

State of Knowledge for Alberta's
Wolverine Population 2020:
Literature Review, Density Estimate,
and Gap Analysis



State of Knowledge for Alberta's Wolverine Population 2020: Literature Review, Density Estimate, and Gap Analysis

Alberta Conservation Association #101, 9 Chippewa Road Sherwood Park, Alberta, Canada T8A 6J7



Report Series Editors

DOUG MANZER Alberta Conservation Association P.O. Box 92, Provincial Bldg. Blairmore, AB T0K 0E0 SUE PETERS Alberta Conservation Association #101, 9 Chippewa Rd. Sherwood Park, AB T8A 6J7

Conservation Report Series Type: Data

ISBN: 978-1-989448-13-7

Reproduction and Availability:

This report and its contents may be reproduced in whole, or in part, provided that this title page is included with such reproduction and/or appropriate acknowledgements are provided to the authors and sponsors of this project.

Suggested Citation:

Alberta Conservation Association. 2020. State of Knowledge for Alberta's Wolverine Population 2020: Literature Review, Density Estimate, and Gap Analysis. Data Report, produced for the Alberta Conservation Association, Sherwood Park, Alberta, Canada. 41 pp + App.

Contributors: Andrea Morehouse (Winisk Research and Consulting), Sue Peters (ACA), Robert Anderson (ACA), and Doug Manzer (ACA)

Corresponding contributor: Sue Peters

Cover photo credit: David Fairless

Digital copies of conservation reports can be obtained from:

Alberta Conservation Association

#101, 9 Chippewa Rd.

Sherwood Park, AB T8A 6J7 Toll Free: 1-877-969-9091

Tel: (780) 410-1998 Fax: (780) 464-0990

Email: info@ab-conservation.com Website: www.ab-conservation.com

EXECUTIVE SUMMARY

The wolverine is considered *Data Deficient* in Alberta. Alberta uses criteria developed by the International Union for Conservation of Nature (IUCN) when assessing species' status. IUCN status designations are determined using a variety of criteria including a declining population size, extent of (and changes to) geographic range (e.g., extent of occurrence, or area of occupancy), a determination that population size is small and/or restricted, or a quantitative analysis on the probability of extinction (IUCN 2012). Alberta's designation of *Data Deficient* is used when the available data are inadequate to determine the degree of threat faced by the species.

Several wolverine studies have occurred within Alberta since the provincial status assessment in 2000, and much more information is now available that will be useful for an updated status assessment, including abundance estimates for some regions of the province, areas of occupancy and occurrence, habitat ecology, and response to anthropogenic change. However, the data on population size within the province remains limited. Some extrapolation techniques might allow for coarse estimates at the provincial level, but there are limitations to these options. In particular, there are currently no robust population estimates for the Boreal Forest Natural Region even though this makes up the vast majority of the wolverine distribution in Alberta.

We estimated wolverine density for the Birch Mountains area using data originally collected for an occupancy study from 2016–2017. The study area was 1,976 km² with an estimated density within the range of 0.66–3.00 per 1,000 km² (95% CI). This estimate should be interpreted cautiously because of low precision and the failure to meet spatially explicit capture-recapture model assumptions regarding trap-specific behavioural response. A density estimate in the Rainbow Lake area of Alberta is currently underway; however, the study area was again relatively small and may not be representative for Alberta's Boreal Forest Natural Region as a whole. Wolverine density estimates from studies in various locations in the Rocky Mountains and Foothills natural regions between 2004 and 2020 range from 1.3/1,000 km² to 6.8/1,000 km²; however, differences in field and analysis methods make comparisons across studies difficult and should be interpreted cautiously.

In addition, there are limited available data to provide an estimate of population trend over time. Harvest records can provide an index of harvest and changes in the distribution of harvest, though these records are largely influenced by trapper effort, which has not been accounted for with wolverine harvest to date. In summary, data gaps that continue to exist include a current abundance estimate for the northern portion of the Rocky Mountains and Foothills, a reliable abundance estimate to represent the Boreal Forest Natural Region, and information to account for population trend across the province.

ACKNOWLEDGEMENTS

Thank-you to Andrea Morehouse (Winisk Research and Consulting) for the analysis of the Birch Mountains data and her contribution to the writing of this report. We also thank the Alberta Trappers' Association, particularly Neil Kimmy and Bill Abercrombie, for their significant contribution to the collection of wolverine data in the Birch Mountains. Funding for this state of knowledge report was provided by Alberta Conservation Association.

TABLE OF CONTENTS

EXECUTIVE SUMMARY	ii
ACKNOWLEDGEMENTS	iii
LIST OF TABLES	v
LIST OF FIGURES	vi
1.0 INTRODUCTION	1
2.0 METHODS	1
2.1 Literature Review	1
3.0 RESULTS AND DISCUSSION	2
3.1 Objective 1: A review of the available population information from Alberta and other relevant jurisdictions	2
3.2 Objective 2: An evaluation of whether the available data allow for a provincial population and trend estimate over the last 5-10 years	5
3.3 Objective 3: An assessment of knowledge gaps and list of information needed to answer further questions about wolverine population size and trend within Alberta	7
4.0 CONCLUSION	9
5.0 LITERATURE CITED	10
6.0 APPENDICES	18
Appendix 1: The development of a spatially explicit density estimate for the western periphery of the Birch Mountains	18
Appendix 2: Summary of Alberta wolverine literature and relevant density estimates	34

LIST OF TABLES

Appendix 1 Table 1: The number of individuals detected for the first time per occasion 24
Appendix 1 Table 2: AICc model selection results for wolverines in the Birch Mountains study area using 2016–17 data
Appendix 1 Table 3: Real parameter estimates for the most parsimonious model for wolverines in the Birch Mountains Study Area. Data are from 2016–17
Appendix 1 Table 4: Effect of mask spacing on density estimates for the most parsimonious model, D~1 g0~bk σ ~1
Appendix 1 Table 5: Effect of mask buffer width on density estimates for the most parsimonious model, D \sim 1 g0 \sim bk $\sigma\sim$ 1 as well as the null model, D \sim 1 g0 \sim 1 $\sigma\sim$
Appendix 1 Table 6: Effect of mask buffer width on density estimates for the most parsimonious model, D \sim 1 g0 \sim bk $\sigma\sim$ 1
Appendix 1 Table 7: Real parameter estimates for the most parsimonious model for wolverines in the Birch Mountains Study Area using a 90 km buffer around camera trap locations. Data are from 2016-17
Appendix 1 Table 8: Real parameter estimates for the most parsimonious model without the bk covariate (i.e. the null model) for wolverines in the Birch Mountains Study Area. Data are from 2016-17
Appendix 1 Table 9: Number of detections per individual and the number of locations at which that individual was detected. Also listed are the number of detections occurring at the initial capture site
Appendix 2 Table 1: Summary of Alberta wolverine literature published since the last status assessment (Peterson 1997)
Appendix 2 Table 2: Summary of the available literature on wolverine density in habitats found within Alberta

LIST OF FIGURES

Appendix 1 Figure 1: Map of the Birch Mountains study area in north-central Alberta 18
Appendix 1 Figure 2: Telemetry data and minimum convex polygons of collared wolverines in the Birch Mountains study area. Data are from November 2016 through March 2017
Appendix 1 Figure 3: Detection locations of male and female wolverines in the Birch Mountains November 2016 through March 2017
Appendix 1 Figure 4: The number of detections grouped by monthly intervals
Appendix 1 Figure 5: Detection probability (g0) versus the distance between the animal's home range center and camera trap location for wolverines in the Birch Mountain Study area
Appendix 1 Figure 6: Effect of varying buffer width on estimated density (y-axis) for (a) the null model (D \sim 1 g0 \sim 1 $\sigma\sim$ 1) and (b) the most parsimonious model (D \sim 1 g0 \sim bk $\sigma\sim$ 1)
Appendix 1 Figure 7: Detection probability (g0) versus the distance between the animal's home range center and camera trap location for wolverines in the Birch Mountains Study area
Appendix 1 Figure 8: Detection probability (g0) versus the distance between the animal's home range center and camera trap location for wolverines in the Birch Mountain Study area

1.0 INTRODUCTION

Wolverines are notoriously cryptic and information about their ecology, habitat needs, and population status is often difficult to obtain. Federally, the wolverine is considered a species of *Special Concern* by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2014). Within Alberta, wolverines may be at risk but the species is currently considered *Data Deficient* due to insufficient information on their populations (Alberta Environment and Parks 2017). The status assessment for wolverines resulting in this designation occurred in 2000, based on information available in the late 1990s (Peterson 1997). Since that time, there have been several wolverine studies within Alberta to attempt to better understand the ecology of this evasive species.

This report provides a review of population literature for wolverines and discusses its implications for estimating abundance and trend within Alberta. This report also presents an analysis of the available population data for wolverines in Alberta, including recently obtained data from the Alberta Conservation Association's (ACA) Birch Mountains study area, with the goal of defining our knowledge of a defendable provincial population estimate. A provincial population estimate is an important component of a future status re-assessment of wolverines in Alberta. Additional information relevant to the status assessment, such as trend in population, habitat, distribution, rescue potential, and threats would be covered in a future updated Alberta Wildlife Status Report.

Specifically, the objectives of this report are to provide:

- 1. a review of the available population information from Alberta and other relevant jurisdictions;
- 2. an evaluation of whether the available data allow for a provincial population and trend estimate over the last 5–10 years; and
- 3. an assessment of knowledge gaps and list of information needed to answer further questions about wolverine population size and trend within Alberta.

2.0 METHODS

2.1 Literature Review

To complete Objectives 1 through 3, we reviewed the available wolverine literature, specifically focussing on literature that has been published since the last status report (Peterson 1997). We focussed on studies completed in Alberta or in other relevant jurisdictions (e.g., other regions with similar habitat). In our review of the available density and abundance literature, we focussed only on publications conducted in habitats present in Alberta (e.g., we excluded studies conducted in arctic habitats).

As part of Objective 1, we attempted to calculate a spatially explicit density estimate for the western periphery of the Birch Mountains using data collected in 2016–2017. See Appendix 1 for the details of the methods and results.

3.0 RESULTS AND DISCUSSION

3.1 Objective 1: A review of the available population information from Alberta and other relevant jurisdictions

Several wolverine studies have occurred within Alberta since the provincial status assessment in 2000, which was based on Peterson (1997). Broadly, the recent work occurring within Alberta can be grouped into seven main themes: population assessments, habitat ecology, genetics, trapper harvest, behaviour, foraging ecology, and occupancy monitoring (Appendix 2 Table 1). Until recently, work has been focussed in the Rocky Mountain region. Wolverine distribution in the United States is largely limited to mountainous areas, and consequently a large portion of North American research has focussed on this ecosystem (e.g., Hornocker and Hash 1981, Inman et al. 2012, Fisher et al. 2013, Kortello et al. 2019, Sawaya et al. 2019). Thus, perhaps one of the biggest contributions to the literature since the last status assessment is the work in the boreal forest of Alberta (e.g., Webb et al. 2016, Scrafford et al. 2017, Scrafford and Boyce 2018, Jokinen et al. 2019). For example, a consistent finding in the literature is that wolverine distribution is largely associated with, and limited by, persistent spring snow cover (e.g., Aubry et al. 2007, Brodie and Post 2010, Copeland et al. 2010). However, recent research from the boreal forest in Alberta suggests this is not the case and an established wolverine population exists in the boreal region despite the lack of spring snow cover (Webb et al. 2013, 2016, 2019).

Similar to research outside of Alberta, wolverines in the province appear to be affected by anthropogenic landscape change (e.g., Heim et al. 2017). In the Rocky Mountains and foothills, wolverine density is higher in areas with less anthropogenic development (Fisher et al. 2013) and wolverine behaviour differs between areas of low and high human disturbance (Stewart et al. 2016). Indeed, genetic work indicates that populations have more gene flow between them when they are exposed to fewer anthropogenic disturbances (Kyle and Strobeck 2001, 2002). Furthermore, wolverine use of habitats is affected by industrial development. For example, Scrafford et al. (2018) showed that roads, regardless of traffic volume, reduced the quality of wolverine habitats and higher-traffic roads might be deleterious. Further work indicates that in at least some areas, wolverines have become adapted to landscapes with high industrial footprints (e.g., Scrafford et al. 2017). In the boreal forests near Rainbow Lake, Alberta, wolverines were attracted to logging areas perhaps because these areas provide foraging opportunities and movement routes for wolverines (Scrafford et al. 2017). Wolverines were even found using anthropogenic features for denning habitat; one wolverine den was found in a slash pile and one den was found in a log deck (Scrafford et al. 2018). Similarly, wolverines in the boreal region use borrow pits as hunting grounds for beavers and one wolverine denned within a beaver lodge at a borrow pit (Scrafford et al. 2020).

