




Research Article

The Sustainability of Wolverine Trapping Mortality in Southern Canada

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ABSTRACT Range declines, habitat connectivity, and trapping have created conservation concern for wolverines throughout their range in North America. Previous researchers used population models and observed estimates of survival and reproduction to infer that current trapping rates limit population growth, except perhaps in the far north where trapping rates are lower. Assessing the sustainability of trapping requires demographic and abundance data that are expensive to acquire and are therefore usually only achievable for small populations, which makes generalization risky. We surveyed wolverines over a large area of southern British Columbia and Alberta, Canada, used spatial capture-recapture models to estimate density, and calculated trapping kill rates using provincial fur harvest data. Wolverine density averaged 2 wolverines/1,000 km² and was positively related to spring snow cover and negatively related to road density. Observed annual trapping mortality was >8.4%/year. This level of mortality is unlikely to be sustainable except in rare cases where movement rates are high among sub-populations and sizable untrapped refuges exist. Our results suggest wolverine trapping is not sustainable because our study area was fragmented by human and natural barriers and few large refuges existed. We recommend future wolverine trapping mortality be reduced by ≥50% throughout southern British Columbia and Alberta to promote population recovery. © 2019 The Authors. The *Journal of Wildlife Management* published by Wiley Periodicals, Inc. on behalf of The Wildlife Society.

KEY WORDS DNA, genetic sampling, genetic tagging, *Gulo gulo*, harvest, spatial capture-recapture, wildlife management.

Range declines, habitat connectivity, and trapping have created conservation concern for wolverines (*Gulo gulo*) throughout their range in North America (Ruggiero et al. 2007, Canadian Wildlife Service 2014). Wolverine populations were extirpated in much of their southern and eastern range post-European contact, and many populations along the current southern range are still partly or entirely isolated from the continuous population in northwest North America (Aubry et al. 2007, Canadian Wildlife Service 2014, Idaho Department of Fish and Game 2014). One conservation risk to wolverine populations in some parts of their range is

the demographic effect of fur trapping (Banci 1994, Krebs et al. 2004, Lofroth and Ott 2007). Trapping is only currently allowed in western and northern Canada and Alaska, USA. Portions of southwest British Columbia, Canada, and most of the lower 48 states have been closed to wolverine trapping for several decades.

Wolverines are described as facultative scavengers and the amount of food they scavenge is related to prey abundance, the proximity of the prey to carrying capacity, and the presence of other large carnivores that kill large prey that wolverines could not kill themselves (van Dijk et al. 2008, Mattisson et al. 2016). In Scandinavia, when reindeer (*Rangifer tarandus*) were abundant, more reindeer calves were killed by wolverines in spring (Mattisson et al. 2016). Wolverine reproduction appears to be contingent on adequate female body condition (Persson 2005), and even experienced adult females regularly fail to reproduce.

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Wolverine survival may also be influenced by food limitation (Sæther et al. 2005). Researchers in southern Sweden reported density dependence in wolverine survival (Broseth et al. 2010). Wolverine growth is limited by food availability, which is moderated by variation in ungulate abundance, vulnerability, and kills by other predators (including people) across space and time. The large potential variation in wolverine vital rates suggests that wolverine population growth could be quite variable across the species' range, which could influence the sustainability of trapping.

The distribution of wolverines and the locations of their dens have been linked to the presence of continuous snow cover during the spring denning period (Copeland et al. 2010, Magoun et al. 2017). Copeland et al. (2010) and Magoun et al. (2017) also reported that radio-telemetry locations and home ranges in spring were mostly in areas of continuous spring snow. There are 3 working hypotheses to explain this link between spring snow and wolverine distribution. The first hypothesis proposes the need for snow to protect the safety and thermoneutrality of the young in the den (Copeland et al. 2017). The second hypothesis is based on the observation that wolverines cache food for winter. Inman et al. (2012a) suggested that wolverines require continuous snow during late-fall to spring to preserve food during winter because food is particularly scarce during this season. Third, wolverines may be physically adapted to snow covered, temperate environments, and these adaptations may exclude them from more moderate environments (Lofroth et al. 2007; Schwartz et al. 2009; Copeland et al. 2010, 2017). Spring snow cover has not been linked to wolverine population density.

Wolverines are most at risk in the montane portion of their range and density has been studied in 2 montane areas in southern Canada (Lofroth and Krebs 2007). Also, M. Barrueto (University of Calgary, unpublished data) presented an earlier analysis of a portion of the data included here. Using live capture data and open capture-recapture models during 4 years of study, Lofroth and Krebs (2007) calculated a mean abundance across years; they also used camera sightings and a closed model to obtain a single estimate of abundance during 1 winter of study. These estimates of abundance were likely biased low because the substantive food baits placed at the capture sites meant previously captured animals were more likely to be recaptured in subsequent trapping sessions than were animals that had never been captured. In contrast, density estimates were not corrected for the partial residency of animals living near the study area boundary, which can underestimate the effective trapping area and lead to positive bias in the density estimate (i.e., closure bias). Wolverine density was also estimated using very similar methods in a sister study in the northern limit of the montane mountains in central British Columbia. These 2 studies yielded density estimates of about 3 individuals/1,000 km² and other estimates of wolverine density in comparable ecosystems were similar (Lofroth and Krebs 2007), except for 1 study in Idaho, USA (Hornocker and Hash 1981), which reported much higher density.

Natural mortality of wolverines has been observed to vary from 4–20% per year (Krebs et al. 2004, Squires et al. 2007, Persson et al. 2009), and reproduction is low for an animal

of this size. Females produce <0.5 female young per year (Persson et al. 2006). Previous researchers used simple population models and observed estimates of survival and reproduction to estimate the influence of trapping mortality on population growth. They concluded that wolverine demographics are sensitive to adult mortality and that current harvest rates in North America may limit population growth, except perhaps in parts of northern Canada and Alaska where trapping mortality rates were lowest (Krebs et al. 2004, Squires et al. 2007, Lofroth and Ott 2007). None of these models incorporated density dependence or accommodated differential sex- and age-based trapping vulnerabilities; therefore, they may have underestimated sustainable harvest rates (Krebs et al. 2004, Squires et al. 2007, Lofroth and Ott 2007).

A specific analysis of harvest sustainability in British Columbia by Lofroth and Ott (2007) suggested recent levels of wolverine kill were sustainable at the provincial scale, but harvest in some areas may not have been sustainable. They reported that uncertainty in the harvest data was an important part of the conservation risk and recommended improved data collection and evaluation. Using a probabilistic modeling approach, Dalerum et al. (2008) included various realistic harvest scenarios and immigration levels in their model and found the model population was sensitive to adult female harvest and that immigration was necessary to ensure long-term viability and avoid local extirpations. Sæther et al. (2005) examined conservation risk in the Scandinavian wolverine population using a population viability approach and they also reported that harvest posed the largest conservation risk to the population. In summary, previous studies of wolverine demography suggest the species can support small, male-dominated harvests and that harvesting isolated populations can cause population decline or extirpation.

Juvenile and yearling (sub-adults collectively) wolverine dispersal begins in January, and males disperse more commonly than females (Magoun and Copeland 1998, Vangen et al. 2001, Gervasi et al. 2015, Copeland et al. 2017). Sub-adults have larger home ranges than adults while they are searching for a permanent range; sub-adult males cover particularly large areas (Inman et al. 2012b). In addition, pregnant female wolverines begin looking for dens in January, and their young are born in February or March (Magoun 1985, Banci 1994, Magoun and Copeland 1998); therefore, breeding females have restricted home ranges during late winter. The variation in home range size among sex and age cohorts in wolverines is likely greater during late winter than at any other time of year. Resident females with young may have seasonal ranges <100 km², whereas dispersing sub-adult males are often nomadic and may have ranges >2,000 km². Hence, we expect considerable bias in all density estimators that do not specifically account for space use and individual variation in detection probability due to these space use patterns (Royle et al. 2011).

The main objective of this study was to evaluate the demographic risk of trapping to wolverine populations in south-east British Columbia and the adjacent Rocky Mountains of southern Alberta. We also investigated the relationship between broad habitat factors and wolverine density so we could

predict density across space and gain insights into the species' habitat needs. Based on previous research, we predicted trapping, roads, and human use would be negatively related to density and that spring snow cover, alpine, and upper elevation forest would be positively related to density.

STUDY AREA

Our study area included the Kootenay-Boundary Region in southeast British Columbia and the southern Rocky Mountains and foothills of southwest Alberta, Canada (Fig. 1). This area includes parts of the Monashee, Selkirk, Purcell, and Rocky mountains and is $>50,000 \text{ km}^2$. The area is montane and the climate, although highly stratified by elevation, is characterized by cold winters, with long periods of snow cover, and hot summers (MacKillop and

Ehman 2016). Many large lakes, highways, and human settlements, which could create resistance to movement, occurred in low elevation valleys. Extensive forest harvest has occurred throughout the area and mining was widespread historically but is much less active currently. Both industries built and continue to build many roads. Winter recreation (e.g., snowmobile use, ski resorts, helicopter or snowcat-access skiing, ski lodges, backcountry skiing) was common in our study area. Provincial and national parks and protected areas occurred throughout the area.

