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ARTICLE

Low wolverine (*Gulo gulo*) density in a national park complex of the Canadian Rocky Mountains

M. Barrueto, M.A. Sawaya, and A.P. Clevenger

Abstract: Large carnivores are sensitive to human-caused extirpation due to large home ranges, low population densities, and low reproductive rates. Protected areas help maintain populations by acting as sources, but human-caused mortality, habitat displacement, and edge effects occurring at protected area boundaries may reduce that function. The national parks Banff, Yoho, and Kootenay in the Canadian Rocky Mountains are refugia for large carnivores, including wolverines (*Gulo gulo* (Linnaeus, 1758)). Despite growing conservation concern, empirical baseline population data for wolverines remain scarce throughout their range, including most of Canada. We hypothesized (*i*) that in these national parks, wolverine density matched values expected for high-quality habitat, and (*ii*) that edge effects decreased density towards park boundaries. We conducted systematic non-invasive genetic sampling surveys covering >7000 km² (2011 and 2013). Using spatial capture–recapture models, we estimated mean (±SE) female (1.5 ± 0.3 and 1.4 ± 0.3 wolverine/1000 km²), male (1.8 ± 0.4 and 1.5 ± 0.3 wolverine/1000 km²), and combined (3.3 ± 0.5 and 3.0 ± 0.4 wolverine/1000 km²) densities for 2011 and 2013, respectively. These estimates were lower than predictions based on density extrapolation from nearby high-quality habitat, and density decreased towards park boundaries. To benefit the population, we recommend creating buffer zones around parks that protect female habitat and prohibit harvest.

Key words: wolverine, *Gulo gulo*, density, spatial capture–recapture, apparent survival, edge effect, protected area, non-invasive genetic sampling.

Résumé : Les grands carnivores sont vulnérables à la disparition locale causée par l'humain en raison de leurs grands domaines vitaux et leurs faibles densités de population et taux de reproduction. Les aires protégées aident à maintenir leurs populations en servant de sources, mais la mortalité causée par les humains, le déplacement d'habitats et les effets de bordure aux limites des aires protégées peuvent compromettre cette fonction. Les parcs nationaux de Banff, Yoho et Kootenay, dans les Rocheuses canadiennes, servent de refuges pour de grands carnivores, dont le carcajou (*Gulo gulo* (Linnaeus, 1758)). Bien que la conservation de cette espèce soit de plus en plus préoccupante, les données démographiques empiriques de référence demeurent rares pour toute son aire de répartition, dont la majeure partie du Canada. Nous avons postulé que (*i*) dans ces parcs nationaux, la densité de carcajous correspond aux valeurs attendues pour des habitats de haute qualité et que (*ii*) des effets de bordure réduisent cette densité à l'approche des limites des parcs. Nous avons réalisé des relevés systématiques d'échantillonnage génétique non invasif couvrant >7000 km² (2011 et 2013). En utilisant des modèles spatiaux de capture–recapture, nous avons estimé les densités moyennes (±ET) de femelles (1,5 ± 0,3 et 1,4 ± 0,3 carcajou/1000 km²), de mâles (1,8 ± 0,4 et 1,5 ± 0,3 carcajou/1000 km²) et des femelles et mâles combinés (3,3 ± 0,5 et 3,0 ± 0,4 carcajou/1000 km²) pour 2011 et 2013, respectivement. Ces estimations sont plus faibles que les prédictions basées sur l'extrapolation de la densité observée dans des habitats de haute qualité avoisinants, et les densités diminuent à l'approche des limites des parcs. Pour soutenir la population, nous recommandons de créer des zones tampons autour des parcs qui protègent les habitats des femelles et où les prises sont interdites. [Traduit par la Rédaction]

Mots-clés : carcajou, *Gulo gulo*, densité, modèle de capture–recapture spatial, survie apparente, effet de bordure, aire protégée, échantillonnage génétique non invasif.

Introduction

Large carnivores are sensitive to human-caused extirpation and extinction due to their large home ranges, low population densities, and low reproductive rates (Weaver et al. 1996). Protected areas play an important role in maintaining sustainable populations (Doak 1995; Noss et al. 1999); however, human-caused mortality, habitat displacement, and edge effects occurring within and on the edges of protected areas may affect their efficacy (Woodroffe and Ginsberg 1998; Clevenger et al. 2001; Hebblewhite et al. 2003). Species with individual home ranges that are large compared with protected area size are particularly vulnerable, as

individuals may be forced to live partially outside the protected areas, exposing them to those impacts the park was intended to protect them against. For example, North American parks may not adequately protect focal species (Newmark 1987; Grumbine 1990; Gurd and Nudds 1999). Monitoring species of concern is essential to ensure their persistence. Yet, population estimates for large carnivores can be difficult to obtain, and thus, even baseline data are often lacking (Garshelis 1992; Karanth 1995; Boulanger et al. 2004; Obbard et al. 2010).

Wolverines (*Gulo gulo* (Linnaeus, 1758)) are large terrestrial mustelids with a circumboreal distribution. In Canada, they are harvested in much of their range and are of conservation priority

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due to habitat loss and concerns about harvest sustainability (COSEWIC 2014; BCCDC 2017; SARA 2018). In the contiguous United States, wolverines are recovering from a range contraction post-European contact, but considerable conservation concerns remain (Aubry et al. 2007; Idaho Department of Fish and Game 2014). Despite their large home ranges, adult wolverines are territorial, which leads to low adult densities even in high-quality habitat (Inman et al. 2012). Finally, a strong association with persistent spring snow cover (PSSC) across much but not all of their range suggests that wolverines may be susceptible to impacts from climate change (Aubry et al. 2007; Brodie and Post 2010; Copeland et al. 2010; Webb et al. 2016). Because of this, the geographic extent and connectivity of suitable wolverine habitat in western North America is forecasted to decline (McKelvey et al. 2011). Yet, despite these concerns about current and future population sustainability, information on wolverine population density in southern Canada is available for only two study areas (Lofroth and Krebs 2007; Fisher et al. 2013). Our study, taking place in the Canadian Rocky Mountains, was conducted to help fill this gap.

The three national parks Banff (BNP), Yoho (YNP), and Kootenay (KNP) in the Canadian Rocky Mountains form a contiguous national parks complex (NPC), comprising over 9000 km². They delineate the northern end of the trans-border region, which is a corridor for wolverine movement between Canada and the United States (Schwartz et al. 2009), and the most likely long-term prospect for trans-boundary habitat connectivity (Copeland et al. 2010). Owing to their low reproductive rates and the largely additive effects of human-caused mortality, harvested wolverine populations are often unsustainable without immigration from source populations (Krebs et al. 2004; Lofroth and Ott 2007; Dalerum et al. 2008) and require large refugia without harvest (Vangen et al. 2001; Flagstad et al. 2004). The NPC serves as a refugium for many of the region's large carnivores (Weaver et al. 1996; Landry et al. 2001). However, little is known about the status of its wolverine population (Suitor 2005).

Our study is the first to estimate wolverine population density within the NPC and had two main objectives. First, we tested the hypothesis that density was consistent with predictions of 6.2 individuals/1000 km², values indicative of high-quality wolverine habitat (Lofroth and Krebs 2007), analyzing data from two years of non-invasive genetic sampling within an open population spatial capture–recapture (SCR) model (Royle et al. 2014). Second, we tested the hypothesis that trapping at the edges of the park boundaries resulted in an edge effect within the protected area with lower densities towards park boundaries, and we examined if PSSC impacted wolverine density positively. We further compared density estimates of one- and two-year models to test if the additional year of sampling positively impacted the precision of the density estimate.

