

Mapping the Wolverine Way

Understanding landscape and human effects on wolverine abundance, distribution and connectivity in the Canadian Crown of the Continent (CCoC) ecosystem

2016 Summary Report



© Andreas Lie

Anthony P Clevenger, Western Transportation Institute, Montana State University,
Bozeman, Montana USA

Garth Mowat, British Columbia Ministry of Forests, Lands, and Natural Resource
Operations, Nelson, British Columbia, Canada

Mirjam Barrueto, Wildlife biologist, Canmore, Alberta, Canada

Jason T Fisher, Alberta Innovates, Victoria, British Columbia, Canada

June 2016

CONTENTS

EXECUTIVE SUMMARY

1. Background and context

Canadian Rockies national parks, 2010-13
Canadian Crown of the Continent, 2014-2016
Objectives

2. Study area and methods

Data collection
Occupancy (camera-based)

3. Results

Camera-based sampling

2016 season
Canadian Crown of the Continent, 2014-2016

Genetic-based sampling

2016 season
Canadian Crown of the Continent, 2014-2016

Tree-climbing behaviour - 2016

Non-target species

Summary for 2016
Summary for 2015

Occupancy

Alberta sampling sites – 2014 and 2015
British Columbia sampling sites – 2015 and 2016
British Columbia study area – 2016
Canadian Crown of the Continent 2014-2016

4. Discussion

Occupancy

British Columbia study area – 2016
Canadian Crown of the Continent 2014-2016

5. Outreach and education (2015-2016)

Public presentations

Social media

Other

6. Publications (2010-present)

7. Future (and scheduling)

Genotyping errors
Analyses and science delivery

Partnership

Funding

Acknowledgements

References

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. But 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. However there is limited baseline data on wolverine density, distribution, or gene flow, or the effects of trap-related harvest on their long-term population viability to inform decision-making aimed at conserving wolverines in this area.

In 2016, we completed a 3-year noninvasive 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.

Our 2016 objectives were to complete the final survey of wolverines in the CCoC. These data will then be used to 1) estimate wolverine abundance and density; 2) assess the sustainability of wolverine harvest in the BC Rocky Mountains 3) examine the relationship between human disturbance and landscape alteration on wolverine density and distribution; 4) and assess landscape connectivity and gene flow to identify dispersal corridors for wolverines at a transboundary metapopulation scale.

Study area and methods

Our 2016 study area was located in southeastern British Columbia and focused in two main areas: the Elk and Flathead Valleys. We surveyed wolverine occurrence using a systematic sampling design consistent with our previous wolverine research to enable data pooling and large-scale analyses. We used a noninvasive hair trap and a remote camera aimed at the hair trap to sample each site. Once sites were set, three replicate monthly visits were conducted to incorporate detectability into occupancy estimates.

For this report we estimated the proportion of sampling sites occupied by wolverines with single season models, using the occupancy modeling program Presence. 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). We ran several competing single-season models, each with different assumptions about how detectability and site occupancy varied through time and space.

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 scores. This provided 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.

Results

Camera-based and genetic sampling

During 2016, we deployed 57 sampling sites over an area of 8208 km². We set 13 additional sites to increase the number of individual detections for modeling wolverine abundance. Of the 70 sampling sites, 26 sites (37%) had confirmed wolverine photo-detections and a total of 51 confirmed visits by wolverines at the 26 sites. Of a total of 194 monthly sampling sessions, wolverines visited the sampling sites 26 times (13%).

We collected 1311 hair samples during 2016. A total of 448 hair samples were sent to Wildlife Genetics International (WGI) for analysis for genotype analysis.

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. A total of 125 sites were set in BC, while 37 were set in Alberta. During the 3-year period, 45 sites (29%) had confirmed wolverine photo-detections. Wolverines were never detected at 71% (n=108) of the sampling sites.

A total of 2453 hair samples were collected at 162 sampling sites from 2014 to 2016. We collected 162 samples during 2014, 980 samples during 2015, and 1311 samples during 2016. A total of 935 hair and 26 scat samples were sent to a genetics lab in Missoula, Montana for genotype analysis.

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 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.

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.

Occupancy

We analyzed several subsets of the data: Alberta sites (2014 and 2015), BC sites (2015), 2016 BC sites only, and finally the combined Alberta and BC data sets (2014-16). Here we summarize the results from the 2016 BC survey and the combined 3-year data set from the CCoC.

2016

In the 2016 BC dataset, detection probability did not vary with survey or as a trend among surveys, although the top model indicated variation by survey, however, it was not well supported. Occupancy probability did not vary by an east-west gradient; however, there was evidence for a north-south gradient in occupancy probability, with higher occupancy at more northern sites.

Combined sites

Our methodology was consistent during all three years and although climate and related environmental factors may affect detectability differently each year, we expected that effect to be relatively small compared to other variability.

We did find study year (or study area) had an effect on occupancy, in addition to evidence of a north-south gradient in occupancy with more northern sites having a higher occupancy probability. The estimates for occupancy varied by year and north-south gradient (UTMN). Occupancy was highest for 2016 (Elk Valley/Flathead) area, and lowest for 2014 (Waterton Lakes/Crowsnest Pass). The site with the highest estimate (Elk Lakes) was one of the northernmost sites and sampled in 2016, while the site with the lowest estimate of occupancy (Beebe Flats), was one of the southernmost sites and sampled in 2014 ($\psi = 0.10$).

Discussion

The estimate of wolverine occupancy in our 2016 BC Rockies study area was 0.40. Previous estimates of occupancy in the Canadian Rockies were 0.88 in the Banff-Yoho-Kootenay park complex and 0.36 in Kananaskis Country. Our 2014 survey in the Waterton-Crowsnest Pass area had one of the lowest estimates of occupancy in the Canadian Rockies to date ($\psi=0.17$), rivaling the highly impacted west-central Foothills ($\psi = 0.14$).

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, and rivaled the industrially developed Alberta foothills further north. Occupancy increased east to west in the Alberta survey area with higher occupancy close to the Continental Divide.

Wolverine occupancy was greatest in the 2016 BC study area, but varied markedly through space. Similar to our 2015 results, we found a clear pattern of decreasing occupancy from north to south. The 2016 results reinforce the pattern of occupancy observed in the CCoC last year. This north-south gradient in occupancy closely matches wolverine occurrence in the Columbia Mountains, the next major north-south range west of the Canadian Rockies. Here a notable decline in wolverine detections occurred from north to south in the Selkirk and Purcell Mountains, in addition to low genetic connectivity between the south Purcell population and other populations in southeastern British Columbia.

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.

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. Our research to date has revealed wolverines are more abundant in rugged and remote areas protected from human activity and landscape disturbance. Similar patterns of wolverine occurrence in the Columbia Mountains also were documented, 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 proximity to source populations, may account for the north to south gradient in distribution in both ranges.

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 scales. The results we present are preliminary; nonetheless our data summary suggests lower populations than expected and lower connectivity near 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.

