Canadian Journal of
Zoology

Article

Climatic conditions limit wolverine distribution in the Cascade Range of southwestern North America

Keith B. Aubry[a], **Catherine M. Raley**[a], **Andrew J. Shirk**[b], **Kevin S. McKelvey**[c], **and Jeffrey P. Copeland**[d]

[a]US Forest Service, Pacific Northwest Research Station, 3625 93rd Avenue SW, Olympia, WA 98512, USA; [b]School of the Environment, University of Washington, Climate Impacts Group, P.O. Box 355674, Seattle, WA 98195, USA; [c]US Forest Service, Rocky Mountain Research Station, 800 East Beckwith, Missoula, MT 59801, USA; [d]The Wolverine Foundation, 4444 Packsaddle Road, Tetonia, ID 83452, USA

Corresponding author: **Keith B. Aubry** (email: keith.aubry@usda.gov)

Abstract

Recolonization of the Cascade Range in southern British Columbia, Canada, and Washington, USA, by wolverines (*Gulo gulo* (L., 1758)) is an ongoing process whose ultimate outcome is unknown. A reliable species distribution model for the wolverine in the Cascades (i.e., their first-order habitat selection) is urgently needed to help inform management and conservation strategies. Using Argos location data obtained on 10 resident adult wolverines (six females, four males) from 2008 to 2016, we generated a multi-covariate species distribution model for the wolverine in the Cascades. Our final model included three climatic covariates and their quadratic terms: Proximity to the Transitional Zone Near Alpine Tree Line, Number of Frost-free Days per Year, and Annual Precipitation as Snow. Model validations indicated that our model was robust and could identify areas of potential wolverine distribution in the Cascades reliably. Our model provides evidence that wolverine distribution in the Cascades is constrained by climatic conditions and that snowy and cold environments define the geographic areas that are overwhelmingly associated with resident wolverines. In addition, our model provides a reliable basis for monitoring the direct effects of climate change on wolverines in the Cascade Range and for predicting the extent to which climate change may impact their populations under various scenarios.

Key words: alpine tree line, Argos satellite telemetry, Cascade Range, *Gulo gulo*, habitat selection, species distribution modeling, wolverine

Introduction

Glaciations and ice-age refugia have had a profound influence on the structure of populations, species, and communities in North America (Hewitt 2000), and comparative phylogeographic studies have helped elucidate the evolutionary history of many modern taxa (Arbogast and Kenagy 2001; Shafer et al. 2010). Phylogeographic patterns among contemporary wolverines (*Gulo gulo* (L., 1758)) in North America indicate that all extant populations, including those that currently occupy the northern Cascade Range and Rocky Mountains in the contiguous USA (Aubry et al. 2007), were descended from lineages that had been isolated in the northern ice-free refugium (Beringia) during the last glaciation (Tomasik and Cook 2005; Cegelski et al. 2006). However, fossil evidence (Neomap 2013) and genetic analyses of historical wolverine specimens from the contiguous USA (McKelvey et al. 2014) demonstrate that wolverine populations that once occupied disjunct islands or peninsulas of alpine tundra throughout the Cascade Range, Sierra Nevada, and Rocky Mountains in the western contiguous USA (Aubry et al. 2007) had been isolated in the southern ice-free refugium (the contiguous USA) during the last glaciation. Historically, these southern populations contained genetic characteristics that differed from those of northern wolverines and may therefore have evolved unique adaptations to the high-elevation montane ecosystems they occupied (McKelvey et al. 2014). Thus, prior to the extirpation of wolverines in the contiguous USA during the early to mid-1900s (Aubry et al. 2007), the southern border of western Canada represented a zone of secondary contact or "suture zone" (Remington 1968) between wolverine lineages that had evolved in isolation during the Pleistocene.

Although the northern Rockies in the western USA were recolonized by Canadian wolverines relatively early in the 20th century (Newby and Wright 1955; Newby and McDougal 1964), recolonization of the Cascade Range began much later. Wolverines were detected on multiple occasions in Washington state during the 1960s and 1970s, but those records were from anomalous habitat conditions in low-elevation areas of eastern Washington, indicating that they were dispersers and not representative of self-sustaining populations (Aubry et al. 2007). Verifiable wolverine records (those associated with physical evidence) from high-elevation areas in the Cascade Range did not begin to accumulate until the 1990s[1]. In recent decades, the wolverine has expanded its geographic distribution in the Cascade Range and has now been detected in multiple locations from the northern extent of the Cascades near the Fraser River in southern British Columbia, Canada (this study) south to Mount Adams in southern Washington, USA (J. Akins, Cascades Carnivore Project, personal communication), and they continue to be reported from new locations within the Cascades. Thus, the recolonization of the Cascade Range by wolverines is ongoing, and the ultimate outcome of this natural experiment remains unknown. Resource managers and conservationists do not know whether areas currently unoccupied by wolverines in the Cascades contain suitable habitat conditions that may eventually be colonized, nor if some recent verifiable records represent transient individuals that do not reside in the habitat conditions in which they were detected. It is also unknown whether portions of the Cascade Range contain key connectivity corridors or bottlenecks that may affect gene flow within the Cascades, nor if some areas containing suitable habitat conditions for wolverines are geographically isolated from other such areas.