Elevation ranged from 400 m to $>3,000 \text{ m}$, with major variation in summer and winter precipitation. In general, the mountains become less rugged from north to south, which led to lower precipitation, though precipitation also roughly declined from west to east. Low elevation forests

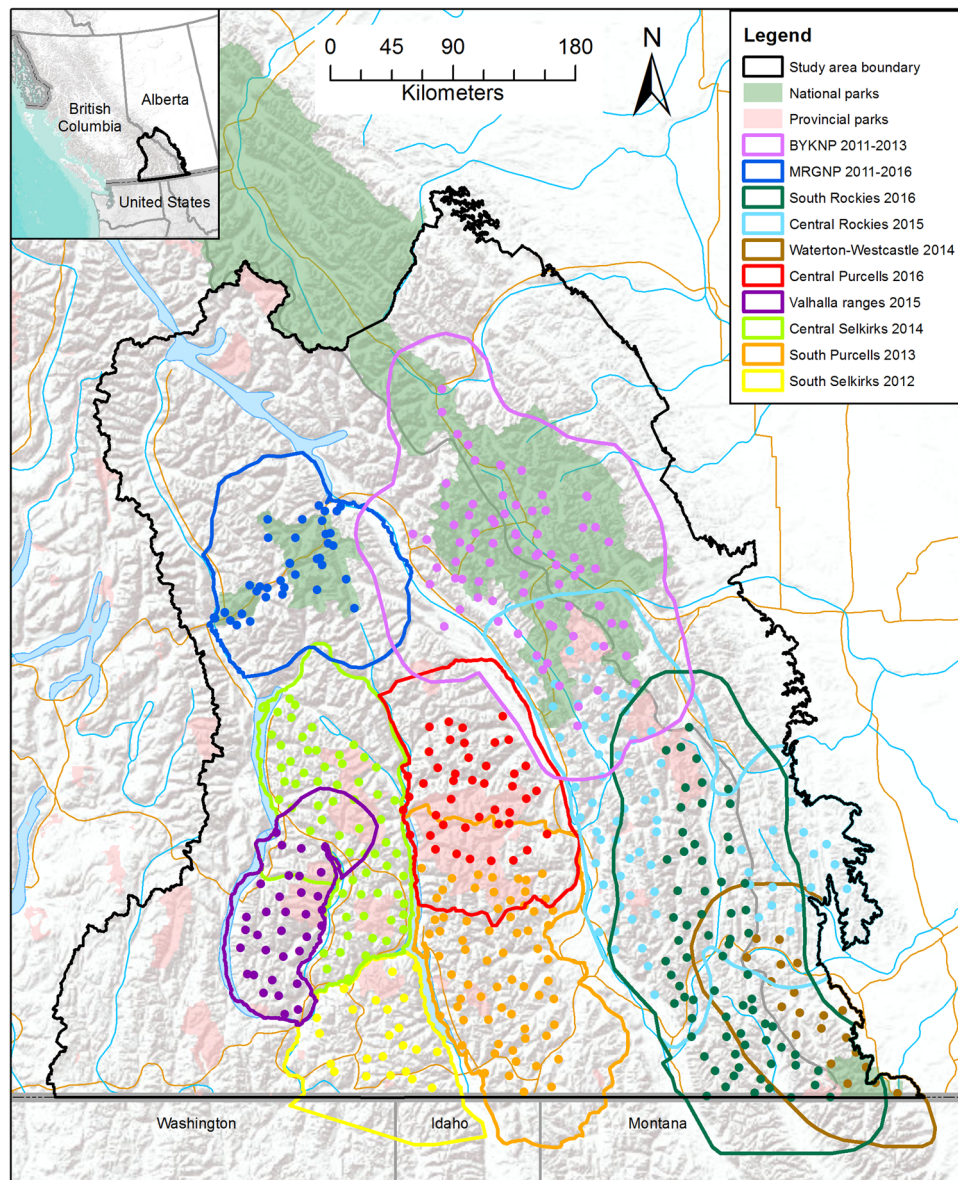


Figure 1. Wolverine winter sampling areas 2011–2016 in southwest Canada showing trap locations and spatially explicit capture-recapture mask boundaries for each sampling area in matching colors. We created mask boundaries by assuming large lakes were hard population boundaries. Where natural boundaries did not exist, we extended the mask approximately 40 km beyond the outer sample sites. In the legend, we provide the year at the end of the winter of sampling after the sampling area name (BYKNP is Banff, Yoho and Kootenay National Parks and MRGNP indicates Mount Revelstoke and Glacier National Parks).

were composed of western red cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), Douglas fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), lodgepole pine (*Pinus contorta*), trembling aspen (*Populus tremuloides*), and western larch (*Larix occidentalis*). At higher elevations, Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) forests transitioned to treeless alpine meadows, rock, and ice (MacKillop and Ehman 2016).

Potential wolverine ungulate prey included mountain goats (*Oreamnos americanus*), mountain caribou, mountain sheep (*Ovis canadensis*), moose (*Alces alces*), elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*O. virginianus*). Only mountain goats and caribou inhabited high elevations consistently during winter; goats were irregular in their distribution and rarely abundant (Poole 2006). Caribou have declined to <200 individuals as of 2018 (A. Reid, British Columbia Ministry of Forests, Lands and Natural Resource Operations and Rural Development [FLNRORD], personal communication) and were confined to 4 areas with large expanses of the study area without caribou. Small-mammal prey included hoary marmots (*Marmota caligata*), Columbian ground squirrels (*Urocitellus columbianus*), snowshoe hares (*Lepus americanus*), American pikas (*Ochotona princeps*), and porcupines (*Erethizon dorsatum*; Lofroth et al. 2007).

METHODS

Wolverine DNA Sampling and Trapping Harvest Rate

We collected samples from wolverines during late winter by remotely removing hair and occasionally collecting scat

samples. We sampled 8 areas in southeast British Columbia and southwest Alberta between 2012 and 2016: 5 areas in the West Kootenays from 2012 to 2016 and 3 areas in the East Kootenays and southwest Alberta from 2014 to 2016 (Fig. 1). We partitioned each area into 10-km by 10-km cells that approximated the minimum size of a female home range. We set 1 or 2 bait sites in each cell and checked them twice in the West Kootenays and 3 times in the East Kootenays at roughly monthly intervals (Table 1). We began sampling in late December in the East Kootenays and in late January in the West Kootenays, and we removed the sites between late March and mid-April. Because of the rugged nature of the terrain, we selected sites for ease of access and used local knowledge of wildlife movements when available. We made hair traps by attaching bait to a tree (~2 m from the ground or snow surface) and wrapping barbed wire around the tree below the bait to capture hair from animals that climbed the tree to get the bait, similar to Mulders et al. (2007; Fig. 2). We used a deer or elk head as bait in the West Kootenays and a skinned beaver (*Castor canadensis*) carcass in the East Kootenays and Alberta. Each time we re-visited the site, we examined the barbed wire for hairs, collected any hair samples present, burned each barb to clean the wire of remaining hairs, and replenished the bait if necessary. We collected hair samples in paper envelopes and stored them in a dry environment. In the East Kootenays we also attached a camera to a nearby tree to photograph animals that visited the site. During each visit to the bait site, we looked for wolverine tracks and scat. We also included data from 5 additional sites that were sampled contemporarily, using similar methods, for environmental

Table 1. Wolverine sampling effort and detection success in southeast British Columbia and southwest Alberta, Canada, 2011–2016. Year is the year at the end of the sampling winter, and the area sampled is the mask area for each sampling area. We detected 126 unique individuals in our study area; we detected some of these individuals in multiple sampling areas or years, so when we summed the individuals detected in each sampling area-year, the total was 153 individuals. Detections are the total number of individual detections across all sampling occasions (each individual could only be detected once per occasion, regardless of how many sites they visited during that occasion). Spatial detections also include multiple detections of an individual within an occasion, as long as those detections occur at different sampling sites.