Our next steps are to estimate wolverine abundance and density; identify the biophysical and human-related factors that best explain wolverine distribution and densities; and assess landscape and genetic connectivity to identify key areas of dispersal and population connectivity. Moreover, our wolverine density estimates will inform management of wolverine harvest in the CCoC 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.

Conclusions

- The Canadian Crown of the Continent (CCoC) has been identified as a potential corridor for wolverine movement into the US and the most likely long-term prospect for transboundary wolverine habitat and genetic connectivity given climate change scenarios.
- A combination of expanding logging, energy development and motorized recreation, along with a growing road network in the CCoC threatens to fragment and diminish connections in this critical transboundary linkage between the US and Canada.
- There is limited information on wolverines in the CCoC and lack of science-based data to inform decision-making with regards to wolverine abundance, trap-related harvest on population viability and identification of core areas and regional and transboundary connectivity. To provide data for management noninvasive surveys of the wolverine population in the CCoC were conducted from 2014 to 2016.
- Wolverine occupancy in the CCoC differed markedly between years and study areas; this is likely at least partly result of habitat quality – as a function of natural landcover and human disturbance - among areas sampled each year.
- There was a clear pattern of decreasing occupancy from north to south in the 2016 study area. These results reinforce the pattern of occupancy observed in 2015. From the combined years, the same trend was seen as wolverine occupancy decreased significantly moving south. The mechanisms for this variability have yet to be explained, but will be the focus of upcoming analysis.

- Current and historic mortality due to fur trapping could also explain our results and will be investigated using the individual detection data, the occupancy data and the trapping records.
- Wolverine camera-detections in the CCoC appear associated with proximity to the Continental Divide, and areas with low levels of landscape disturbance. These results suggest wolverine occupancy is higher in remote areas protected from human disturbance. Similar patterns of wolverine occurrence were documented in the Columbia Mountains, where high rates of detection were within or adjacent to protected areas; provincial parks, nature and wilderness conservancies.
- An effective conservation strategy will require large areas managed at a regional and transboundary metapopulation scale. The results are preliminary yet suggest lower populations than expected and lower connectivity between the US-Canada border and populations to the north.
- Science based data collected in the CCoC will inform management of wolverine harvest and identify limiting landscape factors, connectivity areas and gene flow in a key transboundary linkage in the Crown of the Continent Ecosystem.

1. Background and context

Canadian Rockies National Parks, 2010-13

We initiated wolverine research in the protected areas of Banff, Yoho and Kootenay National Parks in the Canadian Rockies in 2010. The primary focus of this 3-year research was to examine the effects of the 4-lane Trans-Canada Highway on wolverine population connectivity and demographic fragmentation (Sawaya and Clevenger 2014). We used noninvasive survey methods allowing us to collect data from genetic sampling and camera traps. The national parks research prompted a 2-year survey to be conducted in neighbouring Kananaskis Country, Alberta (Fisher and Heim 2012). During winter 2011-12, we surveyed the border area between the national parks and Kananaskis study areas to form a super-study area consisting of protected and non-protected landscapes.

The area between the Canadian national parks and Waterton Lakes-Glacier National Parks on the US-Canadian border is one of only three remaining zones where wolverines, and other large carnivores, can move between Canada and the US. It is a crucial corridor for wolverine dispersal to the highly fragmented wolverine population in the Northern Continental Divide Ecosystem. But a combination of rapidly expanding logging, energy development and motorized recreation, along with a growing road network – to which wolverines negatively respond (Fisher et al. 2013), threatens to fragment and diminish connections in this critical transboundary linkage between the US and Canada (Weaver 2013).

To ensure that wolverines and land resources on both sides of the border are managed to maintain connected populations we initiated multi-year research to better understand wolverine distribution, abundance, core areas and connectivity in the Canadian Crown of the Continent (CCoC).

Canadian Crown of the Continent, 2014-2016

The Crown of the Continent ecosystem is one of North America's most ecologically diverse and jurisdictionally fragmented ecosystems. Encompassing the shared Rocky Mountain region of British Columbia (BC), Alberta and Montana, this 72,000 km² ecological complex covers two nations, one state and two provinces; it spreads across numerous aboriginal lands, municipal authorities, public and private land blocks and working and protected landscapes. It 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 (Cegelski et al. 2006). Wolverines in this region are affected by two of the three landscape stressors (land use and highway barriers), which are exacerbated by climate change as diminishing snowpack reduces denning opportunities (Krebs et al. 2007, Copeland et al. 2010, McKelvey et al. 2011).

The province of Alberta recently created two parks in the CCoC totaling 105,000 ha, and expanding protection in the Castle Wilderness north of Waterton Lakes National Park and along the BC-Alberta border. The western boundary of the Castle is the extraordinary and wildlife rich Flathead Valley of BC, which now stands as the only unprotected part. This biologically diverse area has long been considered critical habitat for grizzly bears and wolverines (Weaver 2001). As a result of the Castle expansion there is pressure on the BC Government to protect the Flathead^{1, 2}. However there is limited baseline data to inform decision-making with regards to wolverine

¹ http://www.flathead.ca/keeping_wilderness_connected_in_the_southern_rockies

² <http://cpawsbc.org/campaigns/flathead>

density and distribution in this area (McLellan and Servheen 2013) or effects of trap-related harvest on long-term population viability (Lofroth and Ott 2007).

In 2016, we completed a 3-year noninvasive sampling effort in the CCoC, which was a key part of a larger 6-year effort that encompassed the entire central and southern Canadian Rockies. This final year focused on surveying the wolverine population in the Elk and Flathead Valleys, the latter being one of the few remaining areas our project has not surveyed to date and recently emerged as a critical piece of the transboundary Crown of the Continent ecosystem.

The results from the 6-year research project will be the first to use spatially explicit data to inform decision-making regarding management of the wolverine population in the Canadian part of this critical transboundary linkage area within the Crown of the Continent ecosystem. Our research results can be potentially merged with noninvasive surveys being initiated in the Northern Continental Divide Ecosystem in fall 2016 (Multi-state Wolverine Working Group 2015). The dovetailing of both landscape scale sampling surveys can be used to manage the transboundary metapopulation and inform land management and transportation planning.

Objectives

The objectives of our 2016 and current research are to conduct the following:

1. Complete the final 6th year survey of wolverine population in the Canadian Crown of the Continent (CCoC) using noninvasive genetic sampling methods in 2016.
2. Conduct and complete genetic analysis of hair and scat samples from winter 2016 survey effort.
3. Use spatial capture-recapture (SCR) models to estimate wolverine abundance and density, and assess the sustainability of wolverine harvest in the BC Rocky Mountains.
4. Use SCR models to examine the relationship between human disturbance and landscape alteration on wolverine density and distribution.
5. From objective 4, assess landscape connectivity and gene flow to identify dispersal corridors for wolverines at a transboundary metapopulation scale.
6. Communicate results to key stakeholders and work with land/natural resource management/transportation agencies on implementing recommendations into planning and management objectives.

