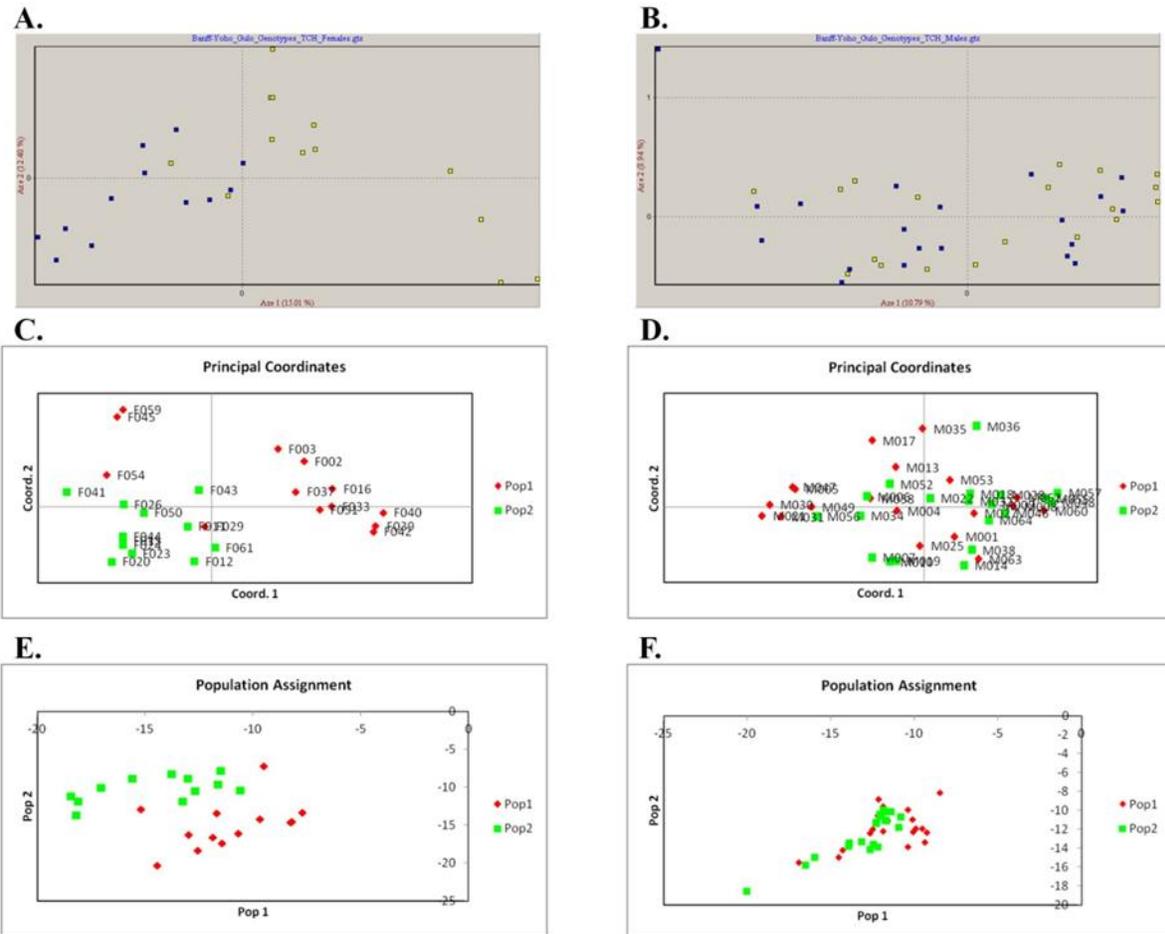


Figure 11. Graphical plots showing Factorial Correspondence Analysis [A) 25 female and B) 39 male], Principle Coordinates Analysis [C) 25 female and D) 39 male] and Assignment Test [E) 25 female and F) 39 male] wolverines detected to the north (red) or south (green) of the Trans-Canada Highway in the parks complex between 2011 and 2013.

Mitochondrial DNA sequencing identified four different haplotypes within the population of 64 wolverines. 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.

5.4 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 is increasingly important to understand what landscape features influence population structure of snow-dependent species to optimize mitigation strategies 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.

5.4.1 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 sample 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, whereas male detections were more dispersed (Figure 11). However, the greater number of detections and more widespread distribution were not surprising considering the well-documented mobility of the male wolverine.

5.4.2 Transportation Effects on Population Structure

Our results show that many female and male wolverines call the parks complex home, but transportation infrastructure affects the two sexes differently. 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.