Sampling area ^a	Year	Area sampled (km ²)	Sites sampled	Detection occasions	Individuals detected	Detections (spatial detections)	\bar{x} trap spacing (km)
Rocky Mountains							
BYKNP	2011	19,617	48	3	23	46 (46)	8.5
BYKNP	2012	19,617	10	3	8	14 (14)	12.9
BYKNP	2013	19,617	64	3	26	62 (63)	7.6
Waterton-Westcastle	2014	7,347	20	3	1	1 (1)	9.3
Central Rockies	2015	18,785	78	3	11	21 (28)	8.7
South Rockies	2016	18,714	75	3	11	22 (37)	7.1
Purcell Mountains							
South Purcells	2013	10,833	66	2	8	9 (12)	7.0
Central Purcells	2016	7,910	43	2	8	11 (23)	7.1
Selkirk Mountains							
MRGNP	2011	7,150	6	3	3	4 (4)	9.7
MRGNP	2012	7,150	7	3	9	11 (11)	6.1
MRGNP	2014	7,150	12	3	3	3 (6)	4.4
MRGNP	2015	7,150	6	3	10	15 (20)	12.4
MRGNP	2016	7,150	6	3	10	13 (13)	8.9
South Selkirks	2012	5,452	23	2	4	5 (6)	7.8
Central Selkirks	2014	7,863	63	2	16	22 (40)	7.0
Valhalla ranges	2015	4,445	33	2	2	2 (2)	7.5
Total			560		153	261 (326)	7.75

^a Sampling areas included Banff, Kootenay and Yoho National Parks (BYKNP) and Mount Revelstoke and Glacier National Parks (MRGNP).



Figure 2. Photo of hair capture site used in the West Kootenay (A) and the East Kootenay and Alberta portion (B) of our wolverine study area in southwest Canada. The bait is nailed several meters off the ground or snow and barbed wire is wrapped around the tree to remove hair from the target animal as it climbs the tree to feed on the bait.

impact assessment. Animal care was regulated by the British Columbia Ministry of FLNRORD Animal Care Committee. We did not need an animal care permit for this work because the sampling methods were considered non-invasive.

Additionally, we collected data using similar methods in 2 areas centered around national parks. The primary objective of these studies was to examine movement across the highways that crossed the parks (Sawaya et al. 2019). We collected data for 5 years near Revelstoke in Mount Revelstoke and Glacier National Parks, and for 3 years in Banff, Kootenay, and Yoho National Parks. These studies used 3 sampling sessions and beaver as bait, as in our East Kootenay studies.

We sent the hair samples to Wildlife Genetics International (WGI) in Nelson, British Columbia for microsatellite genotyping. We selected only samples that had >1 guard hair with a root or >5 underfur hairs for analysis, and WGI used up to 10 guard hairs or approximately 30 underfur

hairs in an extraction. Technicians extracted DNA using QIAGEN DNeasy Tissue kits, following the manufacturer's instructions (Qiagen, Toronto, ON, Canada). Species identification was based on a sequence-based analysis of a segment of the mitochondrial 16S rRNA gene (Johnson and O'Brien 1997). For samples that yielded wolverine DNA, WGI used multilocus genotyping, consisting of a ZFX-ZFY sex marker and 7 additional microsatellite markers, for individual identification. Error checking followed established rules (Paetkau 2003), which have been tested using grizzly bear (*Ursus arctos*) hair and deliver low error rates (Kendall et al. 2009). Samples from the studies in the national parks were first analyzed at the Rocky Mountain Research Station laboratory in Missoula, Montana using nearly identical methods. We later reanalyzed 1 sample from each individual at Wildlife Genetics International to verify that individual identities were comparable between the labs and studies so the datasets could be combined.

We estimated wolverine trapping harvest rates using government-collected kill data. In British Columbia and Alberta, trapping is regulated by a registered trapline system where licensed trappers must own a registered trapline or have permission to trap on private land or someone else's trapline. Registered traplines are exclusive areas whose boundaries rarely change, though ownership may transfer. Most public land that is not park is included in a registered trapline, and traplines even occur in some recent provincial parks. Very few areas are trapped by ≥ 1 person, so trapping effort tends to be dispersed in Canada (Slough et al. 1987). In southeast British Columbia and southwest Alberta trappers may trap wolverines between 1 November and 31 January; each trapper may catch 1 wolverine/year in Alberta, but there is no limit in British Columbia. Trapper kill is recorded by mandatory reporting in southern British Columbia and Alberta and by the fur sales recording system throughout British Columbia. Hunters must submit all wolverines they kill to a government inspector, though few wolverines are killed by hunters. Wolverines are also occasionally killed in highway collisions but few of these are recorded. Lofroth and Ott (2007), Hatler and Beal (2003), and Webb et al. (2013) provide additional details on wolverine trapping and management in British Columbia and Alberta.

Spatial Capture-Recapture Analysis

We used spatially explicit capture-recapture (SECR) analysis to estimate wolverine density (Efford 2004, 2018). This method is fast becoming the standard method for estimating animal density (Royle et al. 2013). Spatial capture-recapture methods estimate 3 parameters: detection, a spatial parameter, and density. The detection parameter can be likened to the detection probability in non-spatial capture-recapture; however, in SECR, detection probability declines with distance from the animal's putative home range center. A link function models the shape of the decline in detection; we used the default logit link. The spatial parameter, termed sigma, is an index of the range size during sampling and,

along with the trap and animal location data, is used to estimate range centers of individuals in and near the sampling area. Density is the response variable and commonly the parameter of interest.

Detection Covariates

Covariates can be fit to all estimated parameters to reduce bias, improve model fit, or better predict density within or beyond the study area. Covariates can also be fit to trap sites and individuals to accommodate heterogeneity in detection or space, or among individuals, but there is a limit to the number and type of covariates that can be fit simultaneously (Efford 2018). We fit detection parameters first and then fit density covariates to minimize the number of model runs using spatial covariates because each analysis using spatial density covariates took 1–2 days. We accommodated variation in sampling effort by directly coding the number of days each trap was set into the trap data file in the usage field. Detection success for wolverines commonly increases from mid to late winter (Broseth et al. 2010, Royle et al. 2011), so we allowed the detection parameter to vary among trapping sessions, expecting increased detection in later sessions. Female ranges are smaller than male ranges, but we initially ran analyses combined for each sex because we had small sample sizes, and smaller range size is often compensated for by higher detection success (Efford and Mowat 2014). Combined sex models often yield nearly identical density estimates to separate models for each sex. After selecting our best model, we ran separate analyses for males and females to better understand the influence of covariates on the density of each sex. We expected considerable variation in range size among individuals which would reduce precision and could bias the estimate of density.

Our hair traps were far apart (~8 km on average; Table 1) and included a substantive meat reward. Many individuals had few traps in their home range and were more likely to visit a site they had already visited than visit a different site, especially given the food reward. Hence, we expected repeated detections of an individual wolverine would be more likely at sites where they were previously detected, and we allowed for this explicitly in our model structure. This trap-based behavior response has been detected in other wolverine studies (Mulders et al. 2007, Royle et al. 2011) and many other carnivore species where baited sites were used and is explicitly accommodated in SECR.

Snow depth varied among years and sites during our study, so we measured snow depth on the final visit to each trap site and used this as a trap covariate to accommodate this possible source of capture variation. We used the final snow depth measure because we could only include 1 measure per trap and snow depth was most variable in the final detection occasion. We also tested to see if the difference in baits used in the East and West Kootenays measurably influenced detection success. Lastly, we included a binary parameter that allowed for different detection success based on which lab originally analyzed the genetic data to examine whether genotyping success affected detection success.

We calculated mean annual home range sizes for all wolverine radio-telemetry studies conducted in the montane region of western North America. Where possible, we chose extensive home range estimates such as 95% minimum convex polygon estimates and did not use core estimates (Table S1, available online in Supporting Information). We weighted the mean from each study by the sample size of individual animals and used the mean home range estimate to calculate sigma values. Sigma is the parameter that scales for density in SECR models, and it can be calculated as $\sigma = r/2.45$ where r is the radius of the 95% home range (Sun et al. 2014). We compared these independently calculated sigma values to those estimated by SECR analysis of our detection data to examine whether our estimates of sigma aligned with other independent measures of wolverine space use.

Density Covariates

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

We predicted that wolverine density would be greater in higher elevation ecosystems. Wolverines appear to use higher elevations at all times of year and especially in winter (Krebs et al. 2007, Inman et al. 2012b). We assumed that wolverines do not choose elevation itself but rather prefer plant associations and climate envelopes typical of higher elevation or latitudes (Copeland et al. 2010). Additionally, females den at higher elevations in montane areas (Krebs et al. 2007). We used ecological mapping (MacKillop and Ehman 2016) to divide our study area into 3 broad zonal ecosystems: low elevation forests, which were wetter in our western study areas than in our eastern study areas; sub-alpine forest of Engelmann spruce-subalpine fir (ESSF), typical of upper elevations in North American montane forests; and alpine, which included all high elevation communities such as alpine tundra and grassland, parkland and woodland forests, and rock. Because precipitation increases with elevation, both the latter ecosystems were wetter, snow-affected ecosystems. We excluded permanent ice. To test if ecosystem was related to density, we included alpine and ESSF in our models and excluded low elevation forest to create a contrast with the other 2 ecosystems.