Materials and methods

Study area

The study area was in the Canadian Rocky Mountains (51°18′N, 116°12′W), encompassed approximately 7000 km², and included parts of BNP, YNP, and KNP. The climate in all three parks is continental and characterized by relatively long winters and short summers, with decreasing snowfall from west to east (Holland and Coen 1983; Achuff et al. 1984). Uniquely for national parks in North America, BNP and YNP are bisected by a busy transportation corridor consisting of the Trans-Canada Highway (TCH) and a railroad, the Canadian Pacific Railway (CPR) mainline (Fig. 1). Roads can be a barrier to large-mammal movements and can im-

pact gene flow and genetic population structure (Epps et al. 2005; Proctor et al. 2012).

The study area was centred on three large river valleys. The Bow River Valley within BNP is situated within the front and main ranges of the Canadian Rocky Mountains. Its topography is steep and mountainous, with elevations from 1300 to 3400 m and a valley floor width from 2 to 5 km. Vegetation in the Bow River Valley encompasses montane, subalpine, and alpine ecoregions. Montane habitats are found in low-elevation valley bottoms. The lower Bow Valley is a human-dominated landscape with the TCH, the Banff town site (>10 000 residents), a golf course, three ski areas, CPR, and a secondary highway. The Kicking Horse River is the main east–west aligned watershed in neighboring YNP and is paralleled by the TCH and CPR. It is situated on the west side of the Continental Divide and is characterized by steep rugged terrain with narrow valleys. Differing from the Bow Valley, the Kicking Horse Valley is sparsely populated, with Field (300 residents) as the only town site within YNP. The Vermilion and Kootenay river valleys in KNP are also situated on the west side of the Continental Divide. Major ecosystems here include montane, subalpine, and alpine, with the montane ecosystem occurring at the lowest elevations and primarily valley bottoms. KNP was bisected by a road from its inception as a protected area. Highway 93 S, a two-lane road, follows along the valley bottom and parallels the two major rivers (i.e., Vermilion and Kootenay rivers). We did not quantitatively assess wolverine prey availability and assumed that wolverine prey species such as hoary marmots (*Marmota caligata* (Eschscholtz, 1829)), porcupine (*Erethizon dorsatum* (Linnaeus, 1758)), elk (*Cervus canadensis* (Erxleben, 1777)), white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)), mule deer (*Odocoileus hemionus* (Rafinesque, 1817)), moose (*Alces americanus* (Clinton, 1822)), Rocky Mountain bighorn sheep (*Ovis canadensis* Shaw, 1804), and mountain goats (*Oreamnos americanus* (Blainville, 1816)) were abundant and available throughout the study area (Lofroth et al. 2007; Steenweg et al. 2016).

Hair sampling

The sampling area was delineated by a 30 km buffer around the TCH from Castle Junction (BNP) to the west boundary of YNP. We used non-invasive genetic sampling combined with camera traps (Reconyx, Holmen, Wisconsin, USA), adapting methods used in past wolverine research that have been shown to be reliable as long as detection probability is accounted for (Fisher et al. 2013; Fisher and Bradbury 2014). Our sampling design was based on minimum female home-range sizes (Banci 1994; Krebs et al. 2007). The survey area was divided into 12 km × 12 km grid cells with one to two sampling site per cell, centred around 51°18.3′N, 116°12.24′W (Fig. 1). To maximize detection probability, sampling sites were preferentially placed in mid-elevation drainages. Study duration was three years, with two sampling seasons: the first in winter 2011 (number of sampling stations was $n = 48$) and the second in winter 2013 ($n = 51$). We established and monitored 43 sites within protected areas in 2011. We re-sampled these and established an additional three sites in 2013. Additionally, in 2011 and in 2013, we established and sampled five sites each within grid cells located outside of park boundaries (Fig. 1). In 2011, sampling locations were, on average, 8.19 km (standard deviation (SD) = 2.87 km) apart, with a range of 1.94–15.46 km. In 2013, mean distance between nearest neighbouring sites was 7.36 km (SD = 2.78 km), with a range of 1.94–14.34 km. Mean sampling site elevation was 1690 m (SD = 304 m), with a range of 1101–2314 m. The scaled locations of all sampling sites are provided in Supplementary Table S1[1].

Non-invasive sampling consisted of hair traps baited with a whole skinned beaver (*Castor canadensis* Kuhl, 1820) carcass nailed

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[1]Supplementary tables and text are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2019-0165.

Fig. 1. Map of sampling sites for a multi-year DNA-based wolverine (*Gulo gulo*) survey in the Canadian Rocky Mountains. The 30 km buffer used in single-year models is outlined by the black dashes ("State Space secr" in the legend, where secr is spatially explicit capture–recapture model). The 30 km state space used in the two-year model is outlined by the light purple box online (grey box in print; "State Space mcmc" in the legend, where mcmc is Markov chain Monte Carlo method). Sources for the base map include Esri, HERE, DeLorme, USGS, Intermap, INCREMENT P, NRCan, Esri Japan, METI, Esri China (Hong Kong), Esri Korea, Esri (Thailand), MapmyIndia, NGCC, © OpenStreetMap contributors, and the GIS User Community. This map contains information licensed under the Open Government Licence – British Columbia (https://www2.gov.bc.ca/gov/content/data/open-data/open-government-licence-bc) and the Open Government Licence – Alberta (https://open.alberta.ca/licence) and was created in ArcGIS version 10.5.1 (Esri, Redlands, California, USA). Colour version online.
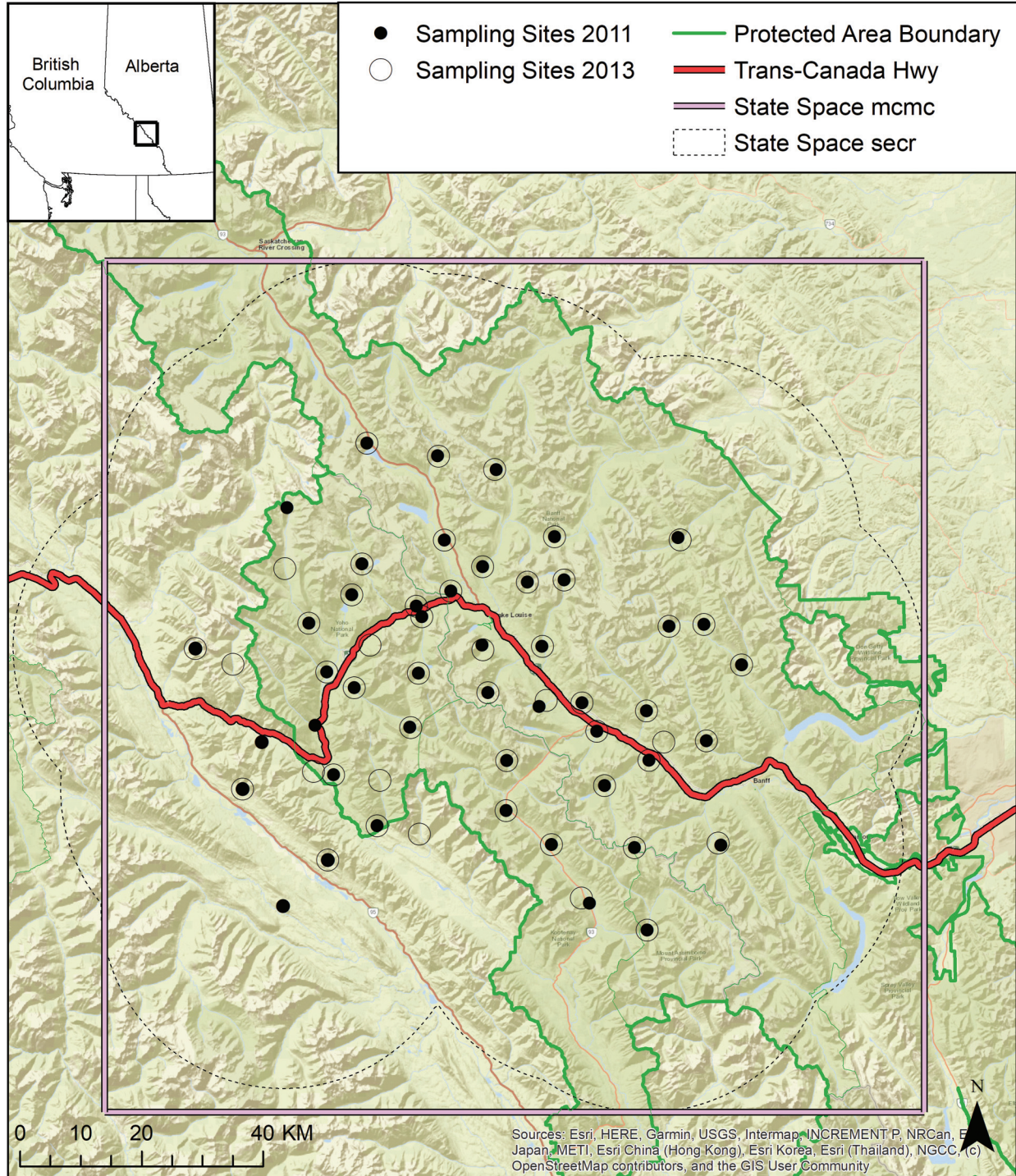
to a tree and secured with baling wire (Fisher et al. 2013). Beaver carcasses were obtained from local trappers in Alberta (Canada) and British Columbia (Canada) and were by-products from pest control programs or the fur trapping trade. Barbed wire was wrapped from the carcass to ca. 1 m above ground level. Sites were set up in mid-December and revisited three times at monthly intervals to rebait, collect hair samples, and service cameras. Wolverine scats found at sampling sites during monthly visits were