The trend in the population estimation literature is for researchers to use spatially explicit capture-recapture (SECR) models and this is true for the recent wolverine literature as well (Appendix 2 Table 2; e.g., Bischof et al. 2019, Barrueto et al. 2020, Mowat et al. 2020). Differences between density and abundance estimates from traditional capture-mark-recapture (CMR) and SECR models are likely (Obbard et al. 2010, Gerber and Parmenter 2015, Whittington and Sawaya 2015). Because of a failure to fully account for animal movement off the sampling grid, ad-hoc estimates of density obtained from CMR methods can be higher than SECR density estimates (Obbard et al. 2010, Gerber et al. 2012, Noss et al. 2012, Rich et al. 2014). As an example, the grizzly bear population in southeastern British Columbia was sampled in 2007 and the data were analyzed using CMR methods, which produced a density estimate of 55 bears/1,000 km² (Alberta Grizzly Bear Inventory Team 2008). However, when the same data set was reanalyzed using SECR methods, the density estimate was 33 bears/1,000 km² or 40% lower than the CMR results (Efford and Mowat 2014). Thus, consistency in methods is important if comparisons between regions are desired.

There has been much effort put into developing and testing monitoring protocols for wolverine (e.g., Mowat 2001, Fisher et al. 2013, Fisher and Bradbury 2014), although there are few actual abundance or density estimates for Alberta (Appendix 2 Table 2). Wolverine distribution in Alberta is limited to the Rocky Mountain, Foothills, Boreal Forest, and Canadian Shield natural regions (Webb et al. 2013), but all Alberta-specific abundance and density estimates have occurred only in the Rocky Mountains and Foothills regions (Appendix 2 Table 2). In the Wilmore Wilderness Area of Alberta during the winters of 2006–07 and 2007–08, Fisher et al. (2013) estimated wolverine density to be 6.8/1,000 km² (CMR). Density estimates for the foothills of westcentral Alberta were lower and ranged from 1.8 to 3.0 wolverines/1,000 km² depending on the year sampled (CMR; 2004–2006) (Fisher et al. 2013, Appendix 2 Table 2). While the Fisher et al. (2013) data represent the first empirical estimates for the Rocky Mountains of Alberta, they are now approximately 15 years old. More recently, Mowat et al. (2020) estimated the wolverine density in the Waterton/West Castle area of southwestern Alberta to be 1.35/1,000 km² (SECR). Further, Mowat et al. (2020) also included density estimates for the Banff, Yoho, and Kootenay national parks region that ranged from 2.05 to 2.83 wolverines/1,000 km² depending on the year sampled (SECR; 2011–2013). Additionally, Mowat et al. (2020) include density estimates for the Central and South Rockies (Fig. 4 in Mowat et al. 2020). These study areas include sampling sites in both Alberta and British Columbia. Density estimates were 1.32 wolverines/1,000 km² and 1.33 wolverines/1,000 km² in the Central and South Rockies, respectively (SECR; Mowat et al. 2020). A recent density estimate for the Banff, Yoho, and Kootenay national parks is slightly higher at 3.0/1,000 km² (SECR; Barrueto et al. 2020). The Barrueto et al. (2020) data uses a subset of the full data set analyzed by Mowat et al. (2020).

Although there is decent data coverage for the Rocky Mountain region, notably missing is an abundance estimate for the Boreal Forest Natural Region of the province. We attempted to estimate density for the Birch Mountains area using ACA data from 2016–2017 (see Appendix 1 for details), but encountered some difficulties as a result of low precision and trap-specific

behavioural response, and the density estimate using SECR methods (1.4/1,000 km²) should be interpreted cautiously. Dr. Matt Scrafford and colleagues have collected a substantial data set of over 50 wolverines detected over three winter field seasons in the boreal forest (Scrafford et al. 2017, 2018, Scrafford and Boyce 2018), and they are currently working on estimating wolverine density and abundance in the Rainbow Lake area (M. Scrafford, personal communication). It is not clear, however, from the published literature what their detection histories and recapture rates might look like. Further, similar to the Birch Mountains study area, their trapping array was small relative to the scale of movement of their collared wolverines (Scrafford 2017, Scrafford et al. 2017); the MCP bounding the live trap locations was 2,380 km² (Scrafford et al. 2017). Thus, an analysis of these data using SECR might encounter similar problems to those described in Appendix 1. Regardless, given the lack of density and abundance estimates for the boreal forest, it will be important to incorporate information from their estimates into wolverine management and conservation once the estimates are available.

Another option we considered was to explore the data collected by Webb et al. (2017), originally intended to assess habitat features associated with wolverine occupancy. Webb et al. (2017) operated run poles within randomly selected 10-km x 10-km township grid cells on registered traplines in the boreal forest. Run poles were checked every two weeks to refresh bait, download pictures, and collect hair samples during the winters from 2013–2016 (Webb et al. 2017). These methods are markedly similar to other wolverine studies that have estimated abundance. Both Lofroth and Krebs (2007) and Mowat et al. (2020) used one to two sampling stations (noninvasive hair collection) within each 10-km x 10-km grid cell overlaid across their study areas. Similarly, Inman et al. (2012) used one sampling station per 12-km x 12-km grid cell over their study area. The key difference is that Webb et al. (2017) generally only selected two random cells per trapline and there was often substantial distance between participating traplines. For example, the average distance between sampling locations during the 2015–16 field season was 280.9 km. Webb et al. (2017) predicted that the best wolverine habitat in the boreal region occurred north of the 56th parallel where road densities are lower, forests are more conifer dominated and climates are cooler. Indeed, more wolverines were detected north of the 56th parallel (Webb et al. 2017). Thus, although the Webb et al. (2017) study was designed to identify habitat variables associated with occupancy, it seemed possible to analyze the detection data in a SECR framework, potentially using only the data north of the 56th parallel. However, we investigated this option and it does not appear feasible. Most detections from the Webb et al. (2017) data occurred during the 2015–16 season, and all detections of individuals occurred at the same site, so there is no spatial movement. In this case, the randomly selected sampling stations are too far apart relative to the spatial movement of wolverines and without redetections at different locations SECR is not able to estimate the sigma parameter. We investigated other years with fewer detections as well and occasionally an individual was detected at a different site, but it was always within the same trapline and occurred rarely. Thus, a density estimate from these data does not appear feasible.

Differences in both field and analysis methods make comparisons of wolverine densities across different studies difficult and should be interpreted cautiously (Appendix 2 Table 2). While there are currently no reliable Alberta-specific density estimates for the boreal region, studies from boreal forests in Ontario and Scandinavia suggest similar density estimates of 1.4/1,000 km² and 1.74/1,000 km², respectively ([CMR] COSEWIC 2014; [open-population spatial capture-recapture] Bischof et al. 2019).

3.2 Objective 2: An evaluation of whether the available data allow for a provincial population and trend estimate over the last 5-10 years

Currently, there is no reliable population estimate available for the Boreal Forest Natural Region of Alberta, even though Alberta's wolverine distribution largely occurs in this region. While recent work by the Alberta Conservation Association and the University of Alberta has provided updated information on wolverine habitat ecology in this region (e.g., Jokinen et al. 2019, Scrafford and Boyce 2018, Scrafford et al. 2017, 2018, Webb et al. 2017), none of the studies were designed to estimate population size. Abundance data, however, are available for the Rocky Mountain and Foothills natural regions (Fisher et al. 2013, Mowat et al. 2020). Though as mentioned previously, the Fisher et al. (2013) data are now 15 years old. Heim et al. (2017) used non-invasive genetic sampling and remote trail cameras to estimate wolverine occupancy in the Banff, Yoho, and Kootenay national parks and adjacent Kananaskis Country, and some of these data have been used by other scientists to estimate density. The Banff, Yoho, and Kootenay national parks data used by Heim et al (2017) were also used in the Mowat et al. (2020) and Barrueto et al. (2020) papers, and both author groups have used these data from 2011 through 2013 to estimate density. Further, Mowat et al. (2020) include density estimate for the Central and South Rockies, and while most of the sampling in these areas occurred in British Columbia, there were some sampling locations in Alberta. Thus, while not necessarily Alberta-specific, there are several data sets for the Rocky Mountains from Banff National Park south to the border with the United States.

Population estimates for the entirety of the Rocky Mountain region, however, would require extrapolating beyond the areas studied. Much research exists on the relationship between habitat selection and abundance (e.g., Boyce and McDonald 1999, Boyce et al. 2016). For most species, habitat is the primary driver of distribution and abundance (Boyce et al. 2016). Habitat selection can be defined as the probability that when a resource unit is encountered, it will be used by the animal (Lele et al. 2013). Habitat selection patterns can be described by resource selection functions (RSFs), which are proportional to the probability of use of a resource unit (Manly et al. 2002). Boyce and McDonald (1999) associated abundance with RSF scores and used this information to extrapolate abundance estimates to unsampled areas. This RSF approach has been used to estimate abundance for several species including black bears (Loosen et al. 2019), grizzly bears (Boyce and Waller 2003), wolves (Mladenoff and Sickley 1998), Amur leopards (Hebblewhite et al. 2011), and wolverines (Inman et al. 2013). A different approach to linking abundance to habitats was used previously in British Columbia (Lofroth and Krebs 2007). Lofroth and Krebs (2007) used empirically derived wolverine density estimates in combination

with a habitat quality rating system developed using wolverine distribution, human development data, and ecosystem mapping to create a predictive model of wolverine distribution and abundance at a provincial scale (Lofroth and Krebs 2007).

Thus, using some method of a habitat-based extrapolation in Alberta could potentially allow for a coarse population estimate in the northern portion of the Rocky Mountain region. As noted previously, abundance data are available for more southern portions of the Rocky Mountain and Foothills natural regions (Fisher et al. 2013, Barrueto et al. 2020, Mowat et al. 2020). Habitatbased extrapolations of abundance estimates require a reference population, and that reference population should be at or near carrying capacity (Boyce and McDonald 1999, Boyce et al. 2016). Often protected areas such as national parks are used as a reference area (e.g., Boyce et al. 2016, Loosen et al. 2019). Within Alberta, density estimates exist for Waterton Lakes National Park (Mowat et al. 2020), Banff, Yoho, and Kootenay national parks (Barrueto et al. 2020, Mowat et al. 2020), and the Wilmore Wilderness Area (Fisher et al. 2013), and these protected areas could potentially serve as a reference population if the assumption is made that they are at or near carrying capacity. Telemetry data from collared individuals are commonly used to develop RSF models, but to our knowledge, wolverine telemetry data are not available for any of these areas. Though commonly used, telemetry data are not required to develop an RSF (e.g., Loosen et al. 2019), but the scale of sampling within these areas might be too sparse (e.g., 1 sampling location/10-km x 10-km grid cell; Mowat et al. 2020) to develop a reasonable RSF, which is required by the Boyce and McDonald (1999) method. The Lofroth and Krebs (2007) method would be another option to consider. If habitat-abundance extrapolation methods are explored, we recommend all available data be reanalyzed using SECR models to ensure consistency between study areas before any extrapolation or additional modeling takes place.