We calculated spring snow cover for each year from 2000–2016 using MODIS data following Copeland et al. (2010). For each pixel and year, we determined if there was persistent spring snow cover from 24 April to 15 May. We then calculated an index of presence of snow (0–17), which

represented the number of years a location had spring snow cover, to test the relationship between spring snow cover and local wolverine density.

We calculated road density using current road data acquired from provincial governments (Supplement S4, available online in Supporting Information). We used open source data for roads in the United States. We also acquired Human Influence Index mapping as an alternative and more generalized measure of disturbance (<http://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-influence-index-geographic>, accessed 17 Mar 2019).

We re-scaled the spatial data for all variables using a moving window analysis with a radius of 10 km, which is roughly the radius of a female home range in late winter. Spatially explicit capture-recapture uses the variable value at the putative home range center to calculate the relationship between density and habitat covariates. We felt wolverine density would be more strongly related to the mean value of each spatial variable in the entire home range, not at a specific site.

We used Akaike's Information Criterion corrected for small sample size (AIC_c) to compare model fit among candidate models. We first compared detection covariates to select which of these variables to include in future spatial modeling. Models that include density covariates take a long time to run and we reduced the number of candidate spatial models by fitting detection variables first because detection models ran more quickly. We chose detection variables based on fit, our knowledge of the detection methods, and wolverine biology. We chose our best density model based on fit and realism and we did not attempt to accommodate uncertainty in model selection because our final model was much better supported than other models.

Population Model

We built an annual discrete-time population model to better understand sustainable harvest rates of wolverines. A number of previous efforts have used population modeling to examine the sustainability of harvest (Krebs et al. 2004, Dalerum et al. 2008, Lofroth and Ott 2007, Squires et al. 2007) or population viability (Sæther et al. 2005). In particular, we wanted to better understand how sex and age-biased harvest affected harvest sustainability, and how environmental stochasticity and density dependence might further influence harvest rates. We used field data from radio-telemetry studies to parameterize reproduction and survival and we used carcass studies to estimate potential reproduction based on *in utero* measures of pregnancy rate and the proportions of each age and sex cohort in the trapped sample. We added environmental stochasticity to the reproduction component of the model because successful reproduction appears to be closely linked to late winter food abundance, which can be as random an event as the discovery of a single ungulate carcass by an individual female (Mattisson et al. 2016).

We structured our model into 5 cohorts: juveniles, yearling females and males, and adult females and males. We split annual survival into an initial pre-harvest rate and a second

post-harvest rate that modestly reduced the initial rate as a function of harvest rate. We incorporated density dependence into reproduction using a theta power function. Only 1 study has estimated theta for wolverines (Sæther et al. 2005), and they reported evidence for strong density dependence near carrying capacity (K ; $\theta = 12.5$). We set K at roughly 50% higher than our observed population estimate because much of the study area appeared to be unoccupied. Density dependence was trivial when K was 50% higher than the starting population size. We used survival rates from Krebs et al. (2004) for yearlings (0.85) and adults (0.88), and a juvenile survival rate (0.68) as measured by Persson et al. (2006). We used the mean reproduction rate observed by 3 field studies (Magoun 1985, Copeland 1996, Persson et al. 2006). This value (0.77 young/year/female) was for adult females only because yearling females have not been observed to reproduce. Stochasticity could be incorporated in all vital rates; however, we allowed it only in the reproductive rate. For each reproductive parameter, we used a beta distribution to generate random realizations that fell within a set expected value (tol) of the parameter approximately 95% of the time. We assumed the sex ratio of litters at birth was equal. Age ratios of trapper killed carcasses were 36% juveniles, 20.2% yearling males, 12.6% yearling females, 20.4% adult males, and 10.8% adult females and we derived these age ratios by taking the mean ratio from 5 mid- to long-term carcass collection studies from northern Canada (Banci and Harestad 1988, Mulders 2000, Awan and Szor 2012, Lee 2016, Kukka et al. 2017). We first ran a model to calculate harvest vulnerabilities for each age and sex based on the age and sex ratio of trapped wolverine samples above. We then used these vulnerability estimates in the subsequent population modeling process. We ran the model for 60 years and focused attention on its long-term steady state behavior. Initial cohort sizes were based on observed age and sex ratios that totaled to our estimate of the population size for the study area. It took about 10 years for the age structure to stabilize for each new model run. We built all models in R (R Core Team 2016; code available online in Supporting Information S5–S6 and at <https://github.com/ctlamb/WolverineSCR>).

RESULTS

Density and Harvest Rate

We sampled wolverines during 6 winters between December 2010 and April 2016 throughout southeast British Columbia and southwest Alberta (Fig. 1). We identified 126 individual wolverines that were detected 326 different times across years, study areas, trapping occasions, and sites (Table 1). Only the 2 study areas in the national parks were sampled in >1 year, and these study areas generated much of the recapture data in the dataset (Table 1; Fig. S1, available online in Supporting Information).

Wolverines were more commonly detected at traps where they had previously been detected, which is expected when food rewards are provided at trap sites. We also expected detection success to increase as the winter progressed, but variation among capture occasions was not supported

Table 2. Model selection table to evaluate possible variation in detection success for wolverines sampled in southeast British Columbia and southwest Alberta, Canada, 2011–2016. We estimated 3 parameters: density (D), detection probability (g0), and a movement parameter (sigma). No density or sigma covariates were included in this analysis. We present the number of model parameters (K), model log likelihood (logLik), Akaike's Information Criterion corrected for small sample size (AIC_c), the difference in AIC_c values (ΔAIC_c), and relative model weight (w_i).

Model ^a	K	logLik	AIC _c	ΔAIC _c	w _i
g0~bk	4	-1,078.20	2,164.68	0.00	0.25
g0~DNA + bk	5	-1,077.14	2,164.70	0.02	0.25
g0~bk + snow depth	5	-1,077.19	2,164.80	0.12	0.23
g0~bait + bk	5	-1,077.42	2,165.24	0.56	0.19
g0~t + bk	6	-1,077.14	2,166.86	2.19	0.08
g0~t	5	-1,101.78	2,213.97	49.29	0.00
g0~1	3	-1,107.33	2,220.83	56.15	0.00
g0~snow depth	4	-1,107.08	2,222.43	57.75	0.00

^a Detection covariates included trap-specific behavior (bk), a categorical variable for each genetic lab (DNA), snow depth at trap site at last check (snow depth), ungulate versus beaver bait (bait), and trapping occasion (t).

(Table 2). The best fitting detection model included separate detection parameters for each sampling area and year, but this model had 19 parameters and was unstable. This model was unrealistic given the small sample sizes in some studies (Table 1) and we did not consider it further. The binary variable representing the 2 genetic labs, snow depth at the trap site, and bait type generated minor improvements in fit so we did not include these variables in further analyses. Only trap-effort and trap-specific behavior were included in future model fitting to account for the variation in detection probability among traps and individuals.

Detection probability when the trap is at the center of the home range (g0) was 0.006 ± 0.001 (SE) for wolverines that were detected at a trap for the first time and 0.023 ± 0.003 for individuals that had already been detected at the same trap. Sigma, the spatial parameter, was 9.8 ± 0.54 km for both sexes combined and 11.2 ± 0.95 km for males and 8.4 ± 0.61 km for females. Sigma values, as calculated from home range data for wolverines living in montane areas, varied from 4.4 km for adult females to 11.4 km for sub-adult males (Table 3). Sub-adults may make such large movements while exploring for a permanent home range that they may effectively emigrate from many study areas (Inman et al. 2012b). The sigma value from our SECR analysis, which was pooled across age-classes, was closer to the size expected for males than females, and the sex-based

Table 3. Mean annual home range size for wolverines in the montane mountains of western North America (1992–2013). Sigma is the movement parameter in spatially explicit capture-recapture and was calculated as $\sigma = r/2.45$ where r is the radius of the 95% home range (Sun et al. 2014).

Sex	Age	Mean home range size (km ²)	Home range radius	Sigma	n
Female	Adult	339	10.4	4.2	28
Female	Sub-adult	787	15.8	6.5	22
Male	Adult	1,097	18.7	7.6	25
Male	Sub-adult	2,333	27.3	11.1	16

Table 4. A comparison of the fit of a selected group of models to estimate density of wolverines in southeast British Columbia and southwest Alberta, Canada, 2011–2016. All models include, sampling effort for each trap, a trap-specific behavior effect on detection, and no covariation for the spatial parameter. Models vary only based on the density covariates included in each model. We present the number of model parameters (K), model log likelihood (logLik), Akaike's Information Criterion corrected for small sample size (AIC_c), the difference in AIC_c values (ΔAIC_c), and relative model weight (w_i).