placed in paper bags and air-dried. Hair samples were stored at room temperature on silica desiccant. All applicable research permits were obtained from the British Columbia provincial (Wildlife Act/Collection permits CB10-68024, CB11-75845, and CB12-84303; Park Use permits 105280 and 105895) and from federal national park authorities (Parks Canada Agency Research and Collection Permit LL-2010-5652). No additional animal care or ethics committee review was required because no wildlife was handled or physically constrained during the study.

Genetic analysis

We conducted genetic analyses on hair and scat samples at the USDA Forest Service Conservation Genetics Laboratory (now known as USDA Forest Service National Genomics Center for Wildlife and Fish Conservation; Missoula, Montana, USA). The laboratory uses protocols for DNA extraction and microsatellite analysis of non-invasive genetic samples (McKelvey and Schwartz 2005; Schwartz et al. 2006). Owing to financial constraints, we were not able to sample every hair sample collected, but we subsampled hair samples using a targeted approach based on available funds. To maximize individual identifications with subsampling, we used camera data to identify sites with ≥1 wolverine and determined the number of hair samples to analyze per site based on the number of wolverines and visits. We categorized hair samples by the number of hairs available. We chose the samples with the most hairs for first attempts at obtaining a genotype. If the initial hair sample selected from each site/session failed, then we attempted to extract DNA from several additional samples from the same site/session (if available) until we obtained positive wolverine genotype(s) or exhausted the samples. For that reason, the number of detections may vary for some individuals, as an unequal number of samples were often analyzed for a given site/session.

Genotyping errors, such as allelic dropout or false alleles, are associated with low-quantity DNA samples from hairs, scats, or other forensic or non-invasive genetic sampling. We used at least two independent approaches to catch and remove these errors. First, DNA from hair samples were run and analyzed at least two times at each microsatellite locus (Taberlet et al. 1996). Allele scores were kept if there was concordance between runs and samples that failed or were inconsistent were culled from the data set. The data set was screened using the program DROPOUT (McKelvey and Schwartz 2005), following the protocol outlined in Schwartz et al. (2006), the program MICRO-CHECKER (Van Oosterhout et al. 2004), and deviations due to Hardy–Weinberg proportions. We tested genotypes from the samples using 15 microsatellite loci used by Schwartz et al. (2009). We evaluated the genotype data by using the "Examining Bimodality" and "Difference In Capture History" tests in DROPOUT (McKelvey and Schwartz 2005). As an extra precaution, final consensus genotypes were also checked for genotyping errors at Wildlife Genetics International (Nelson, British Columbia, Canada), using the methods of Paetkau (2003).

Spatial covariates

To assess edge effects on density, we calculated Euclidean distance in kilometres from the borders of the NPC to each 1000 m × 1000 m pixel centre in the study area. Inside the parks, values were positive and increasing away from park boundaries, whereas outside the parks, the values were set to zero. We bisected the study area along the TCH into a northern part and a southern part to compare density. Snowfall within the study area varies along a west–east gradient and with elevation. To test for a density effect of snow cover, we calculated long-term PSSC as the number of years between 2003 and 2012 that a pixel (500 m × 500 m) was covered in snow between 24 April to 15 May, based on a composite of Moderate Resolution Imaging Spectroradiometer (MODIS) classified satellite images (Copeland et al. 2010). The R package "secr" (Efford 2018), which we used to test for density effects, uses the

covariate value at putative activity centres to estimate the relationship between density and habitat covariates. To approximate the overall home-range characteristic with regards to the covariates, we used a moving window analysis with a 10 km radius to re-scale the two covariates distance to park boundary and spring snow cover. Ten kilometres is approximately the female home-range radius in late winter. To assess if snow cover impacted detection probability of wolverines, we developed a site-specific covariate snow by calculating mean PSSC for a 10 km buffer around each sampling site (Heim et al. 2017). Shrub cover was used as a proxy for avalanche paths and similar preferred wolverine habitat (Heim et al. 2017). To incorporate its impact on detection probability at individual sampling sites, mean percent shrub cover within a 10 km buffer around each site was quantified from a 16-class landcover data set based on LandSat imagery and a digital elevation model (McDermid et al. 2009).

Statistical analysis

Non-invasive molecular techniques have been applied extensively to estimate density of wide-ranging carnivores (Boulanger et al. 2004; Mulders et al. 2007; Kéry et al. 2011; Royle et al. 2014). We used the framework of SCR models, which explicitly incorporate spatial heterogeneity in individual distribution, trap location, and detection probability, and relax the assumption of a geographically closed population (Borchers and Efford 2008; Royle and Young 2008). We assumed demographic closure within each season, as sampling targeted adults and subadults and took place before young of the year left their maternal dens (Royle et al. 2011). In protected areas, adult wolverine year-to-year survival is usually high (Krebs et al. 2004). Spatial Jolly–Seber type open models are an extension of SCR models used where between-year demographic closure assumptions are violated, as was the case for our two-year data (Gardner et al. 2010). They track individual detections over time to estimate demographic parameters such as apparent survival, per-capita recruitment, and population growth rates, and can account for temporal overlap of individuals between years, typical of territorial and relatively long-lived species, but also accommodate shifts in home-range centres between years (Gardner et al. 2010; Whittington and Sawaya 2015). Wolverines use caches, repeatedly visiting sites where food has been stored or encountered previously (Banci 1994). Wolverines often revisit baited camera stations, even once no food remains. Ignoring this behavioural response, termed trap-happiness, can lead to negative bias in density estimates because encounter probability might be overestimated (Royle et al. 2011; Augustine et al. 2014). We included trap-happiness of wolverines in the form of a local trap response (LTR), which is referred to as model M_b (i.e., behavioural response) in classical capture–recapture. It is defined as a trap-, occasion-, and individual-specific variable that changes from 0 to 1 after the first visit by an individual of a specific trap (Royle et al. 2011). All spatial analyses were conducted using ArcMap version 10.5.1. All statistical analyses were conducted using R version 3.6.1. (R Core Team 2019). For open population models, we used the R package "runjags" version 2.0.4-2 (Denwood 2013) to run JAGS version 4.2.0 (Plummer 2003). For the closed SCR models, we used the R package "secr" version 3.2.1 (Efford 2018).