Perhaps the most continuous data set available for Alberta is wolverine harvest records. The previous status report indicated that wolverine harvest showed a pronounced decline in the number of pelts harvested from the northwest region of the province, though other regions showed no discernable trend (Peterson 1997). However, as more recent data were evaluated, the trend shifted. Between 2000 and 2011, the wolverine harvest more than doubled in the northwestern boreal region and increased by 47% in the northeastern boreal region as compared to data from 1989-1999 (Webb et al. 2013). Within Alberta, the majority of harvested wolverines come from the northwestern boreal region of the province (Webb et al. 2013). Although Poole and Mowat (2001) show that the density of harvest locations decreased over time from 1977–1999, they also suggest that the wolverine abundance index based on harvest and pelt price has increased over time. However, they note that their abundance index is certainly biased and emphasize the need for a corrected harvest data set, use of local population data, and finer scale analysis (Poole and Mowat 2001). Indeed, harvest records are not necessarily a good reflection of population trend. For example, harvest data from pelt export records might not account for pelts that are used locally (Peterson 1997, COSEWIC 2004). Further, wolverine pelt price, other fur-bearing species pelt price, weather, furbearer abundance, changes in access, health, work schedules, and rising average income can all affect trapper effort, which would in turn affect harvest records (Peterson 1997, Mullen 2006, Webb et al. 2013).

In short, while numerous studies on wolverine have been conducted since the last status assessment, the data on population size within the province remains limited. As discussed in the preceding paragraphs, some extrapolation techniques might allow for coarse estimates at the provincial level, but there are limitations to these options. In particular, there are currently no robust population estimates for the boreal region even though this makes up the vast majority of the wolverine distribution in Alberta. There are no available data to provide a population trend estimate. As discussed above, harvest records can provide an index of harvest and changes in the distribution of harvest, though these records are largely influenced by trapper effort which is not currently measured.

3.3 Objective 3: An assessment of knowledge gaps and list of information needed to answer further questions about wolverine population size and trend within Alberta

In ideal circumstances, there would be a population estimate for each region of Alberta, similar to what is done for Alberta's grizzly bears (Alberta Sustainable Resource Development 2008, Alberta Environment and Parks 2016). Recognizing that such an effort is likely not feasible given budget constraints, we have focussed on identifying current knowledge gaps and information that could help fill those gaps. Based on our review of the literature, we have outlined several knowledge gaps that should be addressed to answer questions about wolverine population size and trend within Alberta.

3.3.1 Boreal Forest Population Estimate

Notwithstanding the data presented in Appendix 1 from the Birch Mountains, there isn't a reliable estimate that is representative for the entire Boreal Forest Natural Region of Alberta at this time. As discussed under Objective 1 above, work is apparently underway to estimate wolverine density and abundance in the Rainbow Lake area. Although as mentioned, the Rainbow Lake study area is relatively small and may not be representative of the broader region. If a robust and representative density estimate is not completed, ideally, a project specifically designed to estimate wolverine density and abundance in the boreal forest would be implemented. We recommend the use of the program *secrdesign* to simulate different sampling designs. This program allows the user to evaluate different sampling designs and determine the sampling effort required to achieve a density estimate with the desired relative standard error, while also considering logistical constraints.

3.3.2 Rocky Mountains/Foothills Population Estimate

As discussed under Objective 1 above, there are Alberta-specific population estimates for the Wilmore Wilderness Area and surrounding foothills, as well as the Castle/Waterton Parks area in southwestern Alberta (Fisher et al. 2013, Mowat et al. 2020). Mowat et al. (2020) and Barrueto et al. (2020) provide density estimates for the Banff, Yoho, and Kootenay national parks. Further, Mowat et al. (2020) also estimated density for the Central and South Rockies, which

included some sampling locations in Alberta. Mowat et al. (2020) and Barrueto et al. (2020) used SECR to analyze their data. In order to provide the most consistent comparison, ideally the Fisher et al. (2013) data would be re-analyzed using a SECR framework. These data could then be extrapolated beyond their study areas based on habitat associations to provide a rough estimate for the Rocky Mountain and Foothills natural regions.

Obtaining a population estimate for the province, while helpful, provides only a snapshot in time. Repeated surveys would be required to obtain a provincial trend estimate.

3.3.3 Harvest Data

Harvest data have the potential to provide a cost-effective option for long-term monitoring of wolverine populations. However, without a measure of trapper effort, the trends in harvest data, both in terms of the number of harvested individuals as well as the distribution of the harvest, are not necessarily reflective of trends in the wolverine population. The Alberta Conservation Association is currently working with the Alberta Trappers' Association to explore options to evaluate trapper effort. This information will help improve the quality of the harvest data. Additionally, by collecting age-at-harvest data, the utility of this data set would be further expanded. Techniques such as statistical population reconstruction and integrated population models can use harvest data to estimate the abundance of harvested populations (Skalski et al. 2011, Clawson et al. 2016), but they require an estimate of age at harvest as well as trapper effort. Currently, Alberta trappers are required to register harvested wolverines but no data on effort or age class are obtained. Over time, if enough effort and age class data can be collected this may allow for population trend to be documented at a much lower cost than intensive field efforts to estimate abundance.

3.3.4 Provincial Distribution

Although not necessarily a knowledge gap, using an occupancy framework to establish a baseline estimate of wolverine distribution across the province could provide a starting point against which to evaluate future changes in wolverine distribution (Lukacs et al. 2020), and could be indicative of changes to wolverine status (IUCN 2012). Recently, a large-scale study of wolverine occupancy was completed in the continental United States, and this work was the first monitoring program to be completed at the scale at which the wolverine population in the western United States operates (Lukacs et al. 2020). Lukacs et al. (2020) developed a repeatable framework for monitoring wolverines and used that framework to provide a robust estimate of current wolverine distribution. Occupancy modeling has been used to monitor multiple species in Alberta, including wolverines (Whittington et al. 2014, Steenwig et al. 2019). Monitoring changes in occupancy might be more cost-effective than monitoring changes in density and abundance because only presence (rather than individual identification) is required. Similarly, SECR models require redetections of individuals at different spatial detectors to estimate sigma, whereas occupancy models only require presence/absence data. Thus, the required sampling intensity might differ between objectives (i.e., estimating occupancy vs. density). As with any

monitoring effort, ideally an *a priori* power analysis would be completed to determine the level of sampling needed to estimate occupancy and maximize the use of research dollars. Finally, Lukacs et al. (2020) were able to incorporate citizen science into their occupancy mapping (though not the occupancy analysis itself), which provided an opportunity for other groups to engage with the research effort.

4.0 CONCLUSION

The wolverine is considered *Data Deficient* in Alberta. Alberta uses criteria developed by the International Union for Conservation of Nature (IUCN) when assessing species' status. IUCN status designations are determined using a variety of criteria including a declining population size, extent of (and changes to) geographic range (e.g., extent of occurrence, or area of occupancy), a determination that population size is small and/or restricted, or a quantitative analysis on the probability of extinction (IUCN 2012). Alberta's designation of *Data Deficient* is used when the available data are inadequate to determine the degree of threat faced by the species. Since the last status assessment in 2000, several wolverine studies have been completed in Alberta and more information is now available. While data on population trends are missing, abundance estimates for some areas of the province along with new information on harvest trends, areas of occupancy and occurrence, as well as wolverine habitat ecology and response to anthropogenic change will provide information that will be useful for an updated status assessment. Data gaps that continue to exist include a current abundance estimate for the northern portion of the Rocky Mountains and Foothills, a reliable abundance estimate for the Boreal Forest Natural Region, and information on population trend across the province.

5.0 LITERATURE CITED

- Alberta Biodiversity Monitoring Institute. 2018. Wolverine (*Gulo gulo*). Available online at https://www.abmi.ca/home/data-analytics/biobrowser-home/species-profile?tsn=180551 [Accessed 19 February 2010].
- Alberta Environment and Parks. 2016. Alberta grizzly bear (*Urus arctos*) recovery plan, 2017-2022. Alberta Environment and Parks, Alberta Species at Risk Recovery Plan No. 38. Edmonton, Alberta, Canada. *Draft*.
- Alberta Environment and Parks. 2017. Species assessed by the conservation committee. Alberta species at risk. Available online at https://open.alberta.ca/publications/species-assessed-by-the-conservation-committee-alberta-species-at-risk [Accessed 10 February 2020].
- Alberta Grizzly Bear Inventory Team. 2008. Grizzly bear population and density estimates for Alberta bear management unit 6 and British Columbia management units 4-1, 4-2, and 4-23 (2007). Report prepared for the Alberta Sustainable Resource Development, Fish and Wildlife Division, British Columbia Ministry of Forests and Range, British Columbia Ministry of Environment, and Parks Canada. Integrated Ecological Research, Nelson, Canada.
- Alberta Sustainable Resource Development. 2008. Alberta Grizzly Bear Recovery Plan 2008-2013. 2008. Alberta Species at Risk Recovery Plan No. 15, Edmonton, Alberta, Canada.
- 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.
- Banci, V., and A.S. Harestad. 1990. Home range and habitat use of wolverines *Gulo gulo* in Yukon, Canada. Holarctic Ecology 13:195–200.
- Barrueto, M., M. Sawaya, A. Clevenger. 2020. Low wolverine (*Gulo gulo*) density in a national park complex of the Canadian Rocky Mountains. Canadian Journal of Zoology. Available online at https://doi.org/10.1139/cjz-2019-0165.
- Bischof, R., C. Milleret, P. Dupont, J. Chipperfield, H. Brøseth, and J. Kindberg. 2019. RovQuant: Estimating density, abundance and population dynamics of bears, wolverines, and wolves in Scandinavia. MINA fagrapport 63.
- Borchers, D.L., and M.G. Efford. 2008. Spatially explicit maximum likelihood methods for capture-recapture studies. Biometrics 64:377–385.
- Boulanger, J., S.E. Nielsen, and G.B. Stenhouse. 2018. Using spatial mark-recapture for conservation monitoring of grizzly bear populations in Alberta. Scientific Reports 8: DOI:10.1038/s41598-018-23502-3.

- Boyce, M.S., C.J. Johnson, E.H. Merrill, S.E. Nielsen, E.J. Solberg, and B. van Moorter. 2016. Can habitat selection predict abundance? Journal of Animal Ecology 85:11–20.
- Boyce, M.S., and L.L. McDonald. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution 14:268–272.
- Boyce, M.S., and J.S. Waller. 2003. Grizzly bears for the Bitterroot: predicting potential abundance and distribution. Wildlife Society Bulletin 31:670–683.
- Brodie, J.F., and E. Post. 2010. Nonlinear responses of wolverine populations to declining winter snowpack. Population Ecology 52:279–287.
- Burnham, K.P., and D.R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, New York, USA.
- Clawson, M.V., J.R. Skalski, and J.L. Isabelle. 2016. Statistical population reconstruction: a tool to improve how states monitor wildlife trends. The Wildlife Professional March/April:34–37.
- Clevenger, A.P. 2013. Mitigating highways for a ghost: data collection challenges and implications for managing wolverines and transportation corridors. Northwest Science 87:257–264.
- Copeland, J.P. 1996. Biology of the wolverine in central Idaho. Master's Thesis. University of Idaho, Moscow, Idaho.
- Copeland, J.P., E. Cesar, J.M. Peek, C.E. Harris, C.D. Long, and D.L. Hunter. 1995. A live trap for wolverine and other forest carnivores. Wildlife Society Bulletin 23: 535–538.
- Copeland, J.P., and T.E. Kucera. 1997. Wolverine (*Gulo gulo*) in J. E. Harris and C. V. Ogan (Eds.) Mesocarnivores of Northern California: biology, management, and survey techniques, workshop manual. The Wildlife Society: Arcata, California.
- Copeland, J.P., K.S. McKelvey, K.B. Aubry, A. Landa, J. Persson, R.M. Inman, J. Krebs, E. Lofroth, H. Golden, J.R. Squires, A. Magoun, M.K. Schwartz, J. Wilmot, C.L. Copeland, R.E. Yates, I. Kojola, and R. May. 2010. The bioclimatic envelope of the wolverine (*Gulo gulo*): do climatic constraints limit its geographic distribution? Canadian Journal of Zoology 88: 233–246.
- COSEWIC. 2014. COSEWIC assessment and status report on the wolverine *Gulo gulo* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. Available online at https://www.sararegistry.gc.ca/virtual_sara/files/cosewic/sr_Wolverine_2014_e.pdf [Accessed 1 February 2020].