Herein we summarize our 6th and final year of research in addition to the last three years of research conducted in the CCoC.

2. Study area and methods

The 2016 study area was located in the Canadian Crown of the Continent (CCoC) ecosystem in southeastern British Columbia 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 areas and sites sampled during all three years represented a wide range of biophysical attributes, landscape conditions and levels of human disturbance.

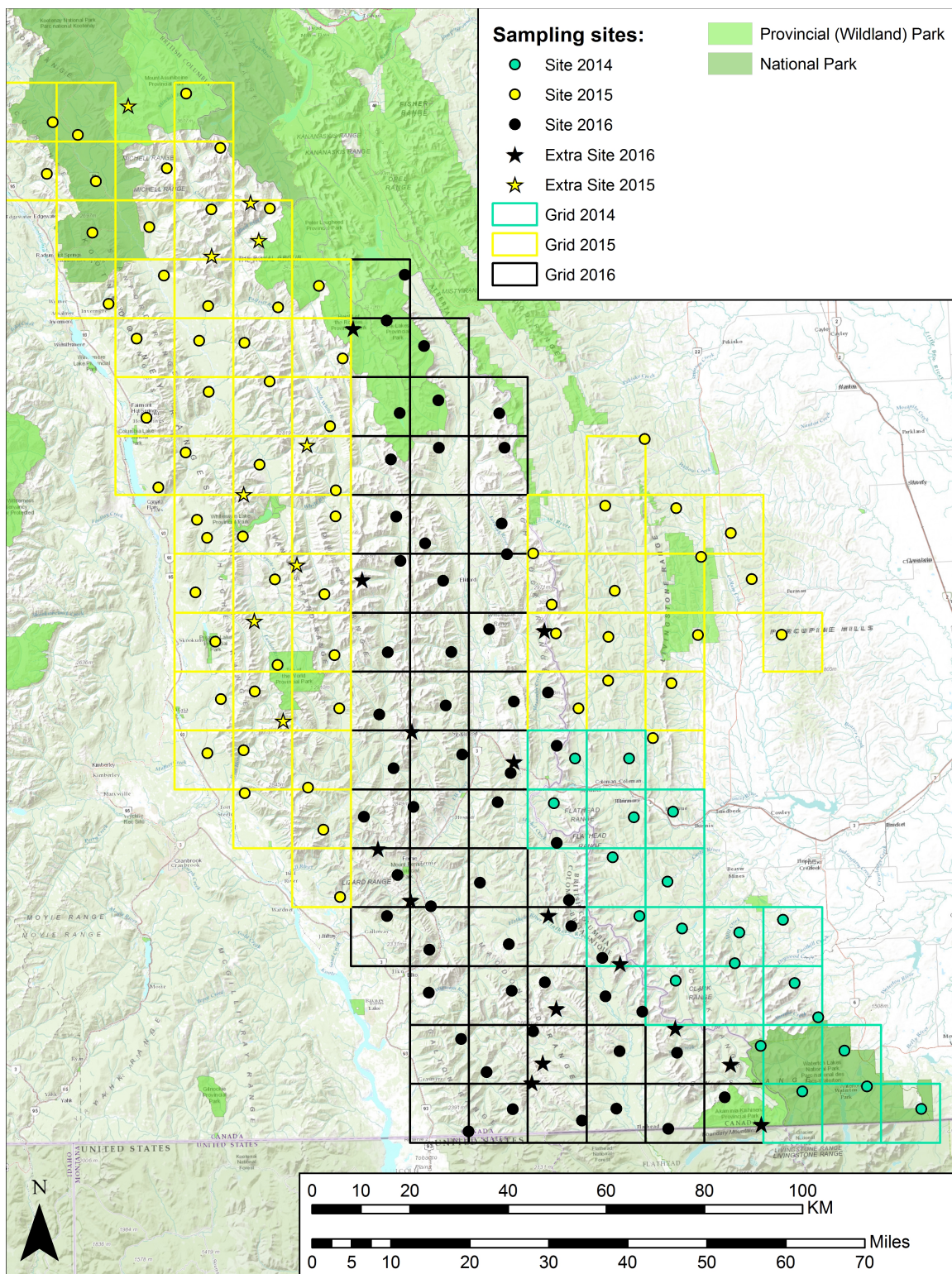


Figure 1. Three study area grids (12 x 12 km) and location of 162 sampling sites for wolverine occurrence in the Canadian Crown of the Continent, 2014-2016.

2.1. Data collection

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 whole 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.

2.2. Occupancy (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 (ver. 10.9;(Hines 2006)). *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. Results