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 affects 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 has 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 is 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 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 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. 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 behavior from snow tracking 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.

CHAPTER 6.0 REFERENCES

- Alberta Fish and Wildlife Division. 2008. Report of Alberta's Endangered Species Conservation Committee, June 2006. Alberta SRD, FWD, Edmonton.
- Aubry, K. B., K. S. Mckelvey, and J. P. Copeland. 2007. Distribution and broadscale habitat relations of the wolverine in the contiguous United States. *Journal of Wildlife Management* 71:2147–2158.
- Awan, M., and J. Boulanger. 2016. Estimates of wolverine density from mark-recapture DNA sampling, Aberdeen Lake, Kivalliq Region, Nunavut, 2013-14. Department of Environment, Government of Nunavut, Igloolik, Nunavut.
- Awan, M., J. B. Boulanger, and J. J. Savikataaq. 2018. Wolverine density and space use near Henik Lake, Kivalliq Region, Nunavut, 2015 and 2016. Department of Environment, Government of Nunavut, Arviat, Nunavut.
- Awan, M., and G. Szor. 2012. Wolverine (*Gulo gulo*) carcass collection and harvest monitoring in Nunavut. Summary report, Department of Environment, Government of Nunavut.
- Banci, V., and A. Harestad. 1988. Reproduction and natality of wolverine (*Gulo gulo*) in Yukon. *Annales Zoologici Fennici* 265–270.
- Banci, V., A. Harestad. 1990. Home range and habitat use of wolverines in Yukon, Canada. *Holarctic Ecology* 13:195-200.
- Barrueto, M., M. Sawaya, and A. Clevenger. Submitted. Low wolverine density in a protected area complex of the Canadian Rocky Mountains. *Scientific Reports*.
- Belkhir, K. 1999. GENETIX, v.4.0. Laboratoire Genome, Populations, Interactions. CNRS UPR, Université Montpellier, France. [In French]

Brodie, J. and E. Post. 2010. Nonlinear responses of wolverine populations to declining winter snowpack. *Population Ecology* 52:279-287.

Broseth, H., O. Flagstad, C. Wardig, M. Johansson, and H. Ellegren. 2010. Large-scale noninvasive genetic monitoring of wolverines using scats reveals density dependent adult survival. *Biological Conservation* 143:113–120.

Burnham, KP, DR Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media.

Canadian Wildlife Service. 2014. COSEWIC assessment and status report on the Wolverine (*Gulo gulo*) in Canada.

Cegelski, C.C., L.P. Waits, and J. Anderson. 2003. Assessing population structure and gene flow in Montana wolverines (*Gulo gulo*) using assignment-based approaches. *Molecular Ecology* 12:2907-2918.

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

Clevenger, A.P., M. Barreto. 2014. Trans-Canada Highway Wildlife and Monitoring Research, Final Report. Part B: Research. Report to Parks Canada Agency, Radium Hot Springs, British Columbia, Canada.

Clevenger, A.P., G. Mowat, J. Fisher. 2015. Mapping the wolverine way: Identifying conservation corridors and transboundary linkages in the Canadian Crown of the Continent. Summary Report 2015 Alberta-British Columbia Survey. Unpublished report.

Copeland, J. P. 1996. Biology of the wolverine in central Idaho. Master's Thesis, University of Idaho Moscow, USA.

- Copeland, J. P., K. S. McKelvey, K. B. Aubry, A. Landa, J. Persson, R. M. Inman, et al. 2010. The bioclimatic envelope of the wolverine (*Gulo gulo*): do climatic constraints limit its geographic distribution? *Canadian Journal of Zoology* 88:233–246.
- Dalerum, F., B. Shults, and K. Kunkel. 2008. Estimating sustainable harvest in wolverine populations using logistic regression. *Journal of Wildlife Management* 72:1125–1132.
- van Dijk, J., L. Gustavsen, A. Myrsterud, R. May, Ø. Flagstad, H. Brøseth, Roy Andersen, Reidar Andersen, H. Steen, and A. Landa. 2008. Diet shift of a facultative scavenger, the wolverine, following recolonization of wolves. *Journal of Animal Ecology* 77:1183–1190.
- EDI & AWR. 2013. Draft Terrestrial Wildlife Baseline Appendix Report, Izok Corridor Project. Draft Terrestrial Wildlife Baseline Appendix Report, Environmental Dynamics Inc. and Aurora Wildlife Research for MMG, Vancouver.
- Efford, M. 2004. Density estimation in live-trapping studies. *Oikos* 106:598–610.
- Efford, M. 2018. secr 3.1-spatially explicit capture–recapture in R. R-CRAN. <<ftp://ess.r-project.org/R-CRAN/web/packages/secr/vignettes/secr-overview.pdf>>. Accessed 29 Aug 2018.
- Efford, M., and J. B. Boulanger. 2018. Analyses of wolverine DNA mark-recapture sampling in the Northwest Territories 2004-2015. Unpublished report for GNWT.
- Efford, M. G., and G. Mowat. 2014. Compensatory heterogeneity in spatially explicit capture-recapture data. *Ecology* 95:1341–1348.
- Evanno, G., S. Regnaut, and J. Goudet. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. *Molecular Ecology* 14: 2611-2620.
- Fisher, J., S. Bradbury, A. Fisher, and L. Nolan. 2009. Wolverines on the edge of Alberta’s Rockies. Alberta Research Council, Edmonton, Alberta.