- Dawson, F.N., A.J. Magoun, J. Bowman, and J.C. Ray. 2010. Wolverine, *Gulo gulo*, home range size and denning habitat in lowland boreal forest in Ontario. Canadian Field Naturalist 124: 139–144.
- Efford, M.G. 2019. Package 'secr'. Available online at https://www.otago.ac.nz/density/pdfs/secr-manual.pdf [Accessed 20 December 2019].
- Efford, M.G. 2019b. Habitat masks in the package secr. Available online at https://www.otago.ac.nz/density/pdfs/secr-habitatmasks.pdf [Accessed 10 December 2019].
- Efford, M.G., and J. Boulanger. 2019. Fast evaluation of study designs for spatially explicit capture-recapture. Methods in Ecology and Evolution 10:1520–1535.
- Efford, M.G., D.K. Dawson, and C.S. Robbins. 2004. DENSITY: software for analyzing capture-recapture data from passive detector arrays. Animal Biodiversity and Conservation 27:217–228.
- Efford, M.G., D.L. Borchers, and A.E. Byron. 2009. Density estimation by spatially explicit capture-recapture: likelihood-based methods. Pages 255–269 *in* D. L. Thomson, E. G. Cooch, and M. J. Conroy, editors. Modeling demographic processes in marked populations. Springer Science and Business Media, New York, New York, USA.
- Efford, M.G., and R.M. Fewster. 2013. Estimating population size by spatially explicit capture-recapture. Oikos 122:918–928.
- Efford, M.G., and G. Mowat. 2014. Compensatory heterogeneity in spatially explicit capture-recapture data. Ecology 95:1341–1348.
- Fisher, J.T. 2003. Assessment of wolverine monitoring methodologies in Alberta: 2002/2003 year-end report. Alberta Research Council Inc., Vegreville, Alberta.
- Fisher, J.T. 2004. Alberta wolverine experimental monitoring project. 2003-2004 annual report. Alberta Research Council Inc., Vegreville, Alberta.
- Fisher, J.T., and S. Bradbury. 2014. A multi-method hierarchical modeling approach to quantifying bias in occupancy from non-invasive genetic tagging studies. Journal of Wildlife Management 78:1087–1095.
- Fisher, J.T., S. Bradburry, B. Anholt, L. Nolan, L. Roy, J.P. Volpe, and M. Wheatley. 2013. Wolverines (*Gulo gulo luscus*) on the Rocky Mountain slopes: natural heterogeneity and landscape alteration as predictors of distribution. Canadian Journal of Zoology 91: 706–716.

- Gerber, B.D., S.M. Karpanty, and M.J. Kelly. 2012. Evaluating the potential biases in carnivore capture-recapture studies associated with the use of lure and varying density estimation techniques using photographic-sampling data of the Malagasy civet. Population Ecology 54:43–54.
- Gerber, B.D., and R.R. Parmenter. 2015. Spatial capture-recapture model performance with known small-mammal densities. Ecological Applications 25:695–705.
- Golden, H.N., J.D. Henry, E.F. Becker, M.I. Goldstein, J.M. Morton, D. Frost Sr., and A.J. Poe. 2007. Estimating wolverine *Gulo gulo* population size using quadrat sampling of tracks in snow. Wildlife Biology 13:52–61.
- Hebblewhite, M., D.G. Miquelle, A.A. Murzin, V.V. Aramilev, and D.G. Pikunov. 2011. Predicting potential habitat and population size for reintroduction of the Far Eastern leopards in the Russian Far East. Biological Conservation 144:2403–2413.
- 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.
- Hornocker, M.G., and H.S. Hash. 1981. Ecology of the wolverine in northwestern Montana. Canadian Journal of Zoology 59:1286–1301.
- 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. Journal of Wildlife Management 76:778–792.
- Inman, R.M., B.L. Brock, K.H. Inman, S.S. Sartorius, B.C. Aber, B. Giddings, S.L. Cain, M.L. Orme, J.A. Fredrick, B.J. Oakleaf, K.L. Alt, E. Odell, and G. Chapron. 2013. Developing priorities for metapopulation conservation at the landscape scale: wolverines in the western United States. Biological Conservation 166:276–286.
- IUCN 2012. IUCN Red List categories and criteria: version 3.1. Second edition. Gland, Switzerland and Cambridge, UK.
- Jokinen, M.E., S.M. Webb, D.L. Manzer, and R.B. Anderson. 2019. Characteristics of wolverine (*Gulo gulo*) dens in the lowland boreal forest of north-central Alberta. The Canadian Field Naturalist 133: 1–15.
- Jůnek, T., P.J. Vymyslická, K. Hozdecká, and P. Hejcmanová. 2015. Application of spatial and closed capture-recapture models on known population of western Derby Eland (*Taurotragus derbianus derbianus*) in Senegal. PLoS ONE 10: e0136525 Available online at 10.1371/journal.pone.0136525.

- Kortello, A., D. Hausleitner, and G. Mowat. 2019. Mechanisms influencing the winter of wolverine *Gulo gulo luscus* in the southern Columbia Mountains, Canada. Wildlife Biology 1:1–13.
- Kyle, C.J., and C. Strobeck. 2001. Genetic structure of North American wolverine (*Gulo gulo*) populations. Molecular Ecology 10:337–347.
- Kyle, C.J., and C. Strobeck. 2002. Connectivity of peripheral and core populations of North American wolverines. Journal of Mammalogy 83:1141–1150.
- Lele, S.R., E.H. Merrill, J. Keim, and M.S. Boyce. 2013. Selection, use, choice, and occupancy: clarifying concepts in resource selection studies. Journal of Animal Ecology 82:1183–1191.
- Lofroth, E.C., and J. Krebs. 2007. The abundance and distribution of wolverines in British Columbia, Canada. Journal of Wildlife Management 71: 2159–2169.
- Loosen, A.E., A.T. Morehouse, and M.S. Boyce. 2019. Land tenure shapes black bear density and abundance on a multi-use landscape. Ecology and Evolution 9:73–89.
- Lukacs, P.M., D.E. Mack, R. Inman, J.A. Gude, J.S. Ivan, R.P. Lanka, J.C. Lewis, R.A. Long, R. Sallabanks, Z. Walker, S. Courville, S. Jackson, R. Kahn, M.K. Schwartz, S.C. Torbit, J.S. Waller, and K. Carroll. 2020. Wolverine occupancy, spatial distribution, and monitoring design. Journal of Wildlife Management 84:841–851.
- Magoun, A.J., C.D. Long, M.K. Schwartz, K.L. Pilgrim, R.E. Lowell, and P. Valkenburg. 2011. Integrating motion-detection cameras and hair snags for wolverine identification. Journal of Wildlife Management 75:731–739.
- Manly, B.F.J., L.L.L. McDonald, D.L. Thomas, T.L. Mcdonald, and W.P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer Academic, Dordrecht, The Netherlands.
- Mladenoff, D.J., and T.A. Sickley. 1998. Assessing potential gray wolf restoration in the northeastern United States: a spatial prediction of favorable habitat and potential population levels. Journal of Wildlife Management 62:1–10.
- Morehouse, A.T., and M.S. Boyce. 2016. Grizzly bears without borders: spatially explicit capture-recapture in southwestern Alberta. Journal of Wildlife Management 80:1152–1166.
- Mowat, G. 2001. Measuring wolverine distribution and abundance in Alberta. Alberta Sustainable Resource Development, Fish and Wildlife Division. Alberta Species at Risk Report No. 32, Edmonton, AB.

- Mowat, G., A.P. Clevenger, A.D. Kortello, D. Hausleitner, M. Barrueto, L. Smit, C. Lamb, B. Dorse, and P.K. Ott. 2020. The sustainability of wolverine trapping mortality in southern Canada. Journal of Wildlife Management 84: 213–226.
- Mowat, G., C. Kyle, and D. Paetkau. 2003. Testing methods for detective wolverine. Alberta Sustainable Resource Development, Fish and Wildlife Division. Alberta Species at Risk Report No. 71, Edmonton, AB.
- 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.
- Mullen, S.M. 2006. Furbearer harvests and landscape change in the Rocky Mountain foothills of Alberta. Master's Thesis. University of Alberta, Edmonton, Alberta.
- Nilsen, E.B., I. Herfindal, and J.D.C. Linnell. 2005. Can intra-specific variation in carnivore home-range size be explained using remote-sensing estimates of environmental productivity? Ecoscience 12:68–75.
- Noss, A.J., B. Gardner, L. Maffei, E. Cuéllar, R. Montaño, A. Romero-Muñoz, R. Sollman, and A.F. O'Connell. 2012. Animal Conservation 15:527–535.
- Obbard, M.E., E.J. Howe, and C.J. Kyle. 2010. Empirical comparison of density estimators for large carnivores. Journal of Applied Ecology 47:76–84.
- Petersen, S. 1997. Status of the Wolverine (*Gulo gulo*) in Alberta. Alberta Environmental Protection, Wildlife Management Division, Wildlife Status Report No. 2., Edmonton, Alberta.
- Poole, K.G., and G. Mowat. 2001. Alberta furbearer harvest data analysis. Alberta Sustainable Resource Development, Fish and Wildlife Division, Alberta Species at Risk Report No. 31., Edmonton, Alberta.
- Rich, L.N., M.J. Kelly, R. Sollmann, A.J. Noss, L. Maffei, R.L. Arispe, A. Paviolo, C.D. De Angelo, Y.E. Di Blanco, and M.S. Di Bitetti. 2014. Comparing capture-recapture, mark-resight, and spatial mark-resight models for estimating puma densities via camera traps. Journal of Mammalogy 95:382–391.
- 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.
- Royle, J.A., R.B. Chandler, R. Sollmann, and B. Gardner. 2014. Spatial capture-recapture. Academic Press, Waltham, Massachusetts, USA.

- Sawaya, M.A., A.P. Clevenger, and M.K. Schwartz. 2019. Demographic fragmentation of a protected wolverine population bisected by a major transportation corridor. Biological Conservation 236:616–625.
- Scrafford, M.A. 2017. Wolverine (*Gulo gulo luscus*) movement, habitat selection, and foraging in a landscape with resource extraction. Dissertation. University of Alberta, Edmonton, Canada.
- Scrafford, M.A., T. Avgar, B. Abercrombie, J. Tigner, and M.S. Boyce. 2017. Wolverine habitat selection in response to anthropogenic disturbance in the western Canadian boreal forest. Forest Ecology and Management 395:27–36.
- Scrafford, M.A., T. Avgar, R. Heeres, and M.S. Boyce. 2018. Roads elicit negative movement and habitat-selection responses by wolverines (*Gulo gulo luscus*). Behavioural Ecology 29:534–542.
- Scrafford, M.A., and M.S. Boyce. 2018. Temporal patterns of wolverine (*Gulo gulo luscus*) foraging in the boreal forest. Journal of Mammalogy 99:639–701.
- Scrafford, M.S., B.R. Norbert, and M.S. Boyce. 2020. Beaver (*Castor canadensis*) use of borrow pits in an industrial landscape in northwestern Alberta. Journal of Environmental Management 269: doi.org/10.1016/j.jenvman.2020.110800
- Skalksi, J.R., J.J. Millspaugh, M.V. Clawson, J.L. Belant, D.R. Etter, B.J. Fawley, and P.D. Friedrich. 2011. Abundance trends of American martens in Michigan based on statistical population reconstruction. Journal of Wildlife Management 75:1767–1773.
- Sirén, A.P.K., P.J. Pekins, P.L. Abdu, and M.J. Ducey. 2016. Identification and density estimate on American Martens (*Martes Americana*) using a novel camera -trap method. Diversity 9: doi:10.3390/d8010003.
- Steenweg, R., M. Hebblewhite, J. Whittington, and K. McKelvey. 2019. Species-specific differences in detection and occupancy probabilities help drive ability to detect trends in occupancy. Ecosphere 10:e02639.
- Stewart, F.E.C., N.A. Heim, A.P. Clevenger, J. Paczkowski, J.P. Volpe, and J.T. Fisher. 2016. Wolverine behaviour varies spatially with anthropogenic footprint: implications for conservation and inferences about declines.
- Slough, B.G. 2007. Status of the wolverine *Gulo gulo* in Canada. Wildlife Biology 13: 76–82.
- 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. doi:10.1371/journal.pone.0088025.