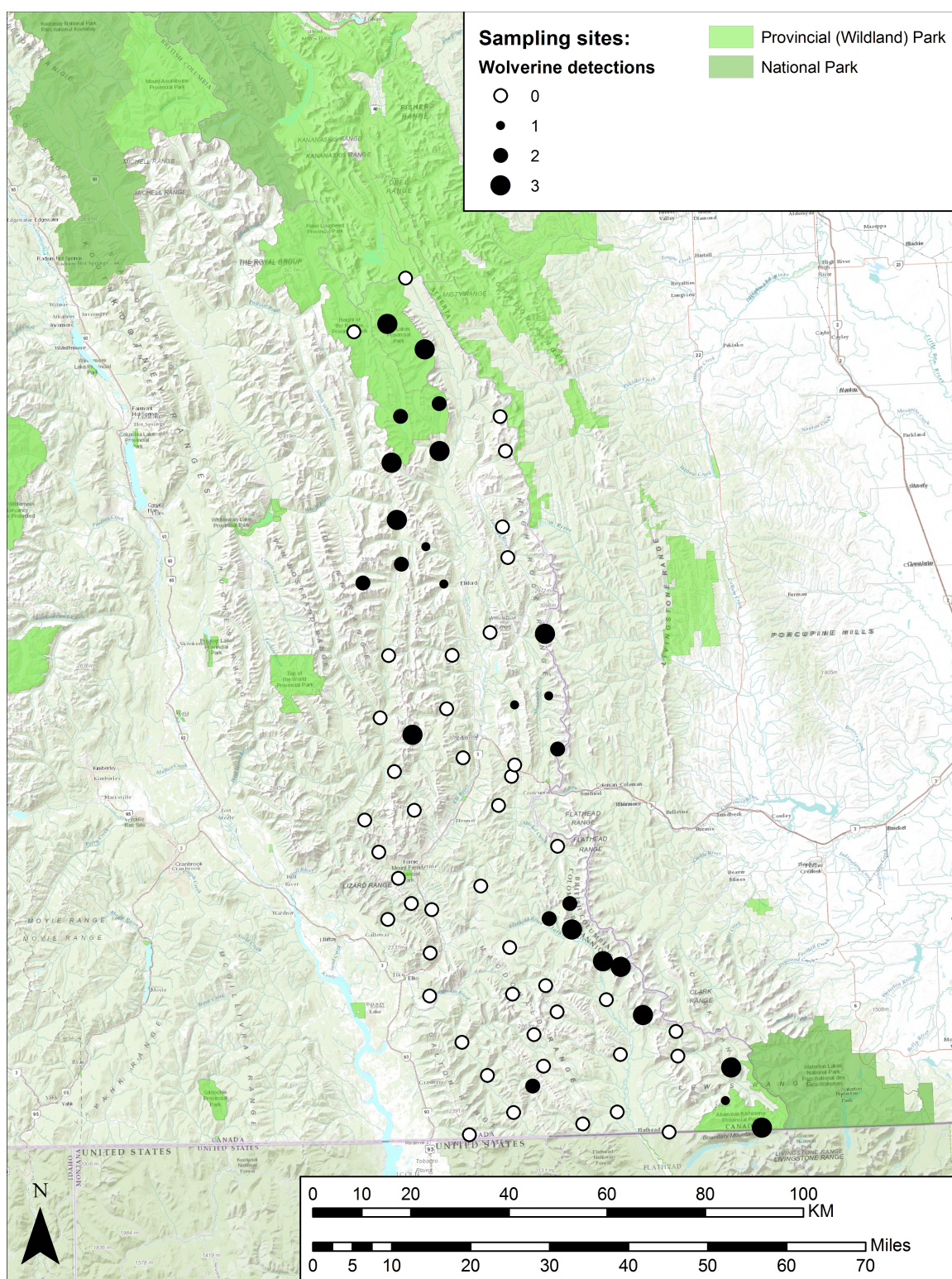
3.1. Camera-based sampling

3.1.1. 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 were sampled 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 a total of 70 sites were set within the 2016 study area.

Of the 70 sampling sites, 26 sites (37%) had confirmed wolverine photo-detections and a total of 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 a total 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 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.



3.1.2. 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). A total of 125 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 two sessions.

Of a total of 441 monthly sampling sessions during the three years, wolverines were detected during 13% (n=60) of sessions.

3.2. Genetic-based sampling

3.2.1. 2016 season

During winter 2016, we collected 1311 hair samples during the three monthly sampling sessions. Not all samples were from wolverines since we collected all hair samples found at the hair traps. We collected 263 samples during session 1, 516 samples during session 2 and 532 samples during session 3. Hair samples were obtained at 80% of 51 sites with confirmed visits by wolverines (n=41).

A total of 448 hair samples were sent to Wildlife Genetics International (WGI) for analysis. These consisted of 378 samples from sites with confirmed wolverine presence and tree climbing activity and 70 hair samples from sites with anecdotal evidence that wolverines visited and may have climbed and left hair at the site. Many samples likely came from the same individual of wolverine or non-target species such as lynx and American marten (see below).

Eighteen putative wolverine scat samples were collected and sent to WGI for analysis.

3.2.2. Canadian Crown of the Continent, 2014-2016

A total of 2453 hair samples were collected at 162 sampling sites from 2014 to 2016. We collected 162 samples during 2014, 980 samples during 2015, and 1311 samples during 2016. A total of 935 hair and 26 scat samples were sent to the US Forest Service Rocky Mountain Research Station Wildlife Genetics lab in Missoula, Montana for genotype analysis.

The lab produced three genotypes, all from the same individual in 2014: a female wolverine that visited the Rowe Creek site in Waterton National Park. This individual was new to the lab and

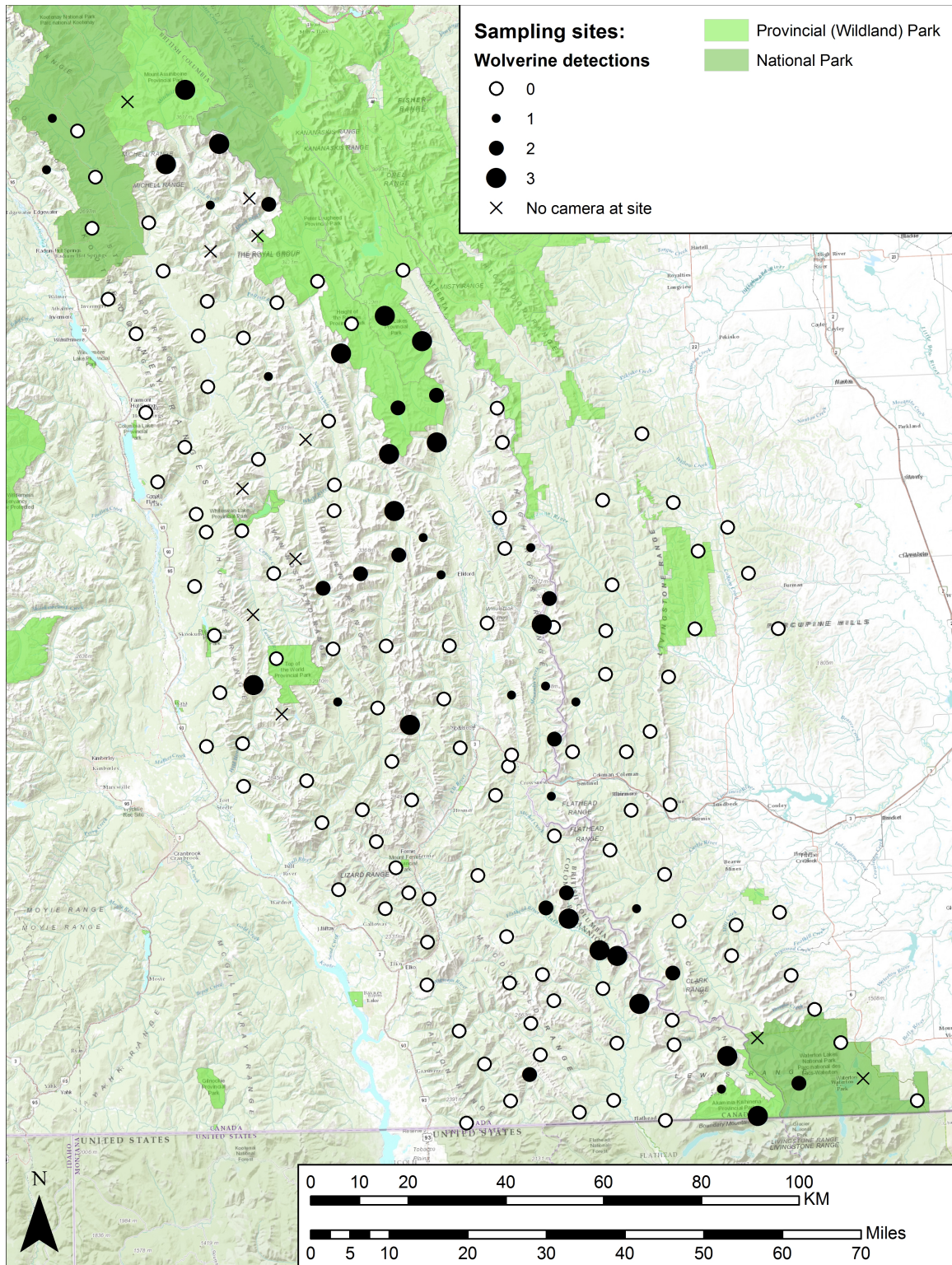


Figure 3. Location of 162 sampling sites and frequency of wolverine detections in the Canadian Crown of the Continent, 2014-2016.

was not identified previously from research conducted in neighbouring Glacier National Park between 2009-2012.