Using both years of data for density estimation, we estimated apparent survival, defined as true survival minus emigration; estimating apparent survival was a valuable opportunity because wolverine vital rates are not well understood (Krebs et al. 2004; Squires et al. 2007). We fitted a two-year open SCR model to the 2011 and 2013 data (not including data from the five sampling stations outside the park boundaries sampled in 2011), using Bayesian Markov chain Monte Carlo (MCMC) methods with data augmentation (Gardner et al. 2010; Whittington and Sawaya 2015). We augmented the population of detected animals by 180 individuals. Individuals (i) could be detected at any of the traps (j) during each of $k = 3$ occasions in both years (t). Probability of detection p_{ijkt} was

modelled as $(y_{ijkt}|z_{it}) \sim$ Bernoulli$(p_{ijk}z_{it})$, using a bivariate (half)normal detection function with $p_{ijkt} = p_0 \cdot \exp(-\alpha_1 d_{ijt}^2)$, where $d_{ijt} = \|x_{jt} - s_{it}\|$ was the distance between trap x_{jt} and activity centre s_{it} and $\alpha_1 = 1/2\sigma_{sex}^2$. The baseline encounter probability p_0 was dependent on an LTR, percent PSSC, percent shrub cover, a linear trend across occasion and sampling year, with respective parameters β_0, β_{LTR}, β_{snow}, β_{shrub}, β_{occ}, and β_{year}. The activity centres (s_{it}) were independent between years (independent movement model), drawn from a uniform distribution across the state space during each year (Royle et al. 2014). Constant movement models where activity centre locations for individuals are the same in both years, and correlated (Markovian) movement models where between-year movements are restricted, can under some circumstances be preferable to independent movement models (Gardner et al. 2018). Whereas most adult wolverines display territoriality and high home-range fidelity through time (Aronsson and Persson 2018), the population that we sampled also included subadult individuals that would be likely to disperse from their natal area between our two sampling seasons (Vangen et al. 2001). We did not use constant or correlated movement models to allow for such long-distance dispersal movements. The state space was defined as a buffer around a rectangle encompassing all trap locations (Fig. 1). To examine potential bias in survival and density estimates depending on the chosen buffer size, we compared results of models with a buffer of approximately 4σ (30 km) and 5σ (40 km) (Gardner et al. 2018).

The observation model was conditional on the latent state variable $z_{i,t}$, which defined an individual i as either alive ($z_{i,t} = 1$) or dead ($z_{i,t} = 0$) at time t, during each iteration of the MCMC sampling process. ψ was the probability that an animal was alive in year $t = 1$, with $z_{i,t=1} \sim$ Bernoulli(ρ). We assigned sex to individuals using the latent covariate sex$_i \sim$ Bernoulli(ψ_{sex}), with sex$_i = 1$ for females. Our data were collected in the winters of 2011 ($t = 1$) and 2013 ($t = 2$), thus sex-specific apparent survival Φ_{sex} and sex-specific recruitment probability γ_{sex} described these processes across a two-year period. Φ_{sex} was the sex-specific probability that an individual i alive at time $t = 1$ was alive at time $t = 2$. Individuals that were not alive at time $t = 1$ were recruited into the population at time $t = 2$ with a sex-specific probability γ_{sex} and $z_{i,t} \sim$ Bernoulli$(\Phi_{sex}z_{i,t} + \gamma_{sex}z_{i,t+1})$. The per-capita recruitment R_{sex} was the number of recruited individuals at time $t = 2$ divided by the number of individuals alive at time $t = 1$. To enable comparison with previously published estimates of yearly survival, we calculated the square roots of the means of our two-year estimates for Φ_{sex}. An approximate 95% home range (HR) was calculated from the scale parameter σ as HR $= \pi \cdot (\sigma \cdot \sqrt{5.99})^2$ (Sun et al. 2014).

Priors for all parameters were non-informative. We used diffuse normal priors with a mean of 0 and a variance of 10^4 for the parameters β_0, β_{LTR}, β_{snow}, β_{shrub}, β_{occ}, and β_{year}. Priors for the probability parameters ρ, ψ_{sex}, γ_{sex}, and Φ_{sex} were Uniform(0, 1). The prior for the scale parameter σ_{sex} was Uniform(0, 50). The priors for the scaled activity centre coordinates were Uniform(–3, 10.5181) for the east–west coordinates and Uniform(–3, 11.0073) for the north–south coordinates. We ran the model with three chains, a burn-in period of 20 000 iterations, and a sample of 20 000 iterations and a thinning rate of five to reduce autocorrelation. We visually inspected trace plots and considered values of Gelman–Rubin convergence diagnostics of <1.1 as evidence for chain convergence (Gelman and Rubin 1992). Bayesian p values were used to assess the goodness of fit of the model by comparing the summed observed and predicted Freeman–Tukey residuals (Gelman et al. 1996; Royle et al. 2014). We calculated Bayesian p values as Pr($T_{observed} > T_{simulated}$). Values <0.05 and >0.95 indicate lack of model fit. Because adult male wolverines usually have larger home ranges than females (Krebs et al. 2007; Persson et al. 2010; Inman et al. 2012), the home-range parameter σ_{sex} was sex-specific. Apparent survival Φ_{sex} was also sex-specific. The baseline

encounter probability p_0 in wolverines is likely sex-specific. Models including this effect did not converge and we proceeded to use one p_0 for males and females combined. R code for the two-year model is provided in Supplementary Text S1[1].

To test for edge effects and impacts of spring snow cover on density, as well as to test if density differed between areas south and north of the TCH, we fitted inhomogeneous density models to the 2011 data collected at all sampled stations, including five stations located outside park boundaries (Fig. 1), using likelihood-based models and the R package "secr" (Borchers and Efford 2008). To avoid pseudo-replication, we did not also fit these density models to the 2013 data because the two years were not independent; 11 of 34 individuals were detected in both years. Adding density covariates to the open population SCR models used for density estimation would allow the use of both years of data, but it was not feasible for us because the open population models already had days-long run times, which were expected to increase even further if density covariates were added. We added sampling effort as the number of trap-nights for each of the three sampling occasions, which is implemented in secr as the "usage" attribute of a "traps" object (Borchers and Efford 2008; Efford 2018). An LTR covariate for encounter probability was included in all models but the null model. We fit models including different combinations of density covariates (distance to park boundary, PSSC, and north or south of highway) and detection probability covariates (PSSC, session (session as linear time and as factor), site elevation), which were selected based on results from wolverine occupancy analyses (Heim et al. 2017; Kortello et al. 2019). We then conducted an overall comparison between the set of candidate models using Akaike's information criterion corrected for small sample size (AIC$_c$) (Anderson and Burnham 2004).

Results

A total of 2563 hair samples were collected from hair traps during 2011 and 2013. Not all samples were from wolverine, as hairs from lynx (*Lynx canadensis* Kerr, 1792), American marten (*Martes americana* (Turton, 1806)), American red squirrel (*Tamiasciurus hudsonicus* (Erxleben, 1777)), and northern flying squirrel (*Glaucomys sabrinus* (Shaw, 1801)) were also collected. Following our subsampling protocols, we attempted to extract DNA from 635 samples; 220 (34%) were successfully genotyped for wolverine. We identified 34 individual wolverines, 15 females and 19 males, for a total of 152 detections (Fig. 2, Table 1). Of the individuals identified in 2011 (Fig. 2), 7 of 11 females and 4 of 12 males were recaptured in 2013. Mean number of detections per individual was similar for both sexes in the first year and increased in the second year (Table 1). Mean number of trap sites that individuals were detected at increased between 2011 and 2013 (Table 1). Most (85.3%) individuals were detected >1 time (Table 1). Across both years, only one female was detected only once (6.67%), compared with four males (21.05%). The female with the most detections had eight confirmed visits at five different trap sites. The male with the most detections was confirmed 13 times at eight different trap sites. Four males and four females were detected on both sides of the TCH, while the other 26 individuals were detected on one side only. Encounter histories of all individuals are provided in Supplementary Table S2[1].