- Tobler, M.W., and G.V.N. Powell. 2013. Estimating jaguar densities with camera traps: problems with current designs and recommendations for future studies. Biological Conservation 159: 109–118.
- Webb, S., B. Abercrombie, R. Anderson, B. Bildson, M. Jokinen, N. Kimmy, and D. Manzer. 2017. Wolverine distribution and habitat associations on registered traplines in Alberta, winters 2011/12 2015/16. Data Report, produced by Alberta Conservation Association and Alberta Trappers' Association, Blairmore and Lethbridge, Alberta, Canada.
- Webb, S.M., R.B. Anderson, M.E. Jokinen, B. Abercrombie, B. Bildson, and D.L. Manzer. 2019. Incorporating local ecological knowledge to explore wolverine distribution in Alberta, Canada. Wildlife Society Bulletin 43:414–424.
- 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. Journal of Wildlife Management 80:1461–1470.
- Webb, S., D. Manzer, R. Anderson, and M. Yokinen. 2013. Wolverine harvest summary from registered traplines in Alberta, 1985–2011. Technical report, T-2013-001, produced by the Alberta Conservation Association, Sherwood Park, Alberta, Canada.
- Whittington, J., K. Heuer, B. Hunt, M. Hebblewhite, and P.M. Lukacs. 2015. Estimating occupancy using spatially and temporally replicated snow surveys. Animal Conservation 18:92–101.
- Whittington, J., and M.A. Sawaya. 2015. A comparison of grizzly bear demographic parameters estimated from non-spatial and spatial open population capture-recapture models. PLoS ONE 10:e0134446.
- Wilton, C.M., E.E. Puckett, J. Beringer, B. Gardner, L.S. Eggert, and J.L. Belant. 2014. Trap array configuration influences estimates and precision of black bear density and abundance. PLoS ONE 9: e111257. doi:10.1371/journal.pone.0111257.

6.0 APPENDICES

APPENDIX 1: The development of a spatially explicit density estimate for the western periphery of the Birch Mountains using Alberta Conservation Association (ACA) data collected in 2016–17. This analysis was conducted by A. Morehouse (Winisk Research and Consulting).

The wolverine research conducted by ACA in the Birch Mountains area of Alberta was designed to quantify wolverine occupancy rates and identify habitat variables associated with home range habitat selection within the Boreal Forest Natural Region. ACA's field methods were tailored to these research objectives and logistical constraints. The development of a spatially explicit density estimate with these data was not originally planned; however, to try to understand population size and trend for status assessment, I undertook the following exercise.

1.1 Study Area

The study took place in northcentral Alberta near Birch Mountains Wildland Park (Figure 1). The study area was a mix of central mixedwood, lower and upper boreal highlands and is representative of Alberta's boreal region. Summers are short and cool, while winters are cold with snow typically covering the ground from November through mid-April. The study area is remote and uninhabited with limited industrial footprint; access is difficult due to extensive wetlands (Jokinen et al. 2019). Although the study area was located on the western periphery of the area known as the "Birch Mountains", elevation only ranged from 500 to 800 m, making the topography unlike that of wolverine range in Alberta's Rocky Mountains.

In addition to wolverines, other carnivores present include fisher (*Pekania pennant*), marten (*Martes americana*), lynx (*Lynx canadensis*), wolf (*Canis lupus*),

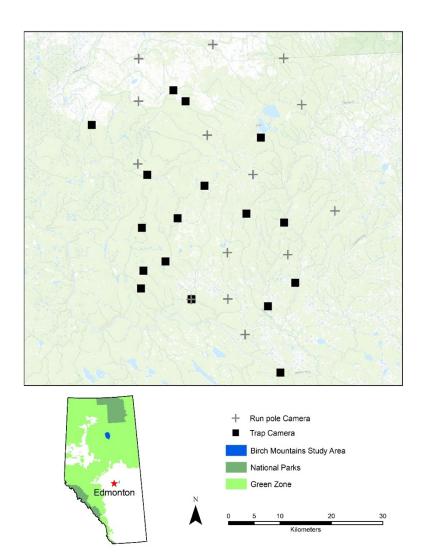


Figure 1: Map of the Birch Mountains study area in north-central Alberta. Squares represent trap camera locations while crosses represent run pole camera locations.

and black bear (*Ursus americanus*). Ungulates within the study area include white-tailed deer (*Odocoileus virginianus*), moose (*Alces americanus*), and caribou (*Rangifer tarandus*) (though caribou are uncommon).

Within the results section, the Birch Mountains Study Area refers to the minimum convex polygon (MCP) encompassing the traps and run poles, which represents an area of 1,976 km². Jokinen et al. (2019) reported a much larger study area size that encompassed more of the home range extent of animals collared at these traps.

1.2 Field Methods

For the purpose of this report, I briefly outline the field methods pertinent to the understanding of the analysis. This section is not meant to be an exhaustive description of the field methods used by the ACA in the collection of data.

The data used in this report come from motion-triggered remote cameras placed at either run poles or log cabin style traps. Wolverines have unique chest markings which can be used to identify individuals (Magoun et al. 2011). The remote trail cameras were situated to capture frontal views of wolverines to allow for individual identification. Data were collected from November 2016 through March 2017.

Run pole camera traps were used to document the presence of individual wolverines based on their unique markings (Magoun et al. 2011). In short, a beaver carcass was suspended between two trees and a horizontal run pole was secured to one of the trees such that the end was

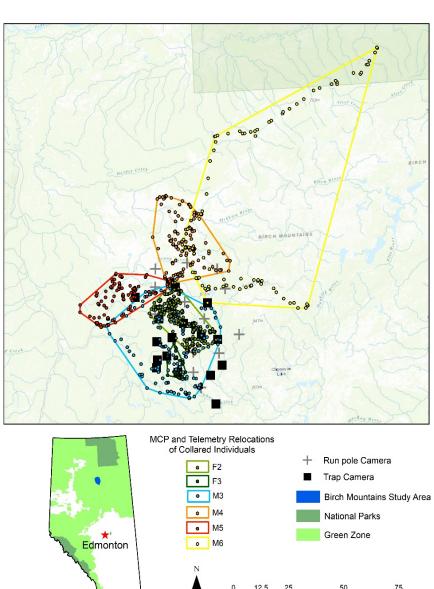


Figure 2: Telemetry data and minimum convex polygons of collared wolverines in the Birch Mountains study area. Data are from November 2016 through March 2017, though not every individual was collared for that entire duration.

directly below the bait (Webb et al. 2017). As a wolverine attempted to get the bait, it would expose its entire chest to a motion-triggered remote camera which was placed in a manner to capture this view (Magoun et al. 2011, Webb et al. 2017). There were 14 run poles in operation during the study period.

Log cabin style traps were used to live-trap wolverines for the purpose of fitting them with GPS radiocollars following methods established by Copeland et al. 1995. At each trap there were two motion-triggered cameras placed to capture individuals that visited the site. Camera trap placement allowed for the identification of individuals. Between November 2016 and March 2017, three female and four male wolverines were trapped and fitted with radiocollars (Figure 2). However, the collar on one of the females never worked; no data were collected, and the collar was removed from the animal. There were 17 trap locations in operation during the study period.

Camera trap images from both traps and run poles were reviewed to identify unique individuals. The end result was a file that contained detections of both known and unknown individuals specific to each site. Only individuals that could be identified were included in the analysis. These camera trap results formed the basis of the capture histories as described in the next section.

1.3 Analysis Methods

I analyzed wolverine encounter histories using spatially explicit capture-recapture (SECR) to estimate density and abundance (Efford et al. 2004, Borchers and Efford 2008, Efford and Fewster 2013). The use of SECR models is rapidly becoming the preferred method of density estimation in the literature. SECR models offer several advantages over traditional capture-recapture methods; they automatically account for capture heterogeneity, are more robust to the closure violation, directly incorporate detection locations, and allow for geographically specific abundance estimates (Efford et al. 2009, Obbard et al. 2010, Efford and Fewster 2013). SECR models fit an observation model and state model to spatial detection histories (Efford et al. 2009, Efford and Fewster 2013). The observation model describes the decaying relationship between detection probability and the distance between an individual's home range center and the trap location. The state model uses a spatial Poisson point process where the intensity of points is equivalent to the density of home range centers.

The observation model estimates two parameters, g0 and σ . The parameter g0 describes the detection probability at the animal's home range center (Efford et al. 2004, 2009). The parameter σ is a spatial scale parameter and describes the area over which an animal can be detected (Efford et al. 2004, 2009). The state model estimates a single parameter, density (D) (Efford et al. 2004, 2009). I used a half-normal detection function to fit each model. Because the number of individuals detected was small, I did not model the sexes separately; this was consistent with other wolverine literature (e.g., Lofroth and Krebs 2007, Royle et al. 2011, Fischer et al. 2013). Further, other research has shown that combined sex models often yield density estimates that are nearly identical to density estimates from sex-specific models (Mowat et al. 2020).

Similar to other camera trap studies (e.g., Royle et al. 2011, Junek et al. 2015, Sirén et al. 2016), I considered each 24-hour period a single occasion. Thus, in total from November 11, 2016 through March 30, 2017 there were 140 occasions. Not all cameras were in operation on any given occasion, and in those instances, sites were coded as "0" in the usage column of the capture history files. I removed repeat detections at the same camera trap during the same occasion.

I used a buffer around all trap locations to define the area of integration (i.e. the habitat mask) for the SECR models. Density estimates are robust to the size of the mask provided the area of integration is sufficiently large (Efford and Fewster 2013, Royle et al. 2014). The area of integration needs to be large enough such that animals outside of this area have a negligible probability of detection (Efford and Fewster 2013, Royle et al. 2014). There are several ways to determine an appropriate buffer size. One option is to use a buffer size that is 3 times the root pooled spatial variance (RPSV), which is a measure of the 2-dimensional dispersion of animal detection locations and a simple measure of animal home-range size (Efford 2019). Alternatively, the suggest.buffer function in the secr package in program R will suggest an appropriate buffer size (Efford 2019b). The buffers suggested by these two methods were similar, ~30 km. I compared the suggested buffers to buffers used in recently published papers that also used SECR models; both papers used a buffer size of 40 km (Royle et al. 2011, Mowat et al. 2020). To error on the side of caution, I went with the larger buffer of 40 km around all trap locations. I used a mask spacing of 2,500 m. Royle et al. 2011 used both a 2 km and 8 km mask spacing and found similar results, and consequently used the 8 km grid spacing because of the computational efficiencies. However, density estimates are more sensitive to mask spacing when detections are few (Boulanger et al. 2018). To be conservative, I used a mask spacing of 2,500 m. I also ran a post-hoc analysis on the top model using the mask.check function in secr to ensure that different buffer and spacing sizes did not substantially influence model results.

I included several detection covariates to help improve model fit. Because each camera trap site was baited, it is reasonable to expect that a wolverine would have repeat detections at a site where they were previously detected. Thus, I included a trap-specific behavioral response (bk) on the detection parameter. Other wolverine studies have also found a trap-specific behavioral response (Mulders et al. 2007, Royle et al. 2011, Mowat et al. 2020). To evaluate any potential difference between run pole and trap cameras, I included trap type as a covariate. I also included a time trend over occasions (T) because detection success for wolverines can vary throughout the winter season (Royle et al. 2011, Fisher et al. 2013, Mowat et al. 2020). The change in detection probability over occasions might better have been modeled as an occasion-specific factor (t in *secr*) but the small sample size and large number of occasions did not allow for fitting such models. The number of covariates that can be fit simultaneously is limited. For example, AICc is undefined when $(n-Npar-1) \le 0$ (i.e. when the number of parameters in the model exceeds the number of detected individuals minus one) (Burnham and Anderson 2002). Thus, the small sample size in this data set did not allow for the fitting of complex models.

I used Akaike's Information Criterion adjusted for small sample sizes (AICc) (Burnham and Anderson 2002) to identify the most parsimonious model (i.e., the model with the lowest AICc

score). I used program R (version 3.6.2, https://www.r-project.org/) and package *secr* (version 4.1.0, http://www.otago.ac.nz/density/SECRinR.html) for all analyses.