In 2015, the lab obtained a total of 55 genotypes from 10 unique individuals (5 female, 5 males). Two males were previously genotyped from samples collected in the Canadian Rockies national parks surveys, while one female was previously genotyped from the Kananaskis survey.

3.3. Tree-climbing behaviour - 2016

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 (Fisher and Bradbury 2014). Thus we are concerned whether wolverines climb the bait tree when they visit and potentially leave hair, which can then be used to genotype individuals.

During the 2016 survey, we assessed tree-climbing behaviour of wolverines at 27 different sites during 52 sampling sessions. Tree-climbing behaviour was characterized as wolverines photographed at a site climbing the bait tree, or an indication that they did climb but were not photographed (*e.g.* jumping out of the tree). At 67% of the visits (35 of 52) wolverines climbed the bait tree at least once, while 33% ($n=17$) of the site visits wolverines were not observed climbing. Broken down by sampling session, 50% of sites visited resulted in climbing (8 of 16 visits) during session one; 68.2% of visits resulted in climbs (15 of 22 visits) during session two, and 86% of site visits during session three resulted in climbing (12 of 14 visits).

Over 90% of the sites-sessions during the 3-year Canadian Rockies national parks survey detected wolverines climbing bait trees (Clevenger and Barrueto 2014), while in Kananaskis Country climbing occurred at 57% (4 of 7 sites) of the sites (Fisher and Heim 2012). Wolverine behavior at hair traps was found to vary markedly across three study areas with different levels of human disturbance (Stewart et al. 2016). Wolverines behaved differently in heavily human-modified landscapes than in lightly human-modified or protected landscapes. Wolverines climbed quickly (if they climbed at all) in non-protected areas, while in more protected areas climbed more and spent more time. Wolverines' behavioral shift in association with human disturbance is additional evidence suggesting that landscape development is likely one of several mechanisms of population decline.

Although failure to climb and leave hair samples can affect detectability, the double-sampling method we used the last three years can help correct for error due to detectability (Fisher and Bradbury 2014). An area of research is using this information to correct density estimates by estimating numbers of individuals missed via genotyping, by incorporating detectability into spatially capture-recapture (SCR) models (Kery et al. 2010).

3.4. Non-target species

In reviewing photographs obtained from the hair trap sites we are able to summarize some of the incidental data collected during the survey. Non-target species are frequently photographed at hair traps during the winter survey. Below we summarize non-target species detection per sampling session (1 - 3 sessions per site) for 2016 and 2015.

Summary for 2016

In 2016, we sampled 70 sites and completed a total of 194 sampling sessions. We detected 19 vertebrate species at the hair traps, including wolverine (Table 1). Mammals smaller than snowshoe hare were often detected but are not summarized here.

Table 1. Summary of non-target species detected at sampling sites during 2016. t = total sampling opportunities or surveys; n = total number of surveys a species was detected; s = the number of sites where a species was detected; ts = the total number of sampled sites; $\text{survey.det} = n/t*100$; $\text{site.det} = s/ts*100$.

Species	t	n	$\text{survey.det}[\%]$	ts	s	$\text{site.det} [\%]$
Lynx	194	81	41.8	70	43	61.4
Bobcat	194	7	3.6	70	3	4.3
Cougar	194	12	6.2	70	8	11.4
Black bear	194	2	1.0	70	2	2.9
Grizzly bear	194	10	5.2	70	10	14.3
Wolf	194	22	11.3	70	17	24.3
Coyote	194	52	26.8	70	32	45.7
Red fox	194	21	10.8	70	15	21.4
American marten	194	85	43.8	70	42	60.0
Snowshoe hare	194	96	49.5	70	47	67.1
Striped skunk	194	3	1.5	70	2	2.9
Moose	194	16	8.2	70	14	20.0
Elk	194	10	5.1	70	7	10.0
White-tail deer	194	12	6.2	70	7	10.0
Mule deer	194	3	1.5	70	3	4.3
Wolverine	194	52	26.8	70	27	38.6
Weasel	194	12	6.2	70	9	12.9
Golden eagle	194	10	5.2	70	8	11.4
Bald eagle	194	1	0.5	70	1	1.4

Summary for 2015

In 2015, we sampled 63 sites with cameras and completed a total of 188 sampling sessions. We detected 18 vertebrate species at the hair traps, including wolverine (Table 2). Non-target species are frequently photographed at hair traps during the winter survey. Below we summarize non-target species detection per sampling session (1 - 3 sessions per site) for 2015.

3.5. Occupancy (camera trap data)

3.3.1. 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

Table 2. Summary of non-target species detected at sampling sites during 2015. t = total sampling opportunities or surveys; n = total number of surveys a species was detected; s = the number of sites where a species was detected; ts = the total number of sampled sites; $\text{survey.det} = n/t*100$; $\text{site.det} = s/ts*100$.

Species	t	n	survey.det[%]	ts	s	site.det [%]
Lynx	188	13	16.9	64	9	14.1
Bobcat	188	17	9.0	64	12	18.8
Cougar	188	21	11.2	64	17	26.6
Black bear	188	2	1.1	64	2	3.1
Grizzly bear	188	5	2.7	64	5	7.8
Wolf	188	36	19.1	64	24	37.5
Coyote	188	32	17.0	64	25	39.1
Red fox	188	18	9.6	64	12	18.8
American marten	188	99	52.7	64	41	64.1
Snowshoe hare	188	34	18.1	64	19	29.7
Striped skunk	188	8	4.3	64	6	9.4
Moose	188	13	6.9	64	9	14.1
Elk	188	11	5.9	64	7	10.9
White-tail deer	188	28	14.9	64	16	25.0
Mule deer	188	16	8.5	64	9	14.1
Wolverine	188	29	15.4	64	15	23.4
Weasel	188	7	3.7	64	5	7.8
Golden eagle	188	6	3.2	64	6	9.4

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, 2 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 6 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 a total of 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 (psi(UTME),p(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 apparent in Figure 3 were reflected in estimates of occupancy probability ψ (UTME; ER = 1.36), and the top model (psi(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 3). 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 (psi(.),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 naive 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 3. 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	Δ AIC	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

3.3.2. British Columbia sampling sites – 2015 and 2016

The combined BC datasets for 2015 and 2016 had a total of 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. With regards to wolverine detected presence at the BC sites: 13 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%.