Using an open population homogeneous density model that included an LTR, as well as encounter probability covariates for occasion, year, shrub cover, and PSSC, we estimated density for both years (2011 and 2013) for the overall population for females only and for males only (Table 2, Fig. 3). First, increasing buffer size from 30 to 40 km did not result in any differences in female survival (0% change); male survival increased by 6%. Density decreased by 2% for both years when the larger buffer was used. The following estimates are from the model with a 30 km buffer. The home-range parameter σ was smaller for females at 7.96 ± 0.54 km

Fig. 2. Map of detected individuals (2011 sampling season) of a DNA-based wolverine (*Gulo gulo*) survey in the Canadian Rocky Mountains. Over three occasions, 23 individuals were detected 63 times total. The numbers (1 to 3) on colour-coded circles represent the number of individuals detected at each sampling station, pooled over occasions. Sampling stations without wolverine detections are marked by plus signs (+). Protected area boundaries are outlined by the thin line, whereas the Trans-Canada Highway is outlined by the thick line. This map contains data from the current study and information licensed under the Open Government Licence – British Columbia (https://www2.gov.bc.ca/gov/content/data/open-data/open-government-licence-bc) and the Open Government Licence – Alberta (https://open.alberta.ca/licence). The map was created in R version 3.6.1 (R Core Team 2019), using the R package "secr" version 3.2.1 (Efford 2018). Colour version online.
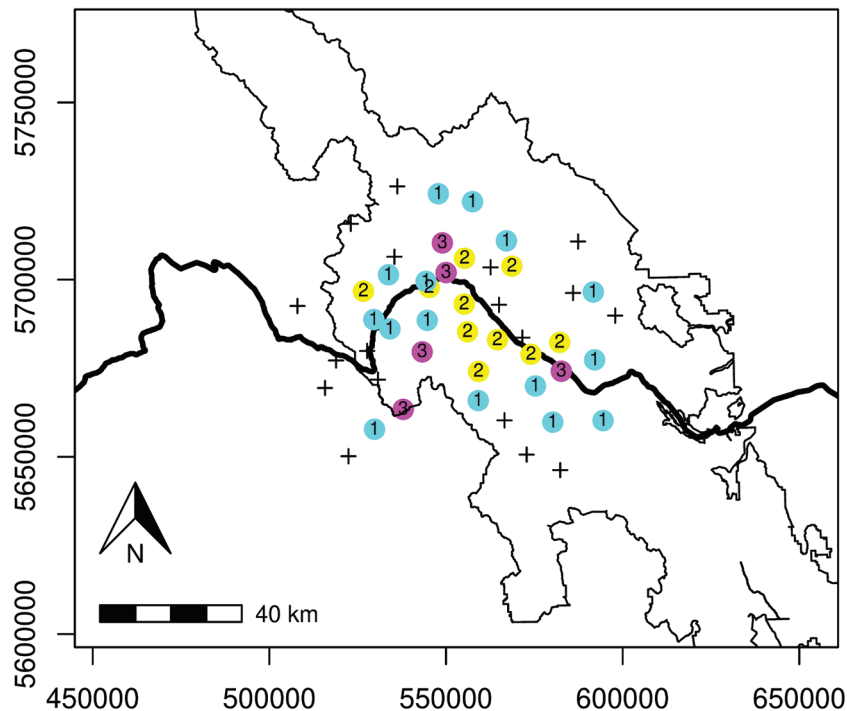

Table 1. Detection results for a multi-year DNA-based wolverine (*Gulo gulo*) survey conducted in 2011 and 2013 in the Canadian Rocky Mountains.

	2011		2013	
	Females	Males	Females	Males
No. of individuals detected	11	12	11	11
No. of new individuals detected per year	11	12	4	7
Mean no. of detections per individual	2.64	2.75	3.64	4.55
Mean no. of sites an individual was detected at	2.09	2.17	2.45	3.18
Percentage of individuals with >1 detection	72.73	66.67	100	90.91

(mean ± SE) than for males at 8.74 ± 0.60 km (Table 2). Approximate 95% HR for females was 1192 km² (95% credible interval = 922–1558 km²) and for males was 1437 km² (95% credible interval = 1110–1893 km²). Mean (±SE) female two-year apparent survival Φ_{female} (0.81 ± 0.14) was higher than the male two-year apparent survival Φ_{male} (0.65 ± 0.19). Mean (±SE) two-year female growth rate λ_{female} was 0.93 ± 0.30 and mean (±SE) two-year male growth rate λ_{male} was 1.05 ± 0.26. The observed (naïve) proportion of females was 0.44, and the mean (±SE) estimated proportion of females was 0.40 ± 0.31. There was a strong positive LTR, and encounter probability was higher at trap sites with high PSSC (Table 2). Encounter probability was not substantially impacted by the percentage of shrub cover around trap locations by year or by sampling occasion (Table 2). A Bayesian *p* value of 0.66 indicated good model fit.

Using a homogeneous density model with an LTR, but no other covariates, and only data from 2011, the mean (±SE) combined density was 3.74 ± 0.91 individuals/1000 km² (95% confidence interval = 2.33–5.99 individuals/1000 km²), the mean (±SE) female density was 1.85 ± 0.66 individuals/1000 km² (95% confidence interval = 0.94–3.66 individuals/1000 km²), and the mean (±SE) male

density was 1.88 ± 0.65 individuals/1000 km² (95% confidence interval = 0.97–3.64 individuals/1000 km²) (Fig. 3). Detection probability for individuals when the sampling station was located at the centre of the home range (g_0) was 0.004 ± 0.001 (mean ± SE) for their first detection at a station and was 0.018 ± 0.005 at stations where they had already been detected previously (second and further visits). For females, these detection probabilities were 0.003 ± 0.001 and 0.019 ± 0.008 (mean ± SE), respectively; for males, these detection probabilities were 0.004 ± 0.001 and 0.017 ± 0.007, respectively. The best-supported model for 2011 was an inhomogeneous density model with a density covariate for distance to park boundaries that positively impacted density and an LTR that positively impacted encounter probability (Table 3). All other models had little support from the data (Table 3). We also reported the effect sizes of the individual density and encounter probability covariates, estimated separately for each covariate by fitting a model that only included an LTR and the respective covariate (Table 4).

Discussion

Our study provides the first empirical estimates of wolverine density in the NPC of the Canadian Rocky Mountains, one of the

Table 2. Parameter estimates for a Bayesian open population two-year spatial capture–recapture model for a multi-year DNA-based wolverine (*Gulo gulo*) survey in the Canadian Rocky Mountains.

Parameter	Mean	SD	0.025% CI	Median	0.975% CI
D_{2011}	3.30	0.51	2.43	3.27	4.44
D_{2013}	2.95	0.44	2.17	2.91	3.91
$D_{2011,female}$	1.51	0.33	1.00	1.48	2.22
$D_{2013,female}$	1.42	0.29	0.95	1.37	2.06
$D_{2011,male}$	1.79	0.39	1.16	1.74	2.64
$D_{2013,male}$	1.53	0.34	0.95	1.48	2.27
Φ_{female}	0.81	0.14	0.48	0.84	0.99
Φ_{male}	0.65	0.19	0.28	0.66	0.97
σ_{female}	7.96	0.54	7.00	7.93	9.10
σ_{male}	8.74	0.60	7.68	8.70	10.03
γ_{female}	0.21	0.26	0.00	0.07	0.90
γ_{male}	0.15	0.22	0.00	0.05	0.85
λ_{female}	0.93	0.30	0.42	0.91	1.61
λ_{male}	1.05	0.26	0.60	1.02	1.66
ψ_{sex}	0.40	0.31	0.08	0.24	0.89
α_0	−1.77	0.34	−2.43	−1.77	−1.13
β_{TRL}	2.31	0.36	1.65	2.30	3.02
β_{occ}	−0.20	0.13	−0.46	−0.20	0.05
β_{snow}	0.30	0.13	0.05	0.30	0.56
β_{shrub}	0.25	0.13	−0.10	0.25	0.51
β_{year}	0.39	0.26	−0.11	0.39	0.92