Model ^a	K	logLik	AIC _c	ΔAIC _c	w _i
Road density + snow	6	-1,037.6	2,087.7	0.0	0.52
Road density + snow + trap harvest	7	-1,037.4	2,089.6	1.9	0.20
Snow	5	-1,039.9	2,090.2	2.5	0.15
HII + snow	6	-1,038.9	2,090.4	2.7	0.13
Road density + alpine	6	-1,042.5	2,097.5	9.8	0.00
Road density + ESSF + alpine	7	-1,042.3	2,099.4	11.7	0.00
Road density + ESSF + alpine + trap harvest	8	-1,041.9	2,100.8	13.1	0.00
Road density	5	-1,045.7	2,101.7	14.0	0.00
Alpine	5	-1,048.2	2,106.8	19.1	0.00
HII	5	-1,063.9	2,138.3	50.5	0.00
ESSF	5	-1,076.4	2,163.2	75.5	0.00
Null	4	-1,078.2	2,164.7	77.0	0.00
Trap harvest	5	-1,077.8	2,166.0	78.2	0.00

^a Snow = the number of years with spring snow cover between 2000–2016, trap harvest = area weighted measure of the number wolverines killed the winter of our sampling, alpine = the proportion of alpine ecosystem, ESSF = the proportion of upper elevation forest, HII = human impact index, which is a cumulative measure based on road density, human habitation, and other human footprints. All variables were smoothed using an 8-km-radius moving window analysis.

values were closer to those expected for sub-adults than adults (Table 3).

After testing the influence of covariates on detection probability, we tested variables we hypothesized would be related to density using the best fit detection model. We did not include spring snow with alpine or ESSF (high elevation forest) in the same model because these variables were strongly correlated (Fig. S2, available online in Supporting Information). Spring snow and road density were most related to estimated density (Table 4); all other variables generated only minor improvements in fit. The trapping mortality variable was not related to density (Table 4). Density varied from 0.9–4.4 wolverines/1,000 km² among our sampling areas (Table S2, available online in Supporting Information) and averaged 2.0/1,000 km² (CI = 1.70–2.5/1,000 km²) across the study area. When we ran the top model separately for each sex, the summed male and female densities were nearly identical to the mean density as estimated by the model that did not accommodate sex. Females were 62% of the estimated population (Table S2). Density was positively related to the annual consistency of spring snow cover and negatively related to road density (Fig. 3).

We used this model to extrapolate wolverine density to our entire study area; estimated density generally declined from north to south (Fig. 4). We derived population estimates for the Kootenay Region of British Columbia, the Alberta portion of our greater study area, and for the 2 areas combined. The wolverine harvest during the 6 years of our field sampling and the 3 years previous averaged 19 animals/year for

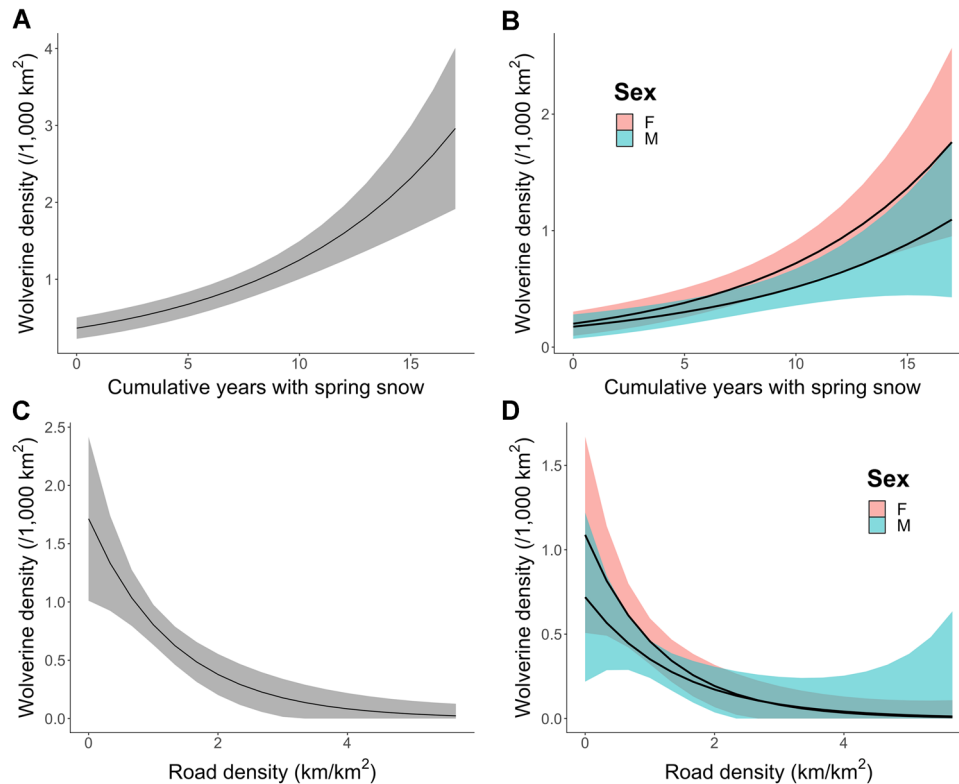


Figure 3. The relationship between spring snow cover, road density, and wolverine density based on our best fit model from southeast British Columbia and southwest Alberta. We built our spring snow map using snow cover data from 2000–2016. The figures on the left are for the combined sex model and the figures on the right are for separate sex models (F = female and M = male); shaded areas are 95% confidence intervals.

the greater study area, 16.6 animals/year in the British Columbia portion and 2.3 animals/year in the Alberta portion of our study area. Our estimate of the annual kill rate for the entire study area was 8.4%. The kill rate in British Columbia was higher than the kill rate in Alberta (Fig. 5) because much of the wolverine distribution in southern Alberta was in national parks (Fig. 4). We also set road density to zero and predicted wolverine abundance without the depressing effect of the road covariate; abundance increased 44% from 226 ± 21.5 to 326 ± 66.2 .

Population Modeling

Our population model suggested the maximum sustainable mortality rate was 6.2%/year when harvest was drawn at random among sex and age classes. We used the mean age structure from published carcass studies to calculate harvest vulnerabilities by age and sex cohorts and found that young age classes were 6–10 times more vulnerable to harvest than adult females. When we incorporated these vulnerabilities in our model, the average maximum sustainable harvest increased to 8.3%. Stochasticity in reproduction caused rapid declines in the sustainable harvest rate from 8.1% at $\text{tol} = 0.05$ to 7.2% at $\text{tol} = 0.1$ to zero when tol was 0.4.

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

Potential reproduction in wolverines is much higher than what has been observed in the field postpartum because many more females, including some yearlings, are pregnant than give birth (Banci 1994, Copeland et al. 2017). When we used *in utero* pregnancy rates in our model, the maximum harvest rate increased to 18–23%; hence, the potential bias caused by using *in utero* reproduction rates is large. We conclude the maximum sustainable harvest rate for wolverines is about 8%, which incorporates the influences of higher trap vulnerability of juveniles and males and realistic stochasticity in juvenile recruitment rates as measured in live wolverine populations.

DISCUSSION

Currently, wolverine trapping is likely not sustainable in southeast British Columbia and southwest Alberta, and our estimated level of mortality presents considerable risk to this population. Although the observed harvest rate (8.4%/year) roughly equaled the theoretical maximum harvest rate (8%) we calculated in our population modeling exercise, the study area includes many parks and protected areas so the harvest rate in the portion of the study where trapping was allowed exceeded sustainable levels. The uncertainty in the recording of the wolverine harvest largely led to under-reporting and this uncertainty is also a risk to this population (Fig. 5). Several other North American researchers have concluded that wolverine harvest in their study populations was not sustainable or was being sustained by immigration (Krebs et al. 2004, Squires et al. 2007, Dalerum et al. 2008).