Similarly to the Alberta surveys, there was a distinct geographical pattern (Figure 3): wolverines were detected 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's 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 4). 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 ($\psi(.), p(.)$): 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 4. Selection of occupancy models for wolverines detected by cameras in the combined BC study area, 2015/2016. 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
$\psi(UTME), p(SURVEY)$	279.29	0	0.16	1.00	5	269.29
$\psi(UTME), p(.)$	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
$\psi(.), p(SESSION)$	280.70	1.41	0.08	0.49	4	272.7
$\psi(YEAR), p(.)$	280.96	1.67	0.07	0.43	3	274.96
$\psi(UTMN), p(.)$	281.15	1.86	0.06	0.39	3	275.15
$\psi(.), p(.)$	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
$\psi(.), p(TREND)$	281.74	2.45	0.05	0.29	3	275.74

3.3.3. 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 5), 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 5. Selection of occupancy models for wolverines detected by cameras in the 2016 BC study area. Detectability (p) could be constant (.), vary independently among SURVEYs, or as a TREND among surveys. Occupancy (ψ) could be constant (.), vary north-south (UTMN), or vary east-west (UTME).

Model	AIC	Δ AIC	AIC weight	Model Likelihood	K	-2*LogLike
$\psi(\text{UTMN}), p(\text{SESSION})$	177.71	0.00	0.24	1.00	5	167.71
$\psi(\text{UTMN}), p(.)$	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
$\psi(.), p(\text{SESSION})$	180.20	2.49	0.07	0.29	4	172.20
$\psi(.), p(.)$	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
$\psi(\text{UTME}), p(.)$	180.58	2.87	0.06	0.24	3	174.58
$\psi(.), p(\text{TREND})$	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

3.3.4. 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(.),p(.)), 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 6 and 7). Also, 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(UTMN+YEAR),p(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 6). 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 6. 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	Δ AIC	AIC weight	Model Likelihood	K	-2*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
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 7. Evidence ratios (ER) of the covariates used in models of combined AB - BC occupancy analysis.

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

4. Discussion

4.1. Occupancy

4.1.1. 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, Gopalaswamy et al. 2012). 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. 2012). The estimate of wolverine occupancy in our 2016 BC Rockies study area was 0.40 (s.e. = 0.04; Table 4). 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.

4.1.2. 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 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 Barrueto 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 in both ranges or their proximity to source populations.

The Canadian Rockies has 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, Squires et al. 2007). 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 (Royle and Young 2008) 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).

5. Outreach and education (2015-2016)

5.1. Public presentations

Municipal District of Bighorn – Living in the Natural Environment series (Feb 2016), *Between Rock and Hard Places: Wolverines in Multi-use Landscapes of Alberta* (T Clevenger).

Lake O'Hara , Yoho National Park, Le Relais Summer Speaker Series (Sep 2015), *Wolverines in the Canadian Rocky Mountains parks* (M Barrueto).

Stewart, F.E.C., N. Heim, A.P. Clevenger, J. Paczkowski, J.P. Volpe, and J.T. Fisher. 2015. Wolverine behavior varies with anthropogenic footprint: Implications for conservation and inferences about declines. Canadian Society for Ecology and Evolution Conference, Saskatoon, Saskatchewan, 21-25 May 2015. (F Stewart)

Stewart, F.E.C., N. Heim, A.P. Clevenger, J. Paczkowski, J.P. Volpe, and J.T. Fisher. 2015. Landscape-scale behavioral response by wolverine to landscape development: evidence for a human-driven landscape of fear? 2015 Conference of Alberta Chapter – The Wildlife Society, Edmonton, Alberta. March 20-22 2015. (F Stewart)

Table 8. Estimates of wolverine occupancy (Ψ) with standard error (SE) and confidence intervals (CI) from the Rocky and Columbia Mountains.

Mountain range Study area	Ψ	se²	CI³	Naïve⁴	Reference
Rocky Mountains					
BC – 2016	0.40	0.06	0.29 - 0.52	0.39	This study
Canadian CoC – 2014-2016	0.32	0.04	0.25 - 0.40	0.30	This study
BC – Alberta 2015	0.25	0.05	0.15-0.38	0.23	Clevenger et al. 2015
Waterton-Crownsnest 2014	0.17	0.09	0.05-0.45	0.08	Clevenger, unpubl. data
Banff-Yoho-Kootenay ¹	0.88	0.05	0.72-0.95	0.79-0.84	Clevenger and Barrueto 2014
Kananaskis Country ¹	0.36	0.11	0.12-0.56	0.25	Fisher and Heim 2012
Willmore Wilderness	0.91	0.04	na	0.89	Fisher et al. 2013
West-central Alberta	0.14	0.07	na	0.11	Fisher et al. 2013
Glacier NP, Montana	na	na	na	0.25	Waller, unpubl. data
Columbia Mountains					
Valhalla and South Monashees	0.56	0.46	na		Kortello and Hausleitner 2015
South Selkirks	0.55	0.13	na		Hausleitner and Kortello 2014
South Purcells	0.38	0.10	na		Kortello and Hausleitner 2013
Purcells	0.71	0.10	0.05-0.45		Kortello and Hausleitner 2012

¹ Multi-season model. ² Standard error. ³ Confidence interval. ⁴ Naïve occupancy (unadjusted).

[PAGE LEFT BLANK INTENTIONALLY]

5.2. Social media

Facebook – This year we created a Facebook page for WolverineWatch.org. The objective was to use this to inform and raise awareness of wolverine conservation, management and research in the Canadian Rockies. Our opening post received more than 29,000 views (posting a video of a wolverine in suburban Lethbridge). We continue to post regularly, including a recent post from our 2016 wolverine survey photograph of a cougar mother with three kittens at one of our hair traps. The posting went viral, receiving more than 1.5 million views.

Instagram - Like Facebook we opened up an Instagram account (Wolverine_Watch) to raise awareness of wolverine conservation and our research in the Canadian Rockies. During our winter 2016 field season we posted regularly, nearly daily, documenting the research, how data are collected, the landscape surveyed for wolverines, and some of frustrations of relying on snowmobiles for travel. We continue to post regularly and currently have over 150 followers.

5.3. Other

- *Highline Magazine* (Bow Valley). Gluttons for punishment, 15 Dec 2015 <http://highlineonline.ca/mapping-the-wolverine-way/>.
- *ZDF Television, Germany* - Documentary about Waterton-Glacier National Parks. Film crew spent one day with us filming fieldwork and field data collection. Hour long documentary will be broadcast by ZDF TV on Christmas eve 2016.
- *Canadian Geographic* – Article on wolverines in western North America and Crown of the Continent ecosystem, prepared by Fraser Los, photographs by Kyle Hamilton. Both Fraser and Kyle spent time in the field with us to help prepared their December 2016 article.
- *BBC Earth* – The Truth About Wolverines, an online article by Niki Wilson that highlighted our work on behavioural aspects of wolverines' response to anthropogenic stressors that garnered global attention. <http://www.bbc.com/earth/story/20150421-the-truth-about-wolverines>.