Using the top model, I derived an abundance estimate for the study area. Abundance estimates derived from SECR models represent the estimate of individuals that have home range centers within the study area. Thus, it is possible that additional wolverines used the Birch Mountains study area but did not have their home ranges centered within the study area and, therefore, are not counted in the estimates of density and abundance (Morehouse and Boyce 2016).

1.4 Results

There were 31 camera trap locations (14 run poles, 17 traps) operated during the study period for a total of 140 occasions. The number of camera sites in operation in any given occasion ranged from 5 through 31, with 28 sites in operation on average per occasion. Within the study area, there were 77 detections of 7 individuals, 3 females and 4 males (Figure 3). Most wolverines were detected for the first time in either November or December, occasions 1 through 51 (Table 1). The number of detections per occasion generally increased throughout the sampling period with the exception of few detections in February, occasions 83-110 (Figure 4). The number of individual wolverines detected in any given occasion ranged from 0 to 3.

The top model included a trap-specific behavioural effect on g0 (Table 2). The top model (D \sim 1 g0 \sim bk sigma \sim 1) estimated a wolverine density in the Birch Mountains study area of 0.58/1,000 km² (95% CI 0.27 – 1.24) (Table 3). From this density estimate, I derived an abundance estimate for the Birch Mountains study area of 1.14 wolverines (95% CI 0.53 – 2.47) (Table 3). Detection probability was higher for previously detected individuals (bk_I) (Table 3, Figure 5).

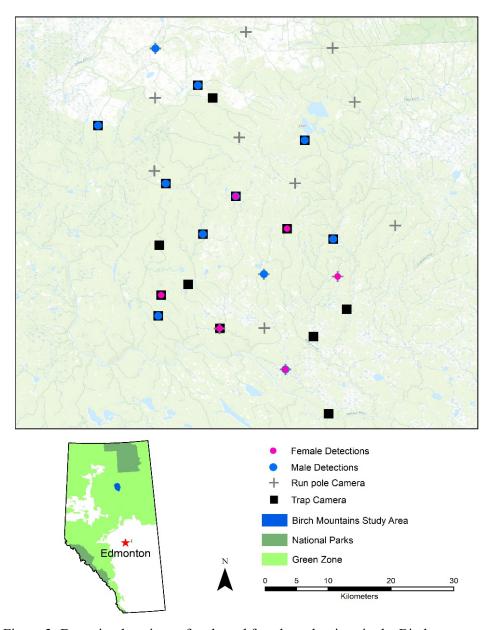


Figure 3: Detection locations of male and female wolverines in the Birch Mountains November 2016 through March 2017. There were 77 detections of 7 individuals (3 females, 4 males).

Table 1: The number of individuals detected for the first time per occasion. Occasions are grouped together by calendar month.

Occasion	Number of individuals detected for first time
1-20 (November)	2
21 - 51 (December)	2
52-82 (January)	0
83-110 (February)	2
111-140 (March	1

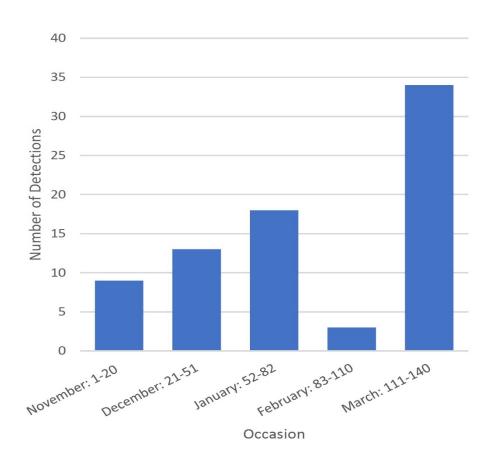


Figure 4: The number of detections grouped by monthly intervals. Occasion range is provided after each month.

Table 2: AICc model selection results for wolverines in the Birch Mountains study area using 2016–17 data. K = the number of parameters, $LL = \log \text{likelihood}$, AICc = Akaike Information Criterion for small samples sizes, $\Delta \text{AICc} = \text{the difference}$ in AICc values between the model and the most supported model for each stage, $w_i = \text{model}$ weight for each stage.

Model	K	LL	AICc	ΔAICc	wi
D~1 g0~bk sigma~1	4	-387.084	802.167	0	1
D~1 g0~bk + T sigma~1	5	-385.219	840.439	38.272	0
D~1 g0~bk + Type sigma~1	5	-386.088	842.176	40.009	0
D~1 g0~bk sigma~Type		-386.544	843.088	40.921	0
D~1 g0~b sigma~1		-440.664	909.328	107.161	0
D~1 g0~1 sigma~1		-454.809	923.618	121.451	0
D~1 g0~T sigma~1	4	-452.82	933.64	131.473	0
D~1 g0~Type sigma~1	4	-453.366	934.732	132.565	0
D~1 g0~Type sigma~Type	5	-453.357	976.714	174.547	0

Table 3: Real parameter estimates for the most parsimonious model for wolverines in the Birch Mountains Study Area. Data are from 2016–17. Detection probability (g0) is given for initial detection (bk0) and for previously detected individuals (bk1). Σ is reported in kilometers. Expected number of home-range centers (N) and associated confidence intervals for the Birch Mountains Study area are also reported. Abundance estimates are derived from the most parsimonious model.

Density (wolverines/1,000 km²)	SE	95% CI	g0 (SE)	σ(SE)	MCP Expected N	95% CI
0.58ª	0.23	0.27 – 1.24	bk ₀ : 0.004 (0.002) bk ₁ : 0.194 (0.068)	24.49 (3.47)	1.14	0.53 – 2.47

 $^{\circ}$ model = D \sim 1 g0 \sim bk sigma \sim 1

1.5 Post-Hoc Analyses

As noted in the methods section, I used the mask.check function in secr to ensure that different buffer and spacing sizes did not substantially influence model results for the most parsimonious model described in the results section above (D \sim 1 g0 \sim bk $\sigma\sim$ 1). The function examines the effect of buffer width and mask spacing by refitting an entire model at user-specified spacings and buffer widths (Efford 2019b). Assuming an appropriate buffer has been chosen, there should be only minor differences in the resulting density estimates because SECR is robust to buffer width as long as the area of integration is large enough such that animals outside this area have a negligible probability of detection (Efford and Fewster 2013, Royle et al. 2014). In this analysis, density estimates were robust to mask spacing (Table 4) but not to buffer width (Table 5).

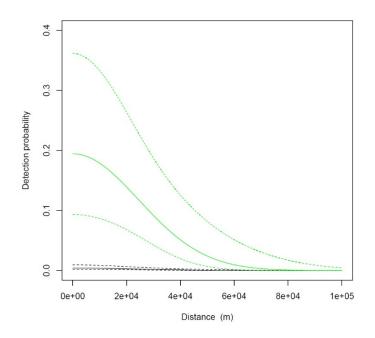


Figure 5: Detection probability (g0) versus the distance between the animal's home range center and camera trap location (i.e. σ , the spatial scale over which the individual can be detected) for wolverines in the Birch Mountain Study area. The plotted model is the most parsimonious model, D~1 g0~bk sigma~1. Detection probability is plotted for bk = 0 (black line) and bk = 1 (green line). Dashed lines are the 95% confidence intervals.

Table 4: Effect of mask spacing on density estimates for the most parsimonious model, $D\sim1$ g0 \sim bk $\sigma\sim1$. Buffer width was held constant at 40 km. Model log likelihood (LL) and standard error (SE) are also reported.

Spacing (m)	LL	Density (wolverines/1,000 km²)	SE
1500	-387.08	0.58	0.23
2500^{a}	-387.08	0.58	0.23
3500	-387.08	0.58	0.23

^a actual spacing used in models

Table 5: Effect of mask buffer width on density estimates for the most parsimonious model, D \sim 1 g0 \sim bk $\sigma\sim$ 1 as well as the null model, D \sim 1 g0 \sim 1 $\sigma\sim$. Mask spacing was held constant at 2500 m. Model log likelihood (LL) and standard error (SE) are also reported.

Model	Buffer Width (km)	LL	Density (wolverines/1,000 km²)	SE
m2, D~1 g0~bk σ~1	30	-386.63	0.80	0.32
	40^{a}	-387.08	0.58	0.23
	50	-387.58	0.44	0.18
m0, D~1 g0~1 σ~1	30	-454.81	1.40	0.56
	40^{a}	-454.81	1.40	0.56
	50	-454.81	1.40	0.56

^a actual buffer width used in models

The effect of buffer width on the density estimate was a surprising result given that the buffer of 40 km exceeded the suggested buffer size. Thus, I used *mask.check* to evaluate the effect of buffer size on the null model and found that density estimates were robust to buffer width in this case (Table 5).

To further evaluate buffer width, I used the function *esa.plot* which provides a visualization of changes in density as a function of buffer width. I used this function to compare the null model (m0, D~1 g0~1 σ ~1) to the most parsimonious model (m2, D~1 g0~bk σ ~1). For the null model, density estimates begin to stabilize at a buffer of approximately 25 km (Figure 6). Thus, the 40 km buffer I used is more than sufficient for this model. For the m2 model, however, density estimates do not begin to stabilize until a buffer width of approximately 80 km (Figure 6). I repeated the above steps on all models (i.e., those listed in Table 2), and for all models except those that included a trap-specific behavioral effect (bk), the 40 km buffer is sufficient.

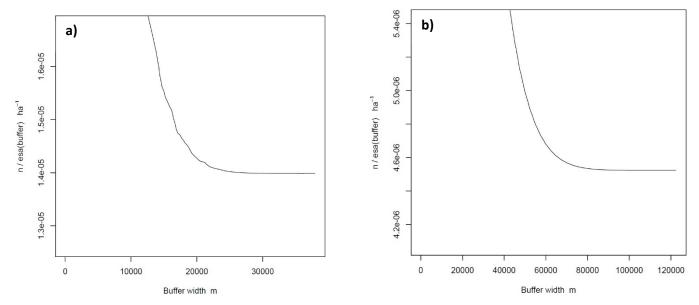


Figure 6: Effect of varying buffer width on estimated density (y-axis) for (a) the null model (D \sim 1 g0 \sim 1 o \sim 1) and (b) the most parsimonious model (D \sim 1 g0 \sim bk o \sim 1).

I used *mask.check* again to evaluate whether density estimates would stabilize at larger buffer sizes for model m2 (Table 6). Density estimates stabilized with a buffer of 80 km or higher, but standard errors of the estimates were high (Table 6). I reran model m2, D \sim 1 g0 \sim bk $\sigma\sim$ 1 with a mask that included a 90 km buffer around trap locations. With the larger buffer, the model estimated a wolverine density in the Birch Mountains study area of 0.71/1,000 km² (95% CI 0.16 – 3.07) (Table 7). The standard error of the estimate and subsequent 95% confidence intervals were larger with the 90 km buffer as compared to the 40 km buffer (Table 7 vs Table 3). Detection probability was higher for previously detected individuals (bk_I), though precision was poor (Table 7, Figure 7). Indeed, confidence intervals go to infinity suggesting this model is not identifiable with the data (Figure 7).

Table 6: Effect of mask buffer width on density estimates for the most parsimonious model, D \sim 1 g0 \sim bk $\sigma\sim$ 1. Mask spacing was held constant at 2500 m. Model log likelihood (LL) and standard error (SE) are also reported.

Buffer Width (km)	LL	Density (wolverines/1,000 km²)	SE
70	-388.18	0.70	0.63
80	-388.18	0.71	0.62
90	-388.18	0.71	0.61
100	-388.18	0.71	0.61
110	-388.18	0.71	0.61

Table 7: Real parameter estimates for the most parsimonious model for wolverines in the Birch Mountains Study Area using a 90 km buffer around camera trap locations. Data are from 2016-17. Detection probability (g0) is given for initial detection (bk0) and for previously detected individuals (bk1). Σ is reported in kilometers.