Fisher, J.T., N. Heim. 2012. Mammalian spatial distribution and habitat selection in a heterogeneous mountain landscape. Year-end report 2011-12. Prepare by Alberta Innovates Technology Futures for Alberta Sustainable Resource Development, Canmore, Alberta.

Fisher, J. T., and S. Bradbury. 2014. A multi-method hierarchical modeling approach to quantifying bias in occupancy from noninvasive genetic tagging studies. *Journal of Wildlife Management* 78:1087–1095.

Fisher, J., S. Bradbury, B. Anholt, L. Nolan, L. Roy, J. Volpe, M. Wheatley. 2013. Wolverines on the Rocky Mountain slopes: natural heterogeneity and landscape alteration as predictors of distribution. *Canadian Journal of Zoology* 91:706-716.

Fisher, J. T., M. Wheatley, and D. I. Mackenzie. 2014. Spatial patterns of breeding success of grizzly bears derived from hierarchical multistate models. *Conservation Biology* 28:1249-1259.

Flagstad, O., E. Hedmark, A. Landa, H. Broseth, J. Persson, R. Andersen, P. Segerstrom, and H. Ellegren. 2004. Colonization history and noninvasive monitoring of a reestablished wolverine population. *Conservation Biology* 18:676–688.

Gervasi, V., H. Brøseth, E. B. Nilsen, H. Ellegren, Ø. Flagstad, and J. D. C. Linnell. 2015. Compensatory immigration counteracts contrasting conservation strategies of wolverines (*Gulo gulo*) within Scandinavia. *Biological Conservation* 191:632–639.

Golden, H. N., J. D. Henry, E. F. Becker, M. I. Goldstein, J. M. Morton, D. Frost, and A. J. Poe. 2007. Estimating wolverine *Gulo gulo* population size using quadrat sampling of tracks in snow. *Wildlife Biology* 13:52–61.

Graves, T., R.B. Chandler, J.A. Royle, P. Beier, K.C. Kendall. 2014. Estimating landscape resistance to dispersal. *Landscape Ecology* 29:1201-1211.

Hatler, D. F., and A. M. M. Beal. 2003. Wolverine. Furbearer management guidelines, Government of British Columbia.

<www.env.gov.bc.ca/fw/wildlife/trapping/docs/wolverine.pdf>. Accessed 29 Aug 2018.

Hausleitner, D., A. Kortello. 2014. Abundance and distribution of wolverine in the Kootenay Region: 2014 field season report: Central Selkirk Mountains. Prepared for Ministry of Forests, Lands and Natural Resource Operations, Nelson, BC.

Heim, N., J. T. Fisher, A. Clevenger, J. Paczkowski, and J. Volpe. 2017. Cumulative effects of climate and landscape change drive spatial distribution of Rocky Mountain wolverine (*Gulo gulo* L.). *Ecology and Evolution* 7:8903–8914.

Heim, N. A. 2015. Complex effects of human-impacted landscapes on the spatial patterns of mammalian carnivores. M.Sc. thesis. University of Victoria.

Holland, W. D. and G. M. Coen. 1983. Ecological land classification of Banff and Jasper National Parks. Vol. I: Summary. Alberta Institute of Pedology, Publ. M-83-2.193 pp.

Hornocker, M. G., and H. S. Hash. 1981. Ecology of the wolverine in northwestern Montana. *Canadian Journal of Zoology* 59:1286–1301.

IDFG. 2014. Management Plan for the Conservation of Wolverines in Idaho 2014-2019. Management Plan.