6. Publications (2010- present)

- Genetic connectivity and demographic fragmentation of wolverines in the Canadian Rocky Mountains. *In prep*. Sawaya, Clevenger.
- Wolverine density in the Canadian Rocky Mountain Parks. *In prep*. Barrueto, Sawaya, Clevenger.
- Heim, N., J. Fisher, A.P. Clevenger, J. Paczkowski, J. Volpe. The climate, or the neighborhood? Multiple factors affecting wolverine distribution in the Canadian Rocky Mountains. *Biological Conservation* (submitted May 2016).
- Steenweg, R., M. Hebblewhite, R. Kays, J. Ahumada, J. Fisher, C. Burton, S. Townsend, C. Carbone, M. Rowcliffe, J. Whittington J. Brodie, J.A. Royle, A. Switalski, A.P.

Clevenger, N. Heim, L. Rich. Scaling up camera traps — monitoring the planet's biodiversity with networks of remote sensors. *Frontiers in Ecology and Environment* (accepted with revisions).

- Stewart, F., N. Heim, A.P. Clevenger, J. Paczkowski, J. Volpe, J. Fisher. 2016. Wolverine varies spatially with anthropogenic footprint: implications for conservation and inferences about declines. *Ecology and Evolution* 6:1493-1503.
- McKelvey, K.S., K.B. Aubry, N.J. Anderson, A.P. Clevenger, J.P. Copeland, K.S. Heinemeyer, R.M. Inman, J. Squires, J.S. Waller, K. Pilgrim, M.K. Schwartz. 2014. Recovery of wolverines in the Western United States : Recent extirpation and re-colonization or range retraction and expansion ? *Journal of Wildlife Management* 78:325-334.

7. Future (and scheduling)

7.1. Genotyping errors in data collected between 2010-2015.

In December 2015, project collaborator Dr. Michael Sawaya, carnivore research ecologist with Sinopah Wildlife Research Associates, discovered that the US Forest Service Rocky Mountain Research Station (RMRS) genetics laboratory in Missoula, MT, which had analysed all of our hair and scat samples collected between 2010-2015, had made substantial genotyping errors leading to the misidentification of a number of wolverines. Originally a total of 64 individuals were identified from noninvasive genetic samples collected between 2010-2013 in Banff and Yoho National Parks. However, on close inspection of microsatellite genotypes and spatial/temporal patterns of individual captures, Dr. Sawaya found laboratory errors (that were confirmed by the RMRS upon re-analysis) in all 3 years of results from the original study. In most cases, genotyping errors caused one individual to be identified as 2+ individuals until the errors were removed and the genotypes were determined to be recaptures of the same animal. Consequently, the original 64 wolverines identified by the RMRS collapsed to 49 unique individuals during the data cleanup process (Table 7.1).

Table 9. Artificially inflated counts and adjusted percentages of individual wolverines that were mis-identified with genotyping errors in microsatellite analysis of noninvasive genetic samples collected in Banff and Yoho National Parks, Alberta.

	Females	Males	Total
Original count	25	39	64
Spurious individuals	9	6	15
Final count	16	33	49
Adjusted percentage	0.36	0.15	0.23

The DNA extracts for all 59 individuals (49 from original Banff-Yoho study and 10 from 2014-2015 DNA sampling grids) and all of the raw genetic material from 2010-2015 has been sent to the Wildlife Genetics International laboratory in Nelson, British Columbia, where they will verify the final multi-locus genotypes and sexes of the 59 individuals identified at the RMRS and analyze samples collected in 2016.

This unexpected and unfortunate incident has caused a significant delay in completing two manuscripts that used the original 64 genotypes and were nearly completed in fall 2015, when we first suspected that there were errors in the dataset. This delay has set us back in terms of reporting results from the 6-year research project, completion of manuscripts to be submitted for publication in peer-reviewed scientific journals, and delivery of the science from the research to key stakeholders.

7.2. Analyses and science delivery

The following two manuscripts are awaiting the results from the re-analysis of the genetic data set from the Canadian Rockies national parks. Once we have confirmation on the genotypes from this data set the manuscripts will be completed and submitted to journals for publication.

A. *Genetic connectivity and demographic fragmentation of wolverines in the Canadian Rocky Mountains* manuscript (schedule: Sept. 2016)

B. *Wolverine density in the Canadian Rocky Mountain Parks* manuscript (schedule: Sept. 2016)

The following are a series of analyses and manuscripts, in order of occurrence, which we will work on and deliver as part of our agreements with funding partners. The results of these studies will inform science-based recommendations for key stakeholders, land/natural resource managers and transportation agencies for 1) managing trapper harvest of wolverines in the southern Rockies, 2) identifying core areas of wolverine habitat and critical linkages and dispersal corridors that link them, and 3) identifying areas of wolverine dispersal within the metapopulation, with special focus on development and transportation networks.

1. *Estimating wolverine abundance and density to assess sustainability of trapper harvest in Alberta and BC Rockies using spatial capture-recapture models (SCR)*; schedule: Dec. 2016)

2. *Understanding the effects of human disturbance and landscape characteristics on wolverine density in the Canadian Rockies*. Spatial capture-recapture analysis will be used to estimate wolverine density in the CCoC and we will apply this method across a gradient of human land-uses and landscape characteristics to understand how they influence wolverine spatial distribution and abundance.

3. *Modeling landscape connectivity of wolverines*: Create landscape resistance (LR) surfaces for wolverines from SCR analysis and other LR modeling methods, based on biophysical (e.g., snowpack, landcover, terrain) and human disturbance (e.g., highways, road density, development). LR models based on least-cost path will identify important dispersal corridors, transboundary linkages and areas required for mitigating fragmentation effects of major east-west aligned highways in the Columbia and Rocky Mountains.

4. *Examining migration and gene flow patterns between wolverine populations in the contiguous US and Canada* using our 6-year data set, data from Schwartz et al. (2009) and newly collected genetic data from the multi-state US wolverine survey.

Partnership

'Mapping the Wolverine Way' is conducted through an international, public-private partnership including the Western Transportation Institute (WTI) at Montana State University, British Columbia Ministry of Forests, Lands and Natural Resource Operations; Alberta Environment and Sustainable Resource Development, Parks Canada Agency, Alberta Innovates Technology Futures, Wildsight BC, and the Yellowstone to Yukon Conservation Initiative.

Funding

Funding for 2016 research came from the Wilburforce Foundation, Woodcock Foundation, Cross Foundation, Liz Claiborne Art Ortenberg Foundation, BC Ministry of Forests, Lands, and Natural Resource Operations, Fish and Wildlife Compensation Program (British Columbia), Columbia Basin Trust, Norcross Foundation and Volgenau Foundation.

Previous funding support came from the US Fish and Wildlife Service Great Northern Landscape Conservation Cooperative, Disney Conservation Fund, Wilburforce and Woodcock Foundations, Cross Foundation, Alberta Conservation Association, the Wolverine Foundation, BC Ministry of Forests, Lands, and Natural Resource Operations and McLean Foundation.