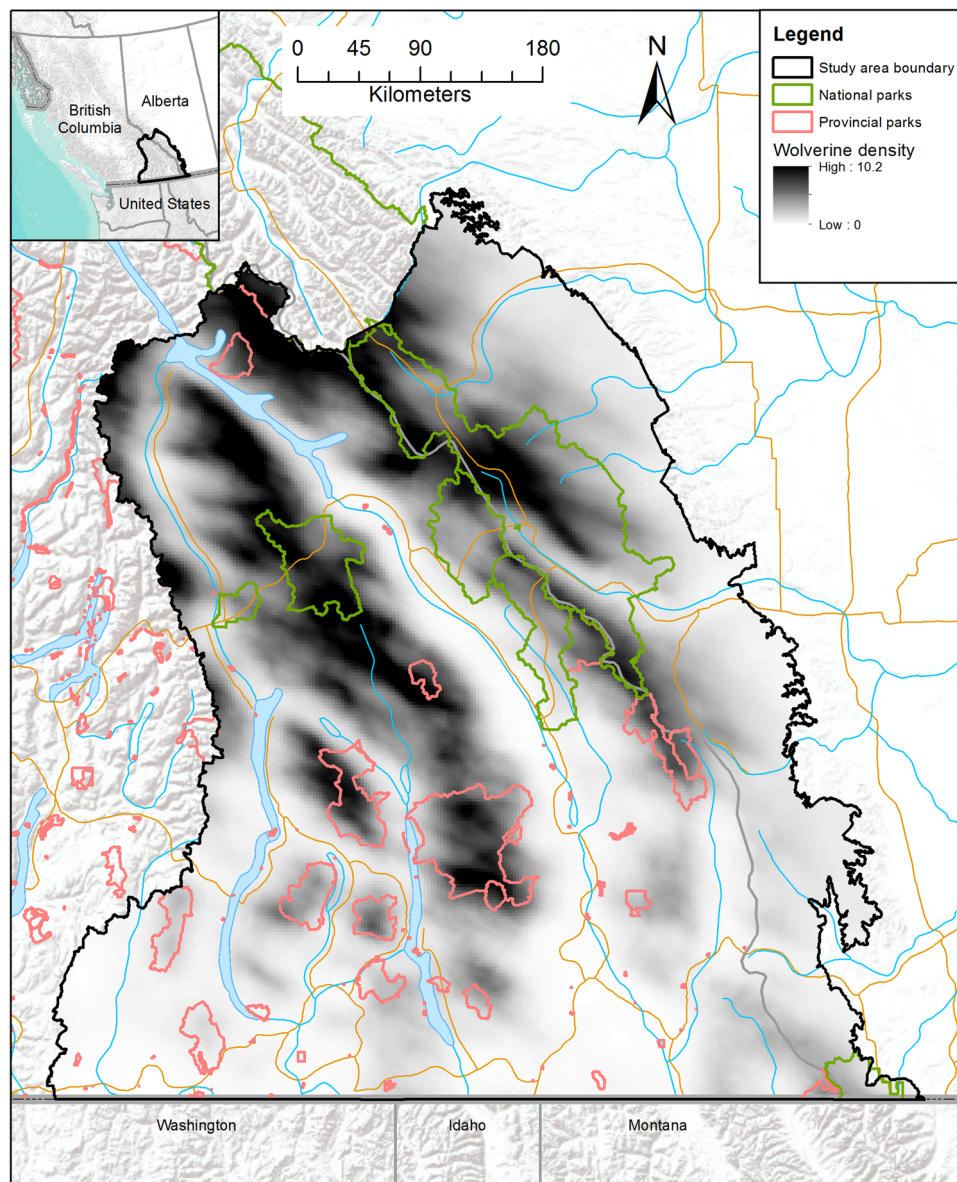


Figure 4. Wolverine density (wolverines/1,000 km²) in southeast British Columbia and southwest Alberta, Canada estimated from spatial capture-recapture analysis of genetically identified wolverines sampled during winter 2011–2016. There was no trapping in national parks, but wolverine trapping was permitted in some provincial parks.

What is the sustainable harvest rate for wolverines in this area? Harvest rates can be considered the policy portion of the harvest regime because the selection of an allowable harvest rate involves social and biological considerations (Mowat et al. 2013). The scientific part of the regime is often described by data. The social component involves the trade-off between the value to society and the perceived risk to the population. Wolverines generate relatively little value to the trapping industry compared to other furbearers like marten (*Martes americana*) or lynx (*Lynx canadensis*), but they do generate moderate value to the few trappers that catch them. About 15 trappers catch wolverines in our study area each year. Conservation risk from harvest is high because wolverines occur in a discontinuous fashion at low densities and have few young, and reproduction is affected by environmental stochasticity (Persson 2005). Because of

their low monetary value and the high conservation risk when this species is trapped, we suggest the target harvest rate should be conservative and less than half the theoretical maximum; we suggest a target harvest rate of $\leq 4\%$ of the population per year.

Pregnancy rates and litter sizes observed before birth suggest most females breed each year, which results in a potential birth rate that is double that observed in the field; however, all field studies of wolverine reproduction suggest females do not reproduce every year (Rauset et al. 2015). The only observation of wild wolverines breeding every year was during an experimental study for a select few females that were fed all winter (Persson 2005). Similarly, no field studies have recorded litter sizes above 3, which is commonly observed *in utero* (Banci 1994). Many recent field studies were on populations that were harvested, some

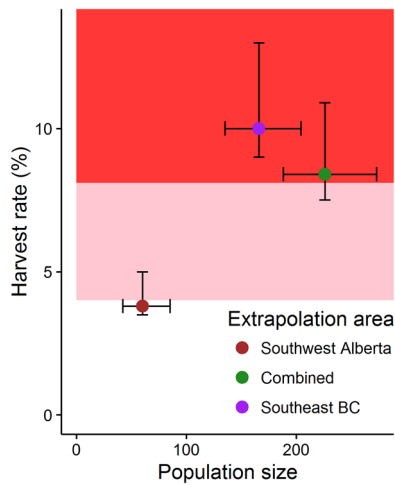


Figure 5. The harvest rate of wolverines based on population estimates extrapolated from spatial capture-recapture analysis of genetically identified wolverines sampled during winter 2011–2016 in southeast British Columbia (BC) and southwest Alberta, Canada. Horizontal error bars are 95% confidence intervals of population estimates, and vertical error bars are our subjective assessment of the likely error in the recording of wolverine trapping kill. Pink shading denotes harvest rates above our recommended level, and red shading denotes harvest rates that are likely not sustainable.

heavily, and none of these studies suggested a density-dependent response in reproduction that approached levels seen *in utero* (Banci 1994, Copeland 1996, Krebs et al. 2004). We conclude that potential reproduction in wolverines is much higher than observed in the wild and any analysis of wolverine population dynamics should use reproductive rates measured in wild populations of wolverines, not those measured *in utero*.

In our population modeling exercise, we found that sub-adult males and sub-adult females were much more vulnerable to trapping (10× and 6×, respectively) than were adult females. Adult males were 3× more vulnerable to trapping than were adult females. In a meta-analysis of survival of North American wolverines, Krebs et al. (2004) also reported sub-adult males were most vulnerable to trapping. Our population model suggested the maximum sustainable harvest rate increased by 2% when accounting for trap vulnerability by sex age class because sub-adults were more vulnerable to harvest. Because adult females had lower mortality *per capita*, reproduction did not decline with an increasing harvest rate as rapidly as it would have if all age cohorts were equally vulnerable to harvest. Greater vulnerability of young animals to trapping moderates the conservation risk of trapping.

Why was the spatial trapping mortality variable not negatively related to density if trapping was limiting wolverine abundance in our study area? This may be because wolverine mortality can only happen in areas that support wolverines, and large portions of our study area appear to support few or no wolverines. This creates a positive relationship between density and trapping kill, at least at low to medium abundance. At higher abundance this relationship may switch, resulting in a non-linear relationship. Also, resident wolverines that are killed may be quickly replaced by

sub-adults, given the large effort sub-adults put into searching for a territory after dispersing from their natal range (Inman et al. 2012b). In the Rocky Mountain national parks, density increased with distance into the park from the park boundary, suggesting trapping outside the parks reduced density measurably (M. Barrueto, University of Calgary, unpublished data).

Population density averaged 2 wolverines/1,000 km² across the study area. Previous density estimates in the montane mountains of western North America were mostly higher than our estimate (range = 1.8–15.4 wolverines/1,000 km²; Table S3, available online in Supporting Information). This difference could be explained by the mortality rate observed in our study area, or the large size of our study area, which included areas of high and low habitat quality. With smaller study areas, researchers may unconsciously select areas of higher than average density to meet sampling objectives (Smallwood and Schonewald 1998). None of the earlier studies, however, corrected for closure bias, which could lead to large over-estimates for animals such as wolverines that have large home ranges and who disperse during the period of study. Wolverine densities appear similar in montane and boreal forests, although only one of the boreal estimates were corrected for closure (Table S3), so it is possible wolverine density in boreal environments is actually lower than in montane environments. Higher densities have been recorded in coastal Alaska and in several places in the arctic; however, again, the highest observed densities were not corrected for closure (Table S3). In a comparative study in arctic Canada, uncorrected density was 2.5-fold greater than the closure-corrected density estimate. Efford and Boulanger (2018) estimated wolverine density using the same data as Mulders et al. (2007), but they corrected for closure bias explicitly using spatial capture-recapture methods. Their estimate was 6.7 wolverines/1,000 km² (CI = 5.4–8.3) compared to 17.2 wolverines/1,000 km² (CI = 16.4–24.3) from the earlier work. It would appear imperative to correct for closure bias in all wolverine inventories given the possibility for large biases, especially if the inventory area is relatively small. In summary, the highest reliable wolverine densities (~10 wolverines/1,000 km²) were observed in coastal Alaska and the Yukon north slope, with moderate densities observed in the central arctic when caribou were abundant (Table S3). Our work suggests densities in montane environments are low compared to densities in environments farther north.