Density (wolverines/1,000 km²)	SE	95% CI	g0 (SE)	σ (SE)
0.71ª	0.61	0.16 – 3.07	bk ₀ : 0.004 (0.002) bk ₁ : 0.150 (0.084)	19.23 (7.23)

 a model = D \sim 1 g0 \sim bk sigma \sim 1

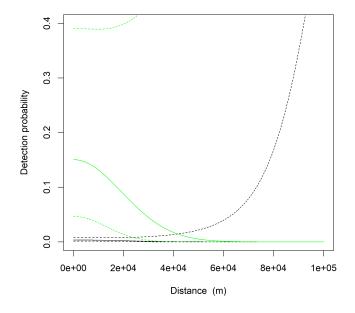


Figure 7: Detection probability (g0) versus the distance between the animal's home range center and camera trap location (i.e. σ , the spatial scale over which the individual can be detected) for wolverines in the Birch Mountains Study area. The plotted model is the most parsimonious model, D~1 g0~bk sigma~1 using a buffer of 90 km around camera trap locations. Detection probability is plotted for bk = 0 (black line) and bk = 1 (green line). Dashed lines are the 95% confidence intervals. The upper confidence interval for previously detected individuals (bk = 1) rapidly goes to infinity and is not fully included in this plot.

Because the trap-specific behavioral effect (bk) appears to be causing erratic model behavior, I re-evaluated model performance using AICc and excluding all models that included the bk covariate. In this case, the most parsimonious model was the null model, D~1 g0~1 σ ~1. Under this model, density was estimated to be 1.4/1,000 km² (95% CI 0.66 – 3.00) in the Birch Mountains Study Area (Table 8). From this density estimate, I derived an abundance estimate for the Birch Mountains study area of 2.78 wolverines (95% CI 1.31 – 5.88) (Table 8). Detection probability was higher under the null model as compared to the bk model and confidence intervals were tighter (Figure 8).

Table 8: Real parameter estimates for the most parsimonious model without the bk covariate (i.e. the null model) for wolverines in the Birch Mountains Study Area. Data are from 2016-17. σ is reported in kilometers. Expected number of home-range centers (N) and associated confidence intervals for the Birch Mountains Study area are also reported. Abundance estimates are derived from the density model.

Density (wolverines/1,000 km²)	SE	95% CI	g0 (SE)	σ(SE)	MCP Expected N	95% CI
1.40 ^a	0.56	0.66 - 3.00	0.23 (0.039)	7.59 (0.58)	2.78	1.31 – 5.88

amodel = D \sim 1 g0 \sim 1 sigma \sim 1

Because the sigma parameter is informed by redetections and there was a large difference in sigma estimates between the null model and the bk model, I examined the number of detections per individual and the number of those detections that occurred at the initial capture site (Table 9). On average, individuals were detected at 3 traps. For several individuals (e.g., M4, M6, F2) the majority of redetections occurred at the initial capture sites (Table 9).

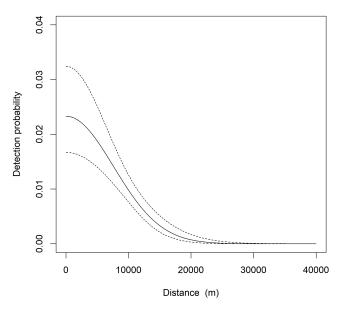


Figure 8: Detection probability (g0) versus the distance between the animal's home range center and camera trap location (i.e., σ , the spatial scale over which the individual can be detected) for wolverines in the Birch Mountain Study area. The plotted model is the most parsimonious model without the bk covariate (i.e., the null model), D \sim 1 g0 \sim 1 sigma \sim 1. Dashed lines are the 95% confidence intervals.

Table 9: Number of detections per individual and the number of locations at which that individual was detected. Also listed are the number of detections occurring at the initial capture site.

Individual	Number of Camera Traps with Detections	Number of Detections	Number of Detections at Initial Capture Site
F2	2	5	4
F3	4	19	10
F4	3	13	3
M3	7	20	1
M4	1	12	12
M5	3	5	1
M6	1	3	3

1.6 Discussion

The results indicate there is variability in model behaviour. In particular, the addition of the trap-specific behavioural response covariate (bk) is problematic. Because camera sites were baited, it is reasonable to expect a trap-specific behavioural response. Indeed, this is often reported in the literature (e.g., Mulders et al. 2007, Royle et al. 2011, Mowat et al. 2020), and AICc identified the bk model as the most parsimonious model. However, post-hoc analyses revealed that the parameter estimates from this model are likely not reliable. Below I detail some potential explanations for the observed results.

Previous studies have found that the trapping array can influence parameter estimates (Wilton et al. 2014). Sun et al. (2014) suggest that trap spacing should ideally be less than two times the sigma estimate. In this data set, trap spacing was 6.4 km which follows the suggested guidelines. In addition to trap spacing, the spatial extent of the trap array can also influence parameter estimates. Tobler and Powell (2013) suggest that trap arrays should be at least the size of an individual's home range to produce unbiased results. Further, individual variation in sigma due to biological differences (e.g., males vs. females, dispersers vs. non-dispersers) can result in biased parameter estimates (Tobler and Powel 2013). Wolverine home range size can vary widely based on habitat and food availability (Copeland and Kucera 1997, Nilsen et al. 2005). In the boreal forest, wolverine home ranges tend to be large. For example, in Ontario's boreal forest, the 95% minimum convex polygon (MCP) for collared wolverines was 2,563 km² for males and 428 km² for females (Dawson et al. 2010). Similarly, in northern Alberta's boreal forest average home range size (100% MCP) varied between males and females as well as between dispersers vs nondispersers and ranged from 306 km² for a non-dispersing female to 4,999 km² for a dispersing male (Scrafford 2017). Given this information on home range size, heterogeneity within the species and the effect of trap array size on parameter estimates, it is likely that the spatial extent of the trap array used in the Birch Mountains Study Area (~2,000 km²) was too small relative to the scale of movement by individuals in the area, thereby making sigma difficult to accurately and precisely estimate – ultimately resulting in biased parameter estimates (Tobler and Powel 2013).

Indeed, even using a 90 km buffer the sigma estimate from the bk model was large at 19.23 km (Table 7). This is 1.7 to 4.6 times higher than other sigma estimates reported in the literature (Table 3 in Mowat et al. 2020). If the sigma estimate is converted to a 95% home range estimate using the equation sigma = r/2.45 (Royle 2014, Sun et al. 2014), the result is an estimated home range size of approximately 6,973 km² – substantially larger than mean wolverine home range sizes reported in the literature and 3.5 times larger than the Birch Mountains trapping array.

In addition to a small trapping array, the bk covariate appears to also influence model behaviour. Trap-specific behavioural effect (bk) models estimate two different detection probabilities: one for animals that have never been caught (bk = 0) and one for previously caught individuals (bk = 1). Given that there is a food reward associated with the camera sites, we would anticipate a higher detection probability for previously caught individuals. As expected, this is the case in these data (Table 3, Table 7). However, the detection probability for individuals that have never been caught

(bk = 0) is an order of magnitude lower than it was under the null model (Table 3 and 7 vs Table 8). If g0 is lowered enough, then sigma is not identifiable because capture events at the detection function tail become increasingly rare. Creating further problems is the fact that the data set informing the sigma parameter is quite thin (Table 9). Although 77 detections of 7 individuals initially seems sufficient (Efford et al. 2004), upon closer examination several of the redetections occurred at the initial capture site (Table 9). For some individuals, all redetections occurred at the initial capture site (Table 9). In these cases, there are no data to inform the estimate of sigma. If buffer size is increased, point estimates will stabilize as seen in Table 6. However, confidence intervals increase and behave erratically (Table 6, 7, Figure 7).

The bottom line is that all of this information suggests that the addition of the bk covariate alerts us to important wolverine behaviour, but the model is not identifiable with the data. This is most likely due to the order of magnitude drop in initial detection probability coupled with a trapping array that is too small relative to the scale of movement of wolverines in this area.

Under the null model, the estimated density is low compared to density estimates from boreal forests in British Columbia (Lofroth and Krebs 2007), though relative density is estimated to generally be lower in Alberta compared to British Columbia (Slough 2007; also note the discussion under Objective 1 in the body of this report re: comparing CMR and more recent SECR estimates). The density estimate of 1.4/1,000 km² is, however, similar to other density estimates from montane habitats in westcentral and southwestern Alberta (Fisher et al. 2003, Mowat et al. 2020). In fact, it is nearly identical to Mowat et al.'s (2020) wolverine density estimate of 1.35 wolverines/1,000 km² in southwestern Alberta as well as estimates from boreal forests in Ontario (1.4/1,000 km²) and Scandinavia (1.74/1,000 km²) (COSEWIC 2014, Bischof et al. 2019). However, the Birch Mountains density estimates have poor precision. Precision of SECR density estimates can be measured by the relative standard error (RSE(\widehat{D}), sometimes also denoted $(CV(\widehat{D}))$, which is equal to the standard error of the estimate divided by the estimate (Efford and Boulagner 2019). An often cited target is a RSE(\widehat{D}) of <20%, though Efford and Boulanger (2019) encourage aiming for greater precision. The RSE(\widehat{D}) of the null model for the Birch Mountains study area was 0.40, indicating poor precision. Precision of the Mowat et al. (2020) estimates were much higher (RSE(\widehat{D}) values range from 0.10 to 0.14). Thus, the null model density estimate for the Birch Mountains study area should be interpreted with caution given that precision is poor and the data suggest there is indeed a strong trap-specific behavioural effect (i.e., "trap happy" individuals).

APPENDIX 2: Summary of Alberta wolverine literature and relevant density estimates.

Table 1: Summary of Alberta wolverine literature published since the last status assessment (Peterson 1997). Included are publication name, primary research theme, and main research findings. Full citation information can be found in the Literature Cited section of this document.

Publication	Theme	Main Findings
Alberta Biodiversity Monitoring Institute 2018	habitat ecology	 Wolverine occurs in boreal forest, foothills, and rocky mountain natural regions Detected too few times to create complex habitat association models
Barrueto et al. 2020	population assessment	 Non-invasive genetic sampling in Banff, Yoho, and Kootenay National Parks in 2011 and 2013 Used spatial capture-recapture models to estimate wolverine density of 3.3 and 3.0 wolverines/1,000 km² in 2011 and 2013 respectively
Brodie and Post 2010 trapper harvest • St. • W. • Ir		 Snowpack has strong nonlinear effects on wolverine population dynamics Wolverine harvest strongly correlated with decline in snowpack In Alberta significant decline in mean spring snowpack depth from 1968 to 2004 Reported number of wolverines harvested annually in Alberta has also declined from 1970 to 2004
Clevenger 2013	habitat ecology, genetics	 Monitored highway crossing structures in Banff 1996 to 2012 Wolverines detected using crossing structures 10 times, 9 at underpass and 1 at overpass Few conclusions can be made because data are so sparse
Fisher 2003 population assessment		 Year-end report for first year of wolverine study in boreal and montane Alberta Recommend each sampling session should be at least 30 days and should run from October through March Snow tracking was the most effective method for detecting wolverine but was also the most susceptible to environmental variation. They do not recommend snow tracking as a stand-alone monitoring protocol. Data were too sparse to provide statistical comparisons between wolverine abundance in the Grand Cache and Chinchaga areas, but there were many more tracks observed in transects surveyed in Grand Cache than in Chinchaga
Fisher 2004	population assessment	 Year-end report for wolverine monitoring in the foothills of Alberta Monitored wolverines using non-invasive genetic sampling and remote trail cameras Detection rates for wolverines were very low Data are preliminary, but wolverine density in foothills might be as low as 1 wolverine per 300 km²