Inman, R. M., A. J. Magoun, J. Persson, and J. Mattisson. 2012a. The wolverine's niche: linking reproductive chronology, caching, competition, and climate. *Journal of Mammalogy* 93:634–644.

Inman, R. M., and M. L. Packila. 2015. Wolverine (*Gulo gulo*) Food Habits in Greater Yellowstone. *The American Midland Naturalist* 173:156–161.

Inman, R. M., M. L. Packila, K. H. Inman, A. J. Mccue, G. C. White, J. Persson, B. C. Aber, M. L. Orme, K. L. Alt, S. L. Cain, J. A. Fredrick, B. J. Oakleaf, and S. S. Sartorius. 2012*b*. Spatial ecology of wolverines at the southern periphery of distribution. *Journal of Wildlife Management* 76:778–792.

Inman, R. et al. 2013. Developing priorities for metapopulation conservation at the landscape scale: Wolverines in the Western United States. *Biological Conservation* 166:276-286.

Johnson, W. E., and S. J. O'Brien. 1997. Phylogenetic reconstruction of the Felidae using 16S rRNA and NADH-5 mitochondrial genes. *Journal of Molecular Evolution* 44:S98–S116.

Kendall, K. C., J. B. Stetz, J. Boulanger, A. C. Macleod, D. Paetkau, and G. C. White. 2009. Demography and genetic structure of a recovering grizzly bear population. *The Journal of Wildlife Management* 73:3–16.

Kery, M., B. Gardner, T. Stoeckle, D. Weber, J.A. Royle. 2010. Use of spatial capture-recapture modeling and DNA to estimate densities of elusive animals. *Conservation Biology* 25: 356-364

Kortello, A., D. Hausleitner 2012. Wolverine population and habitat assessment in the Kootenay Region: 2012 field season report. Prepared for Ministry of Forests, Lands and Natural Resource Operations, Nelson, BC.

Kortello, A., D. Hausleitner 2013. Abundance and distribution of wolverine in the Kootenay Region: 2013 field season report: Purcell Mountains. Prepared for Ministry of Forests, Lands and Natural Resource Operations, Nelson, BC.

Kortello, A., D. Hausleitner 2015. Abundance and distribution of wolverine in the Kootenay Region: 2015 field season report: Valhalla and South Monashee Mountains. Prepared for Ministry of Forests, Lands and Natural Resource Operations, Nelson, BC.

Krebs, J., E. C. Lofroth, and I. Parfitt. 2007. Multiscale habitat use by wolverines in British Columbia, Canada. *Journal of Wildlife Management* 71:2180–2192.

Krebs, J., E. Lofroth, J. Copeland, V. Banci, D. Cooley, H. Golden, A. Magoun, R. Mulders, and B. Shults. 2004. Synthesis of survival rates and causes of mortality in North American wolverines. *Journal of Wildlife Management* 68:493–502.

Kukka, P. M., T. S. Jung, J.-F. Robitaille, and F. K. A. Schmiegelow. 2017. Temporal variation in the population characteristics of harvested wolverine (*Gulo gulo*) in northwestern Canada. *Wildlife Research* 44:497.

Lee, J. 2016. Database Description, Data Summary and Analysis of the Wolverine Harvest from Kugluktuk, Umingmaktok and Bathurst Inlet, Northwest Territories. Manuscript Report, Environment and Natural Resources, Government of the Northwest Territories.

Lofroth, E. C., and J. Krebs. 2007. The abundance and distribution of wolverines in British Columbia, Canada. *Journal of Wildlife Management* 71:2159–2169.

Lofroth, E. C., J. A. Krebs, W. L. Harrower, and D. Lewis. 2007. Food habits of wolverine *Gulo gulo* in montane ecosystems of British Columbia, Canada. *Wildlife Biology* 13 (suppl):31–37.

Lofroth, E. C., and P. K. Ott. 2007. Assessment of the sustainability of wolverine harvest in British Columbia, Canada. *Journal of Wildlife Management* 71:2193–2200.

MacKenzie, D.I., J.D. Nichols, J.A. Royale, K.H. Pollock, L.L. Bailey, J.E. Hines. 2006. *Occupancy estimation and modeling: Inferring patterns and dynamics of species occurrence*. Academic Press, New York, NY.

MacKillop, D. J., and A. J. Ehman. 2016. A Field Guide to Site Classification and Identification for Southeast British Columbia: The South-Central Columbia Mountains. Land Management Handbook 70.