We suggest that some previous studies that did not use SECR methods to analyze their sampling data have substantively over-estimated wolverine abundance. All studies that presented densities >10 wolverines/1,000 km² had study areas <3,000 km² (Table S3). For example, Lofroth and Ott (2007) used density estimates from 2 study areas in British Columbia and extrapolated a population estimate for all of British Columbia. They predicted the Kootenay Region to have 324 wolverines, whereas our model predicted a population of 166. If this difference is a measure of bias in their population estimates, then closure bias could

lead to considerable underestimates of the effect of trapping mortality throughout the wolverine range.

Our data present a positive relationship between wolverine abundance and spring snow cover. This observation supports the hypothesis of Copeland et al. (2010) that the distribution of wolverines is related to the probability that an area has complete snow cover during the late denning period. The circumpolar distribution of known wolverine den sites was related to spring snow in a multi-continent scale analysis (Copeland et al. 2010). Other studies have examined the relationship between spring snow and habitat selection and most find some positive relationship (Copeland et al. 2010, Heim et al. 2017, Kortello et al. 2019), and these relationships appear to be stronger in more topographically complex environments (Webb et al. 2016). Our results demonstrate that spring snow is related to density in montane environments, which suggests a functional relationship with wolverine ecology. Several reasons have been posited for this relationship including the need or preference for snow to cover dens, the need for snow to preserve cached meat, or a preference for snowier areas. We cannot unequivocally test among these hypotheses with our data, but females selected for snow more strongly than males (Fig. 3B), which supports the denning hypothesis more than the 2 alternatives. This is a weak test among these hypotheses because the stronger selection for snow by females could simply be due to the smaller ranges of female wolverines, which allows them to locate their ranges in relatively better habitat conditions. Clarifying the functional relationship between wolverine ecology and spring snow will require detailed study of their autecology.

Wolverine density was negatively related to roads (Fig. 3C) and the functional nature of this relationship is perhaps even less well understood than spring snow. Other workers have reported similar relationships for wolverines (Krebs et al. 2007, Fisher et al. 2013), including an occupancy-based analysis of our West Kootenay data (Kortello et al. 2019). The simplest explanation for this result is the tendency for wolverines to select high elevation areas, which are mostly found above the road network (Inman et al. 2012b, Kortello et al. 2019); however, trappers use roads to access their trapping areas, so this relationship may be partly explained by the recent or historical effects of trapping. Then again, only about 70% of the traplines in the Kootenay are trapped in any year (A. Reid, personal communication), and few trappers try to catch wolverines, though some wolverines are caught as by-catch in traps set for other species. Further, only a small fraction of roads are travelled by trappers during winter, so it seems likely that there are other negative effects of roads on wolverine density. Given other cases of human-caused mortality are rare, either food is less abundant near roads, or wolverines are avoiding roads to the point it influences density.

Helicopter and backcountry skiing were negatively related to winter habitat selection in the north part of our study area (Krebs et al. 2007). Female wolverines have abandoned dens following human disturbance (Pulliainen 1968, Magoun and Copeland 1998), and they do not place den sites near human infrastructure (May et al. 2012). These observations

suggest disturbance can influence habitat use and perhaps density. Forestry roads are also travelled by recreationists on snowmobiles and used during winter logging operations, so perhaps wolverines avoid these collective uses. The human influence variable measures human habitation, which is most correlated with front-country all surface roads. The low explanatory power of this variable compared to forestry roads suggests it is the back-country forestry roads that wolverines are most strongly avoiding. We conclude that the functional significance of the relationship between roads and wolverine density is unclear and requires further study.

Sub-adult wolverines begin to disperse in late winter (Vangen et al. 2001, Gervasi et al. 2015), which presents a potential positive bias to density estimates because recapture rates would be negatively biased if juveniles move out of a study area entirely. This is possible given the large movements that have been documented (Inman et al. 2012b). It is also possible that spatial models may largely correct for this bias, and the estimate of the spatial parameter in this study was higher than expected based on the estimates of home range size. In addition, our trap spacing ($\bar{x} = 7.75$ km) was lower than $2 \times \sigma$ (19.6 km), which is the minimum spacing suggested in recent study design work by Sun et al. (2014). Further, clumping of traps, which occurred in several of our sampling areas (Table 1), has been suggested as a way to better estimate the spacing parameter.

MANAGEMENT IMPLICATIONS

Based on our work, we suggest wolverine trapping mortality should be reduced to $\leq 4\%$ in our greater study area, and perhaps by more than that for an interim period of recovery. Negative human effects on wolverine density could be mitigated by reducing road density, but the uncertainty of the mechanism behind this relationship makes it difficult to identify the best areas to implement closures or traffic restrictions. Many forestry roads in British Columbia have little traffic in winter, especially at higher elevation. Most winter traffic is by snowmobiles for recreation and, to a lesser extent, industry. Given the strong relationship we observed between wolverine density and spring snow, it may be best to select areas with both consistent spring snow cover and roads with substantive winter use when planning access mitigation for wolverine conservation. Denning females are most vulnerable to disturbance and of greatest population importance, so further research to identify denning habitat would offer more area-specific access recommendations and provide the greatest benefit to wolverines.

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LITERATURE CITED

- Aubry, K. B., K. S. McKelvey, and J. P. Copeland. 2007. Distribution and broadscale habitat relations of the wolverine in the contiguous United States. *Journal of Wildlife Management* 71:2147–2158.
- Awan, M., and G. Szor. 2012. Wolverine (*Gulo gulo*) carcass collection and harvest monitoring in Nunavut. Summary report, Department of Environment, Government of Nunavut, Iqaluit, Canada.
- Banci, V. 1994. Wolverine. Pages 99–127 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, L. J. Lyon, and W. J. Zielinski, editors. The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine in the western United States. General Technical Report RM-254. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.
- Banci, V., and A. Harestad. 1988. Reproduction and natality of wolverine (*Gulo gulo*) in Yukon. *Annales Zoologici Fennici* 25:265–270.
- Broseth, H., O. Flagstad, C. Wardig, M. Johansson, and H. Ellegren. 2010. Large-scale noninvasive genetic monitoring of wolverines using scats reveals density dependent adult survival. *Biological Conservation* 143:113–120.
- Canadian Wildlife Service. 2014. COSEWIC assessment and status report on the Wolverine (*Gulo gulo*) in Canada. <http://publications.gc.ca/collections/collection_2014/ec/CW69-14-329-2014-eng.pdf>. Accessed 29 Aug 2018.
- Copeland, J. P. 1996. Biology of the wolverine in central Idaho. Thesis, University of Idaho, Moscow, USA.
- Copeland, J. P., A. Landa, K. Heinemeyer, K. B. Aubry, J. van Dijk, R. May, J. Persson, J. R. Squires, and R. E. Yates. 2017. Social ethology of the wolverine. Pages 389–398 in D. W. Macdonald, C. Newman, and L. A. Harrington, editors. Biology and conservation of musteloids. Oxford University Press, Oxford, United Kingdom.
- 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, et al. 2010. The bioclimatic envelope of the wolverine (*Gulo gulo*): do climatic constraints limit its geographic distribution? *Canadian Journal of Zoology* 88:233–246.
- Dalerum, F., B. Shults, and K. Kunkel. 2008. Estimating sustainable harvest in wolverine populations using logistic regression. *Journal of Wildlife Management* 72:1125–1132.
- van Dijk, J., L. Gustavsen, A. Mysterud, R. May, Ø. Flagstad, H. Brøseth, R. Andersen, R. Andersen, H. Steen, and A. Landa. 2008. Diet shift of a facultative scavenger, the wolverine, following recolonization of wolves. *Journal of Animal Ecology* 77:1183–1190.
- Efford, M. 2004. Density estimation in live-trapping studies. *Oikos* 106:598–610.
- Efford, M. 2018. secr 3.1-spatially explicit capture-recapture in R. R-CRAN. <<http://ess.r-project.org/R-CRAN/web/packages/secr/vignettes/secr-overview.pdf>>. Accessed 29 Aug 2018.
- Efford, M., and J. B. Boulanger. 2018. Analyses of wolverine DNA mark-recapture sampling in the Northwest Territories 2004–2015. Unpublished report for Government of NWT. Integrated Ecological Research, Nelson, Canada.
- Efford, M. G., and G. Mowat. 2014. Compensatory heterogeneity in spatially explicit capture-recapture data. *Ecology* 95:1341–1348.
- Fisher, J. T., S. Bradbury, 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.
- Gervasi, V., H. Brøseth, E. B. Nilsen, H. Ellegren, Ø. Flagstad, and J. D. C. Linnell. 2015. Compensatory immigration counteracts contrasting conservation strategies of wolverines (*Gulo gulo*) within Scandinavia. *Biological Conservation* 191:632–639.
- Hatler, D. F., and A. M. M. Beal. 2003. Wolverine. Furbearer management guidelines, Government of British Columbia. <www.env.gov.bc.ca/fw/wildlife/trapping/docs/wolverine.pdf>. Accessed 29 Aug 2018.
- 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.
- Idaho Department of Fish and Game. 2014. Management Plan for the Conservation of Wolverines in Idaho 2014–2019. Idaho Department of Fish and Game, Boise, USA.
- Inman, R. M., A. J. Magoun, J. Persson, and J. Mattisson. 2012a. The wolverine's niche: linking reproductive chronology, caching, competition, and climate. *Journal of Mammalogy* 93:634–644.
- Inman, R. M., 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, et al. 2012b. Spatial ecology of wolverines at the southern periphery of distribution. *Journal of Wildlife Management* 76:778–792.
- Johnson, W. E., and S. J. O'Brien. 1997. Phylogenetic reconstruction of the Felidae using 16S rRNA and NADH-5 mitochondrial genes. *Journal of Molecular Evolution* 44:S98–S116.
- Kendall, K. C., J. B. Stetz, J. Boulanger, A. C. Macleod, D. Paetkau, and G. C. White. 2009. Demography and genetic structure of a recovering grizzly bear population. *Journal of Wildlife Management* 73:3–16.
- Kortello, A., D. Hausleitner, and G. Mowat. 2019. Mechanisms influencing the winter distribution of wolverine *Gulo gulo luscus* in the southern Columbia Mountains, Canada. *Wildlife Biology* 2019: 1–13.
- Krebs, J., E. Lofroth, J. Copeland, V. Banci, D. Cooley, H. Golden, A. Magoun, R. Mulders, and B. Shults. 2004. Synthesis of survival rates and causes of mortality in North American wolverines. *Journal of Wildlife Management* 68:493–502.
- Krebs, J., E. C. Lofroth, and I. Parfitt. 2007. Multiscale habitat use by wolverines in British Columbia, Canada. *Journal of Wildlife Management* 71:2180–2192.
- Kukka, P. M., T. S. Jung, J.-F. Robitaille, and F. K. A. Schmiegelow. 2017. Temporal variation in the population characteristics of harvested wolverine (*Gulo gulo*) in northwestern Canada. *Wildlife Research* 44:497–503.
- Lee, J. 2016. Database description, data summary and analysis of the wolverine harvest from Kugluktuk, Umingmaktok and Bathurst Inlet,