Publication	Theme	Main Findings
Fisher and Bradbury 2014	population assessment	 Detection error from various sources can bias non-invasive genetic tagging (NGT) occupancy estimates Recommend that NGT studies quantify and correct for detection error using independent survey methods Used cameras and hair snags in Wilmore Wilderness study area Cameras were more likely to detect wolverines than hair traps Detection error is not a problem if detection probabilities are modeled
Fisher et al. 2013	population assessment	 Study of wolverine abundance in Wilmore Wilderness and foothills area Wolverines more abundant in areas protected from anthropogenic development and less likely at sites with oil and gas exploration, forest harvest, or burned areas Estimated density of 6.8 wolverines/1,000 km² in Wilmore Wilderness study area and 3 wolverines/1,000 km² in 2004-5 and 1.8 wolverines/1,000 km² in 2005-6 in foothills study area
Heim et al. 2017	habitat ecology	 Persistent spring snow cover and anthropogenic landscape change are significant predictors of wolverine distribution Wolverine population declines and range shifts likely result from climate change and landscape changer operating together Study took place in Banff, Yohoo, and Kootenay National Parks and Kananaskis Country
Jokinen et al. 2019	habitat ecology	 Examined denning structures of wolverines in lowland boreal forest Females used locally available denning structures despite lack of deep snow, persistent spring snow cover or large boulders as documented in previous literature Provides evidence that wolverines are adapted to exploiting low productivity environments and are not always dependent on snow covers as previously documented
Kyle and Strobeck 2001	genetics	 Genotyped 461 individuals to look at genetic structure of wolverines from northwest Alaska to eastern Manitoba, but no samples from Alberta or Saskatchewan Wolverines from southern regions were anthropogenic factors are strongest had more genetic structuring than more northern populations Populations that are exposed to fewer anthropogenic factors might have more gene flow among them Populations in areas of more disturbance seem to be greatly dependent on large areas of undisturbed habitat and corridors

Publication	Theme	Main Findings
Kyle and Strobeck 2002	genetics	 Builds on data set from Kyle and Strobeck 2001, includes samples from Grand Cache area in Alberta and one area in Saskatchewan High levels of gene flow among all northern wolverine populations studied Observed increasing genetic structure at periphery of southern and eastern distribution, and these may have been partially fragmented from what was at one time a panmictic unit
Mowat 2001	population assessment	 Provides a review of methods available for the inventory of wolverine populations Concludes that non-invasive hair sampling (which was a new technique at the time) is likely the best method to estimate density and abundance
Mowat et al. 2003	population assessment	 Tested the box trap, wire hair corral, and rub pad methods for wolverine population inventory described in Mowat et al. 2003 in west central and central Alberta Box traps and wire hair corrals collected hair samples, but rub pads do not appear to work for detected wolverines Wolverine detection rates were very low and no population estimates were produced
Mowat et al. 2020	population assessment	 Large scale population inventory of wolverines in southeastern British Columbia and southwestern Alberta Estimated density using non-invasive genetic sampling and spatially explicit capture-recapture (SECR) data Across the study area wolverine density averaged 2 wolverines/1,000 km² and was positively related to snow cover and negatively related to road density Estimates pertinent to Alberta include: ✓ Waterton/ West Castle 1.35 wolverines/1,000 km² using 2014 data ✓ Banff, Yoho and Kootenay National Parks 2.83 wolverines/1,000 km² using 2013 data ✓ Central Rockies 1.32 wolverines/1,000 km² using 2015 data ✓ South Rockies 1.33 wolverines/1,000 km² using 2016 data
Sawaya et al. 2019	genetics	 Used population and individual-based genetic analyses to examine genetic structure across the Trans-Canada Highway in Banff, Kootenay, and Yohoo National Parks and surrounding provincial lands Collected 2,586 genetic samples from 2010-13 and identified 49 individuals Detected ample male movement across the Trans-Canada Highway and a lack of genetic differentiation, but female wolverines were highly structured by the highway

Publication	Theme	Main Findings
Scrafford and Boyce 2018	foraging ecology	 Used GPS radiocollars to investigate temporal patterns of wolverine foraging on large prey (ungulate scavenging or beaver predation) in the boreal forest near Rainbow Lake Wolverines encountered large prey more in the spring and spent less time at large prey events in the summer than in the winter The time spent at prey events increased when other wolverines were in the area
Scrafford et al. 2017	habitat ecology	 Used an RSF to analyze wolverine habitat selection patterns during summer and winter in the boreal forest near Rainbow Lake, focussing on logging areas, cutblocks, seismic lines, roads and borrow pits Wolverines were attracted to logging areas. The authors suggest this might be because logging areas provide foraging opportunities and movement routes for wolverines Wolverines avoided low-traffic winter roads in summer and winter, and the authors attribute this to the risk of predation from wolves that used the roads for movement Wolverines were attracted to all season road sections with borrow bits Wolverines were attracted to seismic lines, but note that the age of the feature is important Industrial development can increase the abundance of large prey and predators, which might increase wolverine mortality One wolverine den was found in a slash pile and one den was found in a log deck
Scrafford et al. 2018	habitat ecology	 Used integrated step selection analysis to evaluate wolverine use of industrial roads in boreal forest (Rainbow Lk) Top models indicate that wolverines avoided and increased speed near roads Wolverine movement but not avoidance increased with traffic volume Show that roads, regardless of traffic volume, reduce quality of wolverine habitats and higher-traffic roads might be deleterious
Scrafford et al. 2020	habitat ecology	 Primary objective was to evaluate beaver use of borrow pits in the Rainbow Lake area of Alberta Also noted that wolverines used borrow pits as hunting grounds for beavers Documented a wolverine den within a beaver lodge at a borrow pit

Publication	Theme	Main Findings
Scrafford 2017	habitat ecology	 PhD dissertation, all chapters but one have been published. Notes in this section pertain only to Chapter 4 as other chapters are covered by published papers Examined wolverine dispersal movements Space use differed when a wolverine was in its home range versus dispersing Male wolverines stopped to rest and forage more during dispersal and selected for landscape features that are important to movement efficiency Average home range size of resident wolverines (i.e. non-dispersal) was 306 km² for females and 951 km² for males Average home range size for dispersing wolverines was 1,153 km² for females and 4,999 km² for males
Steenwig et al. 2019	occupancy monitoring	 Used remote cameras placed across 5 national parks in the Canadian Rockies (Jasper, Banff, Yoho, Kootenay, and Waterton) to test for difference in ability of large-scale monitoring program to detect changes in occupancy for 13 different mammal species – including wolverine No bait or lure was used. Cameras were placed on human or wildlife trails, often near trail junctions and/or bear rub trees Wolverines had low detection probability and because of this there was low statistical power to detect trends in wolverine occupancy Power to detect changes in wolverine occupancy could be improved if detection probability was increased by using lure/bait or complimentary survey techniques
Stewart et al. 2016	behaviour	 Used camera images from previous studies to quantify behaviour Considered 4 behaviours: probability that detected wolverine would climb bait tree, time in minutes of wolverine to show up at site, time in minutes for wolverine to climb bait tree given that it climbed, total time spent at site Wolverines behaved differently in heavily modified landscapes Hypothesize that behavioural constraints might indicate an increase in perceived risk in human-modified landscapes
Webb et al. 2013	trapper harvest	 Evaluated long-term wolverine harvest trends The number of registered traplines harvesting a wolverine in a year and the average number of harvested wolverines has increased since the early 1990s Despite lack of consisted spring snow cover, wolverine harvest on some traplines in boreal forest was moderately high Observed high spatial and temporal overlap between lynx and wolverine harvest

Publication	Theme	Main Findings
Webb et al. 2016	trapper harvest, habitat ecology	 Evaluated relationship between wolverines and snow cover using camera traps and long-term fur harvest data Wolverine harvest was highest in northwest boreal forest Mean wolverine harvest density increased by 75% from the 1990s to 2000s in the northwest boreal forest Female wolverines in the Rocky Mountains were located in townships with high amounts of spring snow cover, but females in the boreal forest were located in townships with no spring snow cover. The authors suggest that data from the Rocky Mountains and boreal forest be considered separately when drawing conclusions Wolverines may be more flexible in distribution than previously thought
Webb et al. 2017	trapper harvest, habitat ecology, genetics	 Evaluated broad scale distribution and habitat associations of wolverines using long-term fur harvests, trappers questionnaires, and field data Wolverine occurrence was positively associated with undeveloped forest, deeper winter snow depths, and cooler theoretical temperature index but negatively associated with density of roads and oil and gas wells In the boreal forest, the best habitat was predicted to be north of the 56th parallel where road densities are lower, forests are more conifer dominated, and climate is cooler Identified 56 different wolverines 2013-16, and genetic data revealed 5 wolverine haplotypes, all previously observed in other studies from western United States and Canada
Webb et al. 2019	trapper harvest	 Collaborated with the Alberta Trappers Association to distribute a survey about wolverine sign, harvest history, and opinions about population trend Trapper observations of wolverines were associated with cooler climates and less anthropogenic disturbance The authors hypothesize that wolverine's in the boreal forest are not limited by late spring snow distribution and that anthropogenic disturbance plays a bigger role than climate in the distribution of wolverines in Alberta
Whittington et al. 2015	occupancy monitoring	 Compared four different occupancy models within Banff National Park Developed occupancy models that combined spatially and temporally replicated data and applied them to snow tracking surveys of six species, including wolverine Despite low detection probability, found that snow tracking could be used to monitor trends of wolverine occupancy
Wright and Ernst 2004	habitat ecology	 Examined caches and rest sites in the boreal upland forests of northwestern Alberta and northeastern British Columbia Provide a detailed description of 5 different cache sites. Sites were in areas with relatively good visibility of surrounding area. Well-used cache sites were accessed by wolverine-made trails Resting sites were located in relatively open areas with good visibility

Table 2: Summary of the available literature on wolverine density in habitats found within Alberta. Full citation information can be found in the Literature Cited section of this document.

Density (wolverines/1,000 km²)	Precision (95% CI)	Location	Field Methods	Analysis Methods	Source
15.4		Northwestern Montana	Live capture, radiotelemetry & snow tracking	Not Specified	Hornocker and Hash 1981
4.0 – 11.1		Central Idaho	Live capture, radiotelemetry & snow tracking	Based on assumption all resident wolverines were contacted	Copeland 1996
5.8		Columbia Mountains, British Columbia	Live capture, marking & remote cameras	Jolly-Seber capture-mark- recapture Bowden sight-resight	Lofroth and Krebs 2007
6.2	4.2 – 9.5	Interior mountains in British Columbia		Predictive model based on habitat quality	Lofroth and Krebs 2007
3.5	2.8 - 9.6	Greater Yellowstone Ecosystem	Live captures, snow tracking & genetic sampling	Program MARK, Huggins closed capture models	Inman et al. 2012
6.8		Wilmore Wilderness Area, Alberta	non-invasive genetic sampling	mark-recapture, Rcapture package in program R	Fisher et al. 2013
3.0 (2004-5) 1.8 (2005-6)		Foothills, west central Alberta	non-invasive genetic sampling	mark-recapture, Rcapture package in program R	Fisher et al. 2013
3.0	2.5 – 3.0 (80% CI)	Turnagain Arm and Kenai Mountains, south central Alaska	Aerial track counts	sample-unit probability estimator (SUPE)	Golden et al. 2007

Appendix 2 Table 2 cont.:

Density (wolverines/1,000 km²)	Precision (95% CI)	Location	Field Methods	Analysis Methods	Source
2	1.7 - 2.5	Southeastern British Columbia and Southwestern Alberta	non-invasive genetic sampling	spatially explicit capture- recapture	Mowat et al. 2012
1.3	1.0 - 1.8	Waterton/West-Castle, southwestern Alberta	non-invasive genetic sampling	spatially explicit capture- recapture	Mowat et al. 2020
1.4	1.0 – 1.7	Central Rockies, British Columbia and Southwestern Alberta	non-invasive genetic sampling	spatially explicit capture- recapture	Mowat et al. 2020
3.3 (2011) 3.0 (2013)		Banff, Yoho & Kootenay National Parks, Alberta and British Columbia	non-invasive genetic sampling	spatially explicit capture- recapture	Barrueto et al. 2020
			Boreal		
4.8		Northeastern British Columbia	snow tracking and harvests		Quick 1953
5.6		Kluane Game Sanctuary, Yukon	live capture, radio telemetry, and aerial surveys	Based on known residents only	Banci and Harestad 1990
6.5		Omineca Mountains, British Columbia	Live capture, marking & remote cameras	Jolly-Seber capture-mark- recapture Bowden sight-resight	Lofroth and Krebs 2007
4.1	2.8 - 6.5	Boreal forest in British Columbia		Predictive model based on habitat quality	Lofroth and Krebs 2007
1.4		Boreal forest Ontario	non-invasive genetic sampling	capture-mark-recapture	COSEWIC 2014
1.74	1.66 – 1.83	Norway and Sweden	non-invasive genetic sampling, recoveries of dead animals	open-population spatial capture-recapture	Bischof et al. 2019