Magoun, A. 1985. Population characteristics, ecology, and management of wolverines in northwestern Alaska. Doctoral Thesis, University of Alaska, Fairbanks, Alaska.

Magoun, A. J., and J. P. Copeland. 1998. Characteristics of wolverine reproductive den sites. *Journal of Wildlife Management* 62:1313–1320.

Magoun, A. J., M. D. Robards, M. L. Packila, and T. W. Glass. 2017. Detecting snow at the den-site scale in wolverine denning habitat. *Wildlife Society Bulletin* 41:381–387.

Mattisson, J., G. R. Rauset, J. Odden, H. Andren, J. D. C. Linnell, and J. Persson. 2016. Predation or scavenging? Prey body condition influences decision-making in a facultative predator, the wolverine. *Ecosphere* 7:e01407.

May, R., L. Gorini, J. van Dijk, H. Brøseth, J. D. C. Linnell, and A. Landa. 2012. Habitat characteristics associated with wolverine den sites in Norwegian multiple-use landscapes. *Journal of Zoology* 287:195–204.

McClure, M. L., A. J. Hansen, and R. M. Inman. 2016. Connecting models to movements: testing connectivity model predictions against empirical migration and dispersal data. *Landscape Ecology* 31:1419–1432.

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

McKelvey, K.S., J.P. Copeland, M.K. Schwartz, J.S. Littel, K.B. Aubry, J.R. Squires, S.A. Parks, M.M. Elsner, and G.S. Mauger. 2011. Climate change predicted to shift wolverine distributions, connectivity, and dispersal corridors. *Ecological Applications* 21: 2882-2897.

Mowat, G., D. C. Heard, and C. J. Schwarz. 2013. Predicting Grizzly Bear Density in Western North America. *PLoS ONE* 8:e82757.

Mulders, R., J. Boulanger, and D. Paetkau. 2007. Estimation of population size for wolverines *Gulo gulo* at Daring Lake, Northwest Territories, using DNA based mark-recapture methods. *Wildlife Biology* 13:38–51.

Mulders, R. L. 2000. Wolverine Ecology, Distribution, and Productivity in the Slave Geological Province. Final Report, West Kitikmeot/ Slave Study Society.

Paetkau, D. 2003. An empirical exploration of data quality in DNA-based population inventories. *Molecular Ecology* 12:1375–1387.

Paetkau D, W. Calvert, I. Stirling, and C. Strobeck. 1995. Microsatellite analysis of population structure in Canadian polar bears. *Molecular Ecology* 4: 347-354.

Parks Canada. 1997. Yoho National Park management plan. Ministry of Canadian Heritage, Ottawa, Ontario.

Parks Canada. 2007. Banff National Park management plan. July 2007 Amendment. Ministry of Canadian Heritage, Ottawa, Ontario.

Peakall, R., and P.E. Smouse. 2006. GENALEX 6: genetic analysis in Excel. Population software for teaching and research. *Molecular Ecology Notes* 6: 288-295.

Persson, J. 2005. Female wolverine (*Gulo gulo*) reproduction: reproductive costs and winter food availability. *Canadian Journal of Zoology* 83:1453–1459.

Persson, J., G. Ericsson, and P. Segerstrom. 2009. Human caused mortality in the endangered Scandinavian wolverine population. *Biological Conservation* 142:325–331.

Persson, J., A. Landa, R. Andersen, and P. Segerstrom. 2006. Reproductive characteristics of female wolverines (*Gulo gulo*) in Scandinavia. *Journal of Mammalogy* 87:75–79.

Poole, K. G. 2006. A population review of mountain goats in the Kootenay Region. Unpublished report for British Columbia Ministry of Environment, Nelson, British Columbia.

Pritchard, J.K., M. Stephens, and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. *Genetics* 155: 945-959.

Proctor, M.F., B.N. McLellan, C. Strobeck, and R.M.R. Barclay. 2005. Genetic analysis reveals demographic fragmentation of grizzly bears yielding vulnerably small populations. *Proc. R. Soc. B* 272: 2409-2416.

Proctor, M. et al. 2012. Population fragmentation and inter-ecosystem movements of grizzly bears in western Canada and the northern United States. *Wildlife Monograph* 180:1-46.

Pulliainen, E. 1968. Breeding biology of the wolverine (*Gulo gulo* L.) in Finland. Pages 338–344 *in*. *Annales Zoologici Fennici*. Volume 5. JSTOR.