- Northwest Territories. Environment and Natural Resources, Government of the Northwest Territories, Yellowknife, Canada.
- Lofroth, E. C., and J. Krebs. 2007. The abundance and distribution of wolverines in British Columbia, Canada. *Journal of Wildlife Management* 71:2159–2169.
- Lofroth, E. C., J. A. Krebs, W. L. Harrower, and D. Lewis. 2007. Food habits of wolverine *Gulo gulo* in montane ecosystems of British Columbia, Canada. *Wildlife Biology* 13(suppl):31–37.
- Lofroth, E. C., and P. K. Ott. 2007. Assessment of the sustainability of wolverine harvest in British Columbia, Canada. *Journal of Wildlife Management* 71:2193–2200.
- MacKillop, D. J., and A. J. Ehman. 2016. A field guide to site classification and identification for southeast British Columbia: the south-central Columbia Mountains. Province of British Columbia, Victoria, Canada.
- Magoun, A. 1985. Population characteristics, ecology, and management of wolverines in northwestern Alaska. Dissertation, University of Alaska, Fairbanks, USA.
- Magoun, A. J., and J. P. Copeland. 1998. Characteristics of wolverine reproductive den sites. *Journal of Wildlife Management* 62:1313–1320.
- Magoun, A. J., M. D. Robards, M. L. Packila, and T. W. Glass. 2017. Detecting snow at the den-site scale in wolverine denning habitat. *Wildlife Society Bulletin* 41:381–387.
- Mattisson, J., G. R. Rauset, J. Odden, H. Andren, J. D. C. Linnell, and J. Persson. 2016. Predation or scavenging? Prey body condition influences decision-making in a facultative predator, the wolverine. *Ecosphere* 7: e01407.
- May, R., L. Gorini, J. van Dijk, H. Brøseth, J. D. C. Linnell, and A. Landa. 2012. Habitat characteristics associated with wolverine den sites in Norwegian multiple-use landscapes. *Journal of Zoology* 287:195–204.
- Mowat, G., D. C. Heard, and C. J. Schwarz. 2013. Predicting grizzly bear density in western North America. *PLoS ONE* 8:e82757.
- Mulders, R. L. 2000. Wolverine ecology, distribution, and productivity in the Slave Geological Province. Final Report. West Kitikmeot/Slave Study Society, Yellowknife, Canada.
- 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.
- Paetkau, D. 2003. An empirical exploration of data quality in DNA-based population inventories. *Molecular Ecology* 12:1375–1387.
- Persson, J. 2005. Female wolverine (*Gulo gulo*) reproduction: reproductive costs and winter food availability. *Canadian Journal of Zoology* 83:1453–1459.
- Persson, J., G. Ericsson, and P. Segerstrom. 2009. Human caused mortality in the endangered Scandinavian wolverine population. *Biological Conservation* 142:325–331.
- Persson, J., A. Landa, R. Andersen, and P. Segerstrom. 2006. Reproductive characteristics of female wolverines (*Gulo gulo*) in Scandinavia. *Journal of Mammalogy* 87:75–79.
- Poole, K. G. 2006. A population review of mountain goats in the Kootenay Region. British Columbia Ministry of Environment, Nelson, Canada.
- Pulliaainen, E. 1968. Breeding biology of the wolverine (*Gulo gulo* L.) in Finland. *Annales Zoologici Fennici* 5:338–344.
- R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rauset, G. R., M. Low, and J. Persson. 2015. Reproductive patterns result from age-related sensitivity to resources and reproductive costs in a mammalian carnivore. *Ecology* 96:3153–3164.
- Royle, J. A., R. B. Chandler, R. Sollmann, and B. Gardner. 2013. Spatial capture-recapture. Academic Press, Waltham, Massachusetts, USA.
- Royle, J. A., A. J. Magoun, B. Gardner, P. Valkenburg, and R. E. Lowell. 2011. Density estimation in a wolverine population using spatial capture-recapture models. *Journal of Wildlife Management* 75:604–611.
- Ruggiero, L. F., K. S. McKelvey, K. B. Aubry, J. P. Copeland, D. H. Pletscher, and I. G. Hornocker. 2007. Wolverine conservation and management. *Journal of Wildlife Management* 71:2145–2146.
- Sæther, B.-E., S. Engen, J. Persson, H. Broseth, A. Landa, and T. Willebrand. 2005. Management strategies for the wolverine in Scandinavia. *Journal of Wildlife Management* 69:1001–1014.
- Sawaya, M., A. 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.
- Schwartz, M. K., J. P. Copeland, N. J. Anderson, J. R. Squires, R. M. Inman, K. S. McKelvey, K. L. Pilgrim, L. P. Waits, and S. A. Cushman. 2009. Wolverine gene flow across a narrow climatic niche. *Ecology* 90:3222–3232.
- Slough, B. G., R. H. Jessup, D. I. McKay, and A. B. Stephenson. 1987. Wild furbearer management in western and northern Canada. Pages 1062–1976 in M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, editors. Wild furbearer management and conservation in North America. Ontario Trappers Association, North Bay, Canada.
- Smallwood, K. S., and C. Schonewald. 1998. Study design and interpretation of mammalian carnivore density estimates. *Oecologia* 113:474–491.
- Squires, J. R., J. Copeland, T. J. Ulizio, I. K. Schnvartz, and L. F. Ruggiero. 2007. Sources and patterns of wolverine mortality in western Montana. *Journal of Wildlife Management* 71:2213–2220.
- 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.
- Vangen, K. M., J. Persson, A. Landa, R. Andersen, and P. Segerström. 2001. Characteristics of dispersal in wolverines. *Canadian Journal of Zoology* 79:1641–1649.
- Webb, S. M., R. B. Anderson, D. L. Manzer, B. Abercrombie, B. Bildson, M. A. Scraftford, and M. S. Boyce. 2016. Distribution of female wolverines relative to snow cover, Alberta, Canada. *Journal of Wildlife Management* 80:1461–1470.
- Webb, S. M., D. Manzer, R. Anderson, M. Jokinen, and S. Park. 2013. Wolverine harvest summary from registered traplines in Alberta, 1985–2011. Technical Report. Alberta Conservation Association, Sherwood Park, Canada.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.