Note: Density (D; individuals/1000 km²) was calculated by year for both sexes combined, females, and males. The parameters for two-year survival (Φ_{sex}), scale parameter (σ_{sex}), recruitment parameter (γ_{sex}), two-year growth rate (λ_{sex}), sex ratio (ψ_{sex}), baseline encounter probability (α_0), local trap response (β_{TRL}), trend over time (β_{occ}), snow cover (β_{snow}), shrub cover (β_{shrub}), year effect (β_{year}) did not differ by year. CI is credible interval.

largest contiguous protected areas in southern Canada and an important refugium for large carnivores (Weaver et al. 1996). Mean densities were low compared with previous studies within the wider region (Table 4) (Lofroth and Krebs 2007; Fisher et al. 2013), and lower densities towards park boundaries suggested the presence of an edge effect. As expected for a protected area (Krebs et al. 2004), apparent survival was high and greater for females than males, potentially reflecting an underlying pattern or greater dispersal distances for subadult males. We had hypothesized that wolverine population density in the mountain parks would match a value of 6.2 individuals/1000 km², which is the predicted mean density for high-quality habitats in British Columbia (Lofroth and Krebs 2007). According to those ratings of habitat quality, which relied on ecosystem and wolverine food mapping, on wolverine distribution models and on human development, our study area should consist of high-quality wolverine habitat (Weaver et al. 1996; Suitor 2005; Lofroth and Krebs 2007). Our mean density estimates of 3.3 and 2.95 individuals/1000 km² for 2011 and 2013, respectively, were significantly lower and fell into the range of density values predicted for low- to medium-quality habitat (Fig. 4) (Lofroth and Krebs 2007). Canadian national and many provincial parks do not allow trapping or hunting or other resource extraction, but human presence may incur other costs to wildlife that decreases overall habitat quality and ultimately population densities of sensitive species (Macbeth et al. 2010; Barber et al. 2011; Gaynor et al. 2018; Heinemeyer et al. 2019). Human presence in the NPC varies in intensity and can be high in some areas (Rogala et al. 2011; Steenweg et al. 2016), but in the 2007 models, human disturbance was characterized only by road density, which is low in most protected areas. Other factors not included in the 2007 habitat-quality ratings, such as abundance of competitors or predators, could also impact wolverine density or limit their reproductive output (Durant 1998). Additionally, the two study areas used in the 2007 model calibrations were both small (<4500 km²) and at the time contained substantial numbers of caribou (*Rangifer tarandus* (Linnaeus, 1758)), a key winter food

source for wolverines (Banci 1994; Lofroth et al. 2007). In contrast, our study area historically contained low numbers of caribou that have been absent since 2009, perhaps limiting wolverine abundance despite the availability of other ungulates. Alternatively, although a tempting conceptual idea due to its simplicity, wolverine density and habitat quality may not be directly related, a contention which has long been a focus of ecologists (Van Horne 1983; Weber et al. 2017; Dallas and Hastings 2018). Our results highlight the value that empirical data bring to wildlife management because it tests the accuracy of expert opinion and extrapolation based on limited data, as well as also show that much remains to be learned about wolverine populations and abundance even in protected areas.

Wolverines exhibit intrasexual territoriality, but recent offspring are tolerated by adult, territorial individuals, limiting the maximum number of individuals within any specific area (Inman et al. 2012). High densities can result from a combination of smaller female home ranges, a presence of multiple offspring in parental territories, and limited dispersal opportunities due to geographic barriers (Royle et al. 2011). The low densities that we encountered coupled with large female home-range estimates suggest that the space required for a female to successfully reproduce may be comparatively large in our study area, be it due to low resource availability, high competition, or high predation pressures (Durant 1998). The approximate home range for females (1192 km²) was of similar size as that for males (1437 km²). This pattern was surprising because telemetry studies have established that resident adult female wolverines occupy significantly smaller home ranges than males (Krebs et al. 2007; Persson et al. 2009). However, subadult wolverines of both sexes can undertake large pre-dispersal and dispersal movements (Vangen et al. 2001). The DNA-based methods that we used did not distinguish between age classes; it is likely that subadult wolverines made up a considerable proportion of individuals detected in our sample, in which case our home-range estimates might not solely reflect those of established territorial adults. We caution that wolverine population parameters derived from SCR models should not be equated to those established by telemetry and live-trapping studies without first considering study area size, study duration, and the demographic information available for the detected individuals.

Open population SCR models can be sensitive to specification of the state space and the between-years movement models (Gardner et al. 2018). We used independent activity centres in our two-year model, meaning that individuals could change location of their activity centres between 2011 and 2013, reflecting wolverine biology which includes long-distance dispersal. The minor effects on density and survival following an increase in state space indicated that for our data set, an independent movement model was appropriate. For females, we did not find that the model was sensitive to state-space size; however, for males, there was an increase in survival depending on state-space size (Gardner et al. 2018). This was not unexpected, as telemetry-derived home ranges of male wolverines are large and can surpass 2000 km² (Krebs et al. 2007; Heinemeyer et al. 2019). Despite our sampling area being larger than many previous wolverine study areas, it may not have been large enough to detect large pre-dispersal or dispersal movements of juvenile males, which may bias the male home-range parameter σ low and male density high. Mean male density was indeed higher than mean female density in both years, albeit not significantly so. Non-invasive studies intent on estimating male home-range size and survival would either require even larger study areas or benefit from inclusion of telemetry-derived prior information (Sollmann et al. 2013; Linden et al. 2018).

Apparent two-year survival in our study was higher for females than for males, but 95% credible intervals overlapped. Yearly apparent survival calculated as the square root of the two-year estimates were 0.90 for females and 0.81 for males, values that are consistent with published estimates of true survival in non-

Fig. 3. Wolverine (*Gulo gulo*) density (individuals/1000 km²) for 2011 and 2013 estimated by spatial capture–recapture models for a multi-year DNA-based wolverine survey in the Canadian Rocky Mountains. Bars show the 95% confidence intervals of density estimates for the single-year model (2011 – single-year model) and 95% credible intervals for the two-year model (2011 – two-year model and 2013 – two-year model) for the combined sexes, females, and males, respectively.
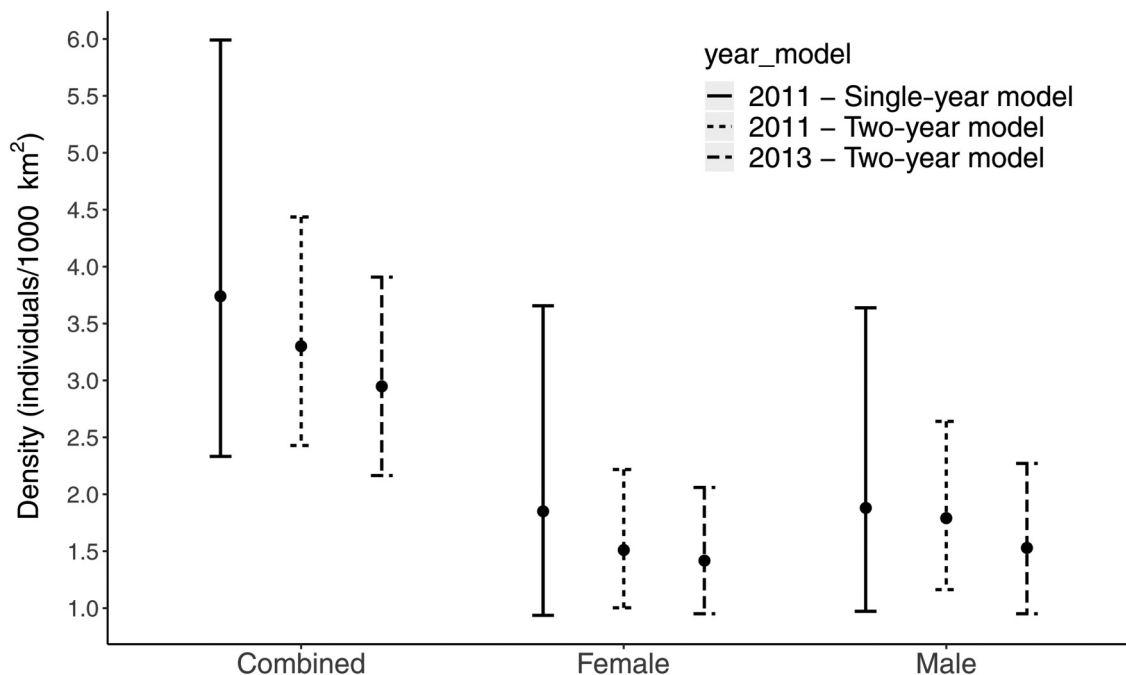