Quick, H. F. 1953. Wolverine, fisher and marten studies in a wilderness region. Pages 513–532 *in*. *Transactions of the North American Wildlife Conference*. Volume 18.

R Core Team. 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <<https://www.R-project.org/>>.

Rauset, G. R., M. Low, and J. Persson. 2015. Reproductive patterns result from age-related sensitivity to resources and reproductive costs in a mammalian carnivore. *Ecology* 96:3153–3164.

Royle, J.A., R.B. Chandler, K.D. Gazenski, T. Graves. 2013. Spatial capture-recapture models for jointly estimating population density and landscape connectivity. *Ecology* 94:287-294.

Royle, J. A., R. B. Chandler, R. Sollmann, and B. Gardner. 2013. Spatial capture-recapture. Academic Press.

Royle, J. A., A. J. Magoun, B. Gardner, P. Valkenburg, and R. E. Lowell. 2011. Density Estimation in a Wolverine Population Using Spatial Capture-Recapture Models. *Journal of Wildlife Management* 75:604–611.

Ruggiero, L. F., K. S. Mckelvey, K. B. Aubry, J. P. Copeland, D. H. Pletscher, and I. G. Hornocker. 2007. Wolverine conservation and management. *Journal of Wildlife Management* 71:2145–2146.

Saether, B. E., S. Engen, J. Persson, H. Broseth, A. Landa, and T. Willebrand. 2005. Management strategies for the wolverine in Scandinavia. *Journal of Wildlife Management* 69:1001–1014.

Sawaya, M.A., A.P. Clevenger, and S.T. Kalinowski. 2013. Demographic connectivity for ursid populations at wildlife crossing structures in Banff National Park. *Conservation Biology* DOI: 10.1111/cobi.12075

Sawaya, M.A., S.T. Kalinowski, and A.P. Clevenger. 2014. Genetic connectivity for two bear species at wildlife crossing structures in Banff National Park. *Proc. R. Soc. B.* 281: 20131705.

Sawaya, M., A. Clevenger, and M. K. Schwartz. Submitted. Demographic fragmentation of a protected wolverine population bisected by a major transportation corridor. *Biological Conservation*.

Schwartz, M. K., J. P. Copeland, N. J. Anderson, J. R. Squires, R. M. Inman, K. S. McKelvey, K. L. Pilgrim, L. P. Waits, and S. A. Cushman. 2009. Wolverine gene flow across a narrow climatic niche. *Ecology* 90:3222–3232.

Slough, B. G., R. H. Jessup, D. I. McKay, and A. B. Stephenson. 1987. Wild furbearer management in western and northern Canada. Pages 1062–1976 *in*. Wild furbearer management and conservation in North America. North Bay, ON: Ontario Trappers Association.

Squires, J. R., J. Copeland, T. J. Ulizio, I. K. Schnvartz, and L. F. Ruggiero. 2007. Sources and patterns of wolverine mortality in western Montana. *Journal of Wildlife Management* 71:2213–2220.

Suitor, M. 2005. Wolverine distribution and abundance in the Canadian Rocky Mountain Parks: Research priorities and techniques. Report for Parks Canada Western Service Centre, Calgary, Alberta.

Sun, C. C., A. K. Fuller, and J. A. Royle. 2014. Trap configuration and spacing influences parameter estimates in spatial capture-recapture models. *PloS one* 9:e88025.

U.S. Fish and Wildlife Service. 2013. Endangered and threatened wildlife and plants: Threatened status for the Distinct Population Segment of the North American wolverine occurring in the contiguous United States. *Federal Register* Vol 78, No. 23, pp. 7864-7890, February 4, 2013.

Vangen, K. M., J. Persson, A. Landa, R. Andersen, and P. Segerström. 2001. Characteristics of dispersal in wolverines. *Canadian Journal of Zoology* 79:1641–1649.

Weaver, J.L., P. Paquet, L. Ruggiero. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. *Conservation Biology* 10: 964-976.

Webb, S. M., R. B. Anderson, D. L. Manzer, B. Abercrombie, B. Bildson, M. A. Scrafford, and M. S. Boyce. 2016. Distribution of female wolverines relative to snow cover, Alberta, Canada. *The Journal of Wildlife Management* 80:1461–1470.

Webb, S. M., D. Manzer, R. Anderson, M. Jokinen, and S. Park. 2013. Wolverine Harvest Summary from Registered Traplines in Alberta, 1985 – 201. Technical Report, Alberta Conservation Association, Sherwood Park, Alberta.