Acknowledgements

There are many people to thank on both sides of the Rockies during the last three years. In Alberta, Maria Didkowski and Greg Hale (Alberta Environment and Sustainable Resource Development, Blairmore, Alberta) assisted and provided in-kind support. In Canmore AESRD, Jon Jorgenson, Jay Honeyman, Brett Boukall and Scott Jevons provided logistical and vehicle support, a full array of remote cameras and GIS support. Bill Dolan and Bryan Sundberg from Alberta Parks helped with permitting and secured housing for us in Alberta. Our 2016 field crew consisted of Troy Malish, Laura Smit, Reg Bunyan and Barb Bertch. Doug Chadwick and John Bergenske have assisted us with fieldwork during the last three years and have been steadfast in supporting and championing the importance of our work throughout the inter-governmental and NGO conservation landscape.

On the BC side, the Ministry of Forests, Lands and Natural Resource Operations (FLNR) in Nelson, Cranbrook, Fernie and Invermere provided critical support and equipment throughout the winters. Bill Hanlon of Hornady Wilderness Society helped with our funding request to the Columbia Basin Trust. We thank Greg Goodison and pilot Dave Hawrys at Ascent Helicopters in Fernie for the many hours of safe flying and generous time and scheduling, not to mention putting up with all the smells that we bring with us. Casey Brennan (Teck Coal) helped with information on access to sampling sites and arranged for our housing within the study area.

Funding for 2016 was obtained from the Wilburforce Foundation, Woodcock Foundation, BC FLNR, Liz Claiborne Art Ortenberg Foundation, Cross Foundation, Columbia Basin Trust, BC Fish and Wildlife Compensation Program, Volgenau Foundation and Norcross Foundation. Support for our research in 2014 and 2015 came from the Wilburforce Foundation, Woodcock Foundation, BC FLNR, US Fish and Wildlife Service Great Northern Landscape Conservation Cooperative, Cross Foundation, Alberta Conservation Association, Disney Wildlife Conservation Foundation, The Wolverine Foundation, and McLean Foundation,

The Yellowstone to Yukon Conservation Initiative and Wildsight BC managed Canadian funding for the project. On the US side, the Montana State University Foundation (MSUF) assisted with locating suitable funders for our work. MSUF and the Western Transportation Institute at Montana State University managed funds south of the border.

References

- Banci, V., A. Harestad. 1990. Home range and habitat use of wolverines in Yukon, Canada. *Holarctic Ecology* 13:195-200.
- Burnham, KP, DR Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Springer Science & Business Media.
- Burton, A. C., E. Neilson, D. Moreira, A. Ladle, R. Steenweg, J. T. Fisher, E. Bayne, and S. Boutin. 2015. Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology* 52:675-685.
- Cegelski, C, L Waits, N Anderson, O Flagstad, C Strobeck, C Kyle. 2006. Genetic diversity and population structure of wolverine (*Gulo gulo*) populations at the southern edge of their current distribution in North America with implications for genetic viability. *Conservation Genetics* 7:197-211.
- Clevenger, A.P., M. Barrueto. 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., 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.
- 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.

- Gopalaswamy, A.M., K.U. Karanth, N. Kumar, D.W. Macdonald. 2012. Estimating tropical forest ungulate densities from sign surveys using abundance models of occupancy. *Animal Conservation* 15:669-679.
- Graves, T., R.B. Chandler, J.A. Royle, P. Beier, K.C. Kendall. 2014. Estimating landscape resistance to dispersal. *Landscape Ecology* 29:1201-1211.
- 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. A. 2015. *Complex effects of human-impacted landscapes on the spatial patterns of mammalian carnivores*. M.Sc. thesis. University of Victoria.
- Hines, J. E. 2006. PRESENCE- Software to estimate patch occupancy and related parameters. USGS-PWRC, Patuxent Wildlife Research Centre, Laurel, MD, USA.
- Inman, R.M., M.L. Packila, K.H. Inman, A. McCue, G. White J. Persson, B. Aber, M Orme, K. Alt, S. Cain, J. Frederick, B. Oakleaf, S. Sartorius. 2012. Spatial ecology of wolverines at the southern periphery of distribution. *Journal of Wildlife Management* 76:778-792.
- 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.A., E.C. 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.
- Krebs, J. R., E. C. Lofroth, and I. A. N. Parfitt. 2007. Multiscale habitat use by wolverines in British Columbia, Canada. *Journal of Wildlife Management* 71:2180.
- Lofroth, E. C., P. K. Ott. 2007. Assessment of the Sustainability of Wolverine Harvest in British Columbia, Canada. *Journal of Wildlife Management* 71:2193.
- 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.
- McKelvey, K. S., J. P. Copeland, M. K. Schwartz, J. S. Littell, K. B. Aubry, J. R. Squires, et al.

2011. Climate change predicted to shift wolverine distributions, connectivity, and dispersal corridors. *Ecological Applications* 21:2882–2897.
- McLellan, M., C. Servheen. 2013. *Flathead wolverine project summary report, 2009-2013*. College of Forestry and Conservation, University of Montana, Missoula, MT. 12 pp.
- Multi-state Wolverine Working Group. 2015. *Coordinated Multi-state Wolverine Baseline Sampling in Montana, Idaho, Wyoming and Washington: Standard Operating Procedures for Camera DNA Stations*. Unpublished report.
- 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.
- Royle, J.A., K.V. Young. 2008. A hierarchical model for spatial capture-recapture data. *Ecology* 89:2281–2289.
- 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.
- Sawaya, MA, AP Clevenger. In prep. Genetic connectivity and demographic fragmentation of wolverines in the Canadian Rocky Mountains.
- Sawaya, MA, AP Clevenger. 2014. Effects of transportation infrastructure on fine-scale genetic structure of wolverines in Banff and Yoho National Parks. Pp 172-190, in: AP Clevenger, M Barrueto (eds). *Trans-Canada Highway Wildlife and Monitoring Research, Final Report. Part B: Research*. Report to Parks Canada Agency, Radium Hot Springs, British Columbia, Canada.
- Schwartz, M., J. Copeland, N. Anderson. 2009. Wolverine gene flow across a narrow climatic niche. *Ecology* 90:3222-3232.
- Squires, J. R., M. K. Schwartz, J. P. Copeland, L. F. Ruggiero, and T. J. Ulizio. 2007. Sources and patterns of wolverine mortality in western Montana. *Journal of Wildlife Management* 71:2213–2220.
- Stewart, F., N. Heim, A.P. Clevenger, J. Paczkowski, J. Volpe, J. Fisher. 2016. Wolverine behaviour varies spatially with anthropogenic footprint: implications for conservation and inferences about declines. *Ecology and Evolution* 6(5):1493-1503.
- Weaver, J. L. 2001. *The Transboundary Flathead: A critical landscape for carnivores in the Rocky Mountains*. Wildlife Conservation Society.
- Weaver, J.L., P. Paquet, L. Ruggiero. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. *Conservation Biology* 10: 964-976.
- Weaver, J. 2013. Safe havens, safe passages for vulnerable fish and wildlife: Critical landscapes in the Southern Canadian Rockies, British Columbia and Montana. *Wildlife Conservation Society Canada Conservation Report No. 6*. Toronto, Ontario, Canada.