Table 3. Comparison of single-year homogeneous and inhomogeneous spatial capture–recapture models (2011 data) for a DNA-based wolverine (*Gulo gulo*) survey in the Canadian Rocky Mountains.

Model	D	p_0	No. of parameters	Log likelihood	AIC_c	ΔAIC_c	AIC_c weight
1	$D \sim distpark$	$p_0 \sim LTR$	5	−213.81	441.16	0.00	0.59
2	$D \sim 1$	$p_0 \sim LTR$	4	−217.14	444.50	3.34	0.11
3	$D \sim distpark$	$p_0 \sim LTR + t$	7	−211.72	444.92	3.76	0.09
4	$D \sim 1$	$p_0 \sim LTR + PSSC\_site$	5	−216.14	445.80	4.64	0.06
5	$D \sim PSSC$	$p_0 \sim LTR$	5	−216.79	447.10	5.94	0.03
6	$D \sim 1$	$p_0 \sim LTR + shrub$	5	−216.81	447.16	6.00	0.03
7	$D \sim 1$	$p_0 \sim LTR + t$	6	−215.06	447.36	6.20	0.03
8	$D \sim 1$	$p_0 \sim LTR + elev$	5	−216.92	447.38	6.22	0.03
9	$D \sim 1$	$p_0 \sim LTR + T$	5	−217.13	447.79	6.63	0.02
10	$D \sim northsouth$	$p_0 \sim LTR$	5	−217.14	447.81	6.65	0.02
11	$D \sim 1$	$p_0 \sim 1$	3	−225.08	457.43	16.27	0.00

Note: The top model included a density covariate (*D*) for distance to park boundary in kilometres (distpark) with areas outside of parks set to zero and a local trap response (LTR) for encounter probability (p_0). Northsouth had two values and referred to the areas north or south of the Trans-Canada Highway. PSSC is the persistent spring snow cover covariate. PSSC_site is the site-specific persistent spring snow cover covariate for a 10 km buffer surrounding a sampling site. Shrub is the percent shrub cover for a 10 km buffer surrounding a sampling site. Elev is the site-specific elevation in kilometres above sea level. *T* is a continuous time covariate (e.g., does encounter probability increase from occasion 1 to occasion 3), whereas *t* is a factorial time covariate for each occasion, not assuming a trend over time. AIC$_c$ is Akaike's information criterion corrected for small sample size.

harvested populations (Krebs et al. 2004; Persson et al. 2009). Our study area is surrounded by harvested areas, and some emigration out of the study area was expected to occur over the two years of study. Better knowledge of the demographic make-up of a wolverine study population may enable estimates of the respective contributions of true survival and emigration and development of more realistic multi-year models. Mean two-year growth rates λ, measured for full years rather than pre-breeding to pre-dispersal (Runge et al. 2006), were close to 1.0 for both males and females, but had very wide confidence intervals, precluding us from making conclusions as to the trajectory of the study population. The number of surplus individuals dispersing per year, which determines a population's ability to act as a source population contributing individuals to surrounding areas, is a function of reproductive rates, survival,

and population size. Thus, even in a scenario where yearly growth rates were as high or higher than the rates determined elsewhere (Krebs et al. 2004; Persson 2005; Persson et al. 2015), the number of hypothetical surplus individuals in our study area would be low because of the low female density.

Wolverine density was higher towards the centres of the protected area. Based on the vulnerability of wolverines to human-caused mortality and the exposure to trapping near the outer boundaries of the NPC, an edge effect due to increased trapping mortality is a possible explanation for the observed pattern (Krebs et al. 2004). Human landscape disturbance negatively affects wolverine habitat occupancy outside of protected areas to the immediate east and south of our study area, and in the southern Columbia Mountains (Heim et al. 2017; Kortello et al. 2019). Al-

Table 4. Coefficient estimates (2011 data) for variables describing spatial capture–recapture models for a DNA-based wolverine (*Gulo gulo*) survey in the Canadian Rocky Mountains.

Covariate	Variable	Coefficient	SE	Confidence interval	
				Lower	Upper
D	Distpark (continuous)	0.07	0.03	0.02	0.12
D	Northsouth (<u>north</u> or south)	0.02	0.54	−1.04	1.07
D	PSSC (continuous)	0.07	0.09	−0.10	0.24
p_0	LTR (<u>initial visit</u> or all further visits)	1.64	0.38	0.89	2.39
p_0	PSSC_site (continuous)	0.10	0.07	−0.04	0.23
p_0	Elev (continuous)	0.31	0.47	−0.61	1.22
p_0	t_{occ2} (<u>1st occasion</u> or 2nd occasion)	0.53	0.33	−0.11	1.17
p_0	t_{occ3} (<u>1st occasion</u> or 3rd occasion)	−0.01	0.37	−0.73	0.72
p_0	T (continuous)	−0.02	0.17	−0.35	0.31
p_0	Shrub (continuous)	0.07	0.08	−0.09	0.22

Note: Coefficients for density and encounter probability included in the models of Table 3 were estimated using two-covariate models, i.e., the null model plus a local trap response (LTR) plus each respective covariate. D stands for density covariate and p_0 stands for encounter probability covariate. Continuous variables are indicated in parentheses. For factorial variables, the categories are indicated in parentheses, with the baseline category underlined. Distpark is distance to park boundary in kilometres, with areas outside of parks set to zero. Northsouth had two values and referred to the areas north or south of the Trans-Canada Highway. PSSC is the persistent spring snow cover covariate. PSSC_site is the site-specific persistent spring snow cover covariate for a 10 km buffer surrounding a sampling site. Elev is the site-specific elevation in kilometres above sea level. t_{occ2} and t_{occ3} are a time effect with one level for each of the three occasions; the base level here is t_{occ1}. T is a linear (on link scale) trend over occasions. Shrub is the percent shrub cover for a 10 km buffer surrounding a sampling site.

Fig. 4. Wolverine (*Gulo gulo*) density (individuals/1000 km²) estimated for 2011 and 2013 by spatial capture–recapture models for a multi-year DNA-based wolverine survey in the Canadian Rocky Mountains. Bars show the 95% credible intervals of empirical density estimates for our study (2011, 2013) and 95% confidence intervals of previously published predictions for low-quality, medium-quality, and high-quality habitats, respectively (Lofroth and Krebs 2007).
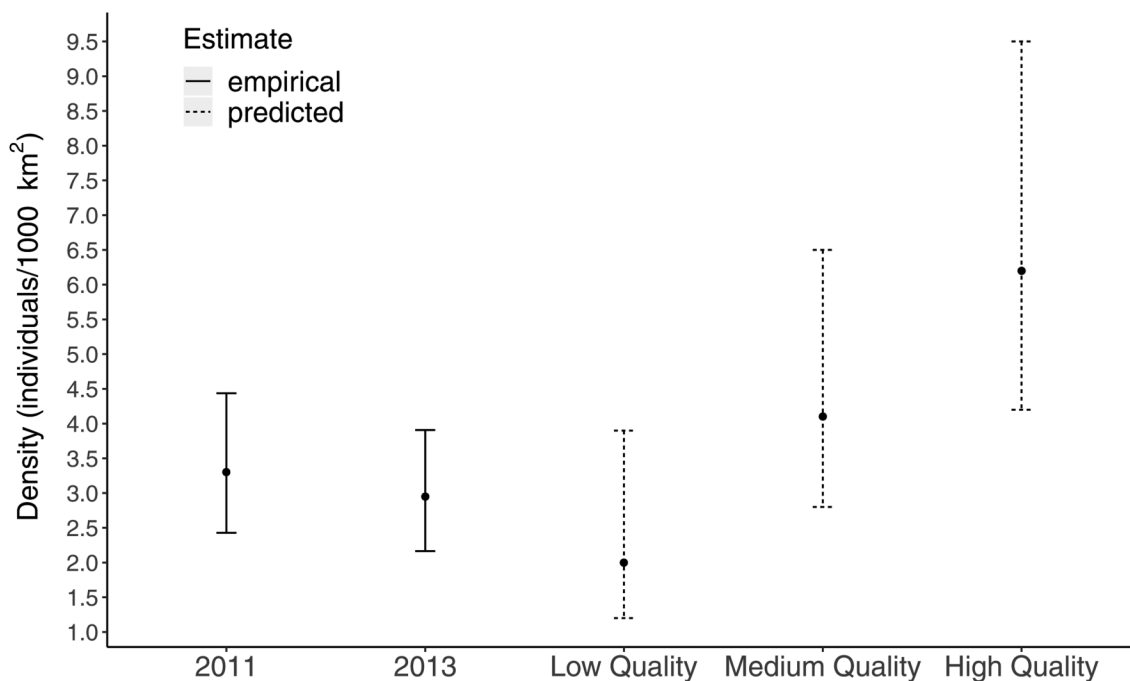
though the low levels of wolverine occupancy of these unprotected areas were mostly driven by anthropogenic changes to the landscape, the processes that mediate these effects may extend into the protected areas, lowering densities towards the edges. The parks that we sampled are small compared with individual wolverine home ranges. Based on our mean density estimates, our entire sampling area (7000 km²) might contain only 22 individual wolverine home-range centres (but more individuals, with home-range centres outside the study area, may be detected at sampling stations); YNP alone (1313 km²) may contain 4 home-range centres and BNP (6641 km²) may contain 21 home-range centres. Even low absolute numbers of additional natural or human-caused mortal-

ity outside park boundaries could thus measurably impact density towards the edges of the parks.

Wolverine distribution worldwide is often associated with PSSC, but the causes for this relationship are not yet fully understood (Aubry et al. 2007; Copeland et al. 2010; Webb et al. 2016; Kortello et al. 2019). In our study, PSSC did not have an impact on density, but did have a positive impact on encounter probability. On a coarse scale, PSSC is present in the majority of our study area except for the lowest valley bottoms and south-facing slopes, and habitat factors such as food availability, predators, or even human activities may have more impact on the distribution of individual wolverine home ranges (Inman et al. 2012). On a finer scale, how-

ever, localized differences in PSSC may result in habitat selection patterns that give rise to uneven encounter probabilities at sampling site locations. Percentage shrub cover surrounding a sampling site did not impact encounter probability, contrasting its positive impact on site occupancy probability in a related analysis that included data from our study area (Heim et al. 2017). Variation of this covariate within our study area may have been too low to result in measurable impacts. The LTR was positive and strong in all models, confirming previous findings that baited traps are successful in attracting wolverines repeatedly (Royle et al. 2011; Fisher et al. 2013). This behaviour has been successfully exploited in other elusive species but raises questions as to how supplemental food may impact survival and reproduction in a multi-year study (Du Preez et al. 2014), as well as how it may impact density. The amount of bait that we used (one beaver carcass per month per station) was substantially lower than the seven adult reindeer carcass equivalents that were provided to individual target females during a food supplementation experiment which concluded that female reproductive rates were affected by food availability (Persson 2005). In addition, at all our sites, American marten usually consumed at least part of the bait. Furthermore, most individuals were detected multiple times, suggesting they were at least temporary residents in the study area. Based on the intrasexual territoriality of adult wolverines and the 30 km buffer that we used in our modeling, we think that it is unlikely that additional individuals from beyond the state space were attracted to bait stations, which would have conflated density. We conclude that the bait provided may have had only minor effects on individual survival and reproduction. Precision for the estimates derived from the open SCR model including two years of data was 45% higher than those derived from single-year models. For additional context, a single-year wolverine data set from a previous study yielded a population density estimate of 9.7 individuals/1000 km^2, with a 95% credible interval of 5.9–15.0 individuals/1000 km^2, nearly five times wider than ours (Royle et al. 2011). We suggest for wolverine surveys that include density estimation, an additional year of sampling the same population may be justified despite the additional financial costs. Multi-year sampling additionally allows estimates of demographic parameters and can capture fluctuations in abundance over time.

Our data were collected within a comparatively large sampling area over three years, and precision of the density estimates was comparatively high (Lofroth and Krebs 2007; Royle et al. 2011). Carnivore density can be positively related to habitat quality (Miquelle et al. 1999; Carbone and Gittleman 2002; Karanth et al. 2004), which, if applicable here, would suggest that the NPC may not contain high-quality wolverine habitat. Yet, density alone can also be a poor proxy for habitat quality and may not be linked directly to reproductive rates, which we did not measure (Van Horne 1983; Pulliam 1988; Furrer and Pasinelli 2016). If a population of adult females was present with consistent reproductive output that exceeds natural mortality, then the NPC could qualify as a source population, despite low overall population density. The large female home ranges indeed suggested that adult and subadult females were detected and thus reproduction was occurring. Yet, the high female apparent survival may be a result of low levels of female dispersal away from the study area, which while consistent with known wolverine behaviour (Vangen et al. 2001; Aronsson and Persson 2018), could be of concern for the harvested areas in the southern Canadian Rocky Mountains and Columbia Mountain ranges. These regions are thought to depend on immigrants from the NPC, including females (Krebs et al. 2004; Lofroth and Ott 2007; Dalerum et al. 2008). In addition, we detected potential signs of an edge effect, with lower density of wolverines closer to park boundaries. Owing to the great spatial requirements of wolverines, most Canadian parks are too small to hold self-sustaining populations (Landry et al. 2001; Fortin et al. 2005). Edge effects effectively decrease the size of a protected area even

further (Woodroffe and Ginsberg 1998). Where regional wolverine population sustainability is a concern, trapping-free buffer zones surrounding protected areas might increase their value as refugia for harvested populations, as would protecting female denning habitat surrounding the parks (Krebs et al. 2004; Golden et al. 2007; Dalerum et al. 2008; Heinemeyer et al. 2019). Management of the wolverine population in the NPC and other protected areas may thus benefit from coordination with surrounding jurisdictions. As an example, wolverines are protected in Sweden but heavily hunted in neighbouring Norway. Compensatory immigration into the hunted population is lowering density near the border within the protected Swedish population and counteracts Norwegian efforts to maintain lower absolute wolverine numbers (Gervasi et al. 2015, 2019).

To maintain and recover wolverine populations in unprotected areas, accurate information on population size, breeding female density, reproductive rates, and levels of female dispersal will be essential. Establishing buffer zones around protected areas that protect female denning habitat and prohibit trapping may increase value of the parks for wolverine conservation by decreasing edge effects on the core protected population. Last, owing to the large home ranges of wolverines and the low abundance that we found even in protected areas, an effective conservation strategy will require large areas managed and monitored at regional and trans-border scales (Krebs et al. 2004; Weaver 2013).

Acknowledgements

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