Wolverines in the Cascade Range represent the southernmost extent of the species' current distribution along the Pacific coast of North America (Aubry et al. 2007), where its distribution is much more constrained in extent than in either the northern portions of the continent or the Rocky Mountains (Wilson 1982; Pasitschniak-Arts and Lariviere 1995; Copeland and Whitman 2003). Moreover, climatic and vegetative conditions in the Cascade Range are subject to maritime influences that do not occur in the Rocky Mountains. The Cascade Range is a relatively isolated, linear mountain chain that is oriented north to south, within which available habitat conditions range from areas of permanent ice and snow near the Cascade crest down in elevation to sea level on the western side and to the treeless Columbia Basin on the eastern side (Franklin and Dyrness 1988). Thus, the occurrence of a resident wolverine population in the Cascade Range[1] provides a unique opportunity to investigate the environmental determinants of the wolverine's geographic distribution (i.e., its first-order habitat selection; Johnson 1980) in montane regions of the western USA and southern Canada (hereinafter, southwestern North America).

Several authors have described the wolverine as a species with relatively broad habitat affinities (e.g., Nowak 1973; Hall 1981; Hash 1987; Hatler et al. 2008). However, recolonization of the western contiguous USA by wolverines from Canada (McKelvey et al. 2014) occurred exclusively within high-elevation montane regions in the Cascade Range and Rocky Mountains that contained relatively large expanses of alpine tundra where environmental conditions are comparable to those that support wolverine populations at northern latitudes (Wilson 1982; Aubry et al. 2007; Slough 2007). These observations indicate that the wolverine is a habitat specialist, and that its geographic distribution is constrained by environmental conditions that are common to arctic, boreal, and alpine regions of the continent. In the tundra and taiga, wolverines occupy landscapes with relatively homogeneous vegetative and physiographic conditions (Slough 2007) where the environmental determinants of their geographic distribution may be difficult to discern. In the more heterogeneous landscapes of southwestern North America, however, we would expect constraints on the wolverine's geographic distribution to be more evident, and the connectivity of their populations to be determined primarily by variation in available habitat conditions (Schwartz et al. 2009).

Copeland et al. (2010) proposed that the wolverine's circumboreal distribution is constrained by their obligate association with persistent spring snow cover for successful reproductive denning, and an upper limit of thermoneutrality. Among nine wolverine telemetry studies conducted in southwestern North America and Scandinavia, the spatial extent of spring snow cover present from 24 April to 15 May delineated by Copeland et al. (2010) encompassed 98% of reproductive dens, 86% of winter locations (December through May), and 95% of summer locations (June through November). Importantly, the latter finding demonstrated that wolverines remained closely associated with the areas delineated by the distribution of spring snow cover even after the snow had melted. Among the seven telemetry studies that were conducted south of 52°N latitude in montane regions of southwestern North America where summer temperatures exceeded 22 °C, 90% of telemetry locations obtained during the summer occurred in areas where the mean maximum August temperature was ≤22 °C (Copeland et al. 2010). These findings were based on large, extensive, and reliable data sets on wolverine occurrence and reproductive dens, and they delineated the wolverine's current distribution throughout the circumboreal region with remarkable accuracy (Copeland et al. 2010).

Inman et al. (2013) developed and validated a predictive model of wolverine distribution in the Greater Yellowstone Ecosystem based on telemetry data obtained during field studies in Wyoming, Idaho, and Montana. They projected their wolverine distribution model throughout the western contiguous USA (see Inman et al. 2013, fig. 2), and compared the geographic extent of the areas they classified as "primary" wolverine habitat to that of Copeland et al.'s (2010) spring snow cover map. Inman et al.'s (2013) model contained four climatic and four non-climatic covariates, whereas Copeland et al.'s (2010) map was derived from a single climatic covariate. Nonetheless, Inman et al. (2013) reported >96% spatial concordance between their model and Copeland et al.'s (2010) snow coverage, indicating the importance of climatic conditions for delineating the spatial extent of both models.

There are long-standing concerns about the conservation status of wolverine populations in the contiguous USA (USFWS 1995, 2013, 2020), Washington state (WDFW 2020), and the province of British Columbia (BCCDC 2021). Several habitat models for the wolverine have been developed or ap-

[1] Aubry, K.B., J. Rohrer, C.M. Raley, and S. Fitkin. 2016. Wolverine distribution and ecology in the North Cascades Ecosystem. Unpublished Final Report, Pacific Northwest Research Station, Olympia, Washington, USA. Available online at http://wolverinefoundation.org/wp-content/uploads/2011/02/NorthCascadesWolverineStudy_Final-Progress-Report2012-2016.pdf [accessed 21 July 2022].

Can. J. Zool. 101: 95–113 (2023) | dx.doi.org/10.1139/cjz-2022-0005

plied in the Cascade Range (Singleton et al. 2002; Rowland et al. 2003; WHCWG 2010; Inman et al. 2013), but those models were based on expert opinion, occurrence records of unknown reliability, or wolverine location data obtained in other regions; consequently, they are of limited value to resource managers. No predictive model of the wolverine's geographic distribution in the Cascade Range has been developed using location data obtained on resident animals. Thus, a reliable and spatially explicit model of the wolverine's geographic distribution in the Cascade Range is urgently needed to help inform future management and conservation strategies. Our objectives in this study were to develop and validate a predictive model of the wolverine's geographic distribution in the Cascade Range of Washington, USA, and British Columbia, Canada, using telemetry data obtained on resident individuals, and compare the structure and composition of our model with other wolverine distribution models developed in southwestern North America.

Materials and methods

Analysis area

The area within which we generated our model (hereinafter, analysis area) was 43 972 km^2 in extent and located in the northern portion of the Cascade Range in southern British Columbia, Canada, and northern Washington, USA (Fig. 1). The northern boundary of our analysis area (50.0°N latitude) was in British Columbia near the southern end of the Fraser River valley, which separates the interior Cascade Range from the Coast Mountains of British Columbia. The southern boundary of our analysis area (47.3°N latitude) was located just north of Snoqualmie Pass in Washington. Federally managed forests and parks account for 73.6% (21 277/28 925 km^2) of the lands in the Washington portion of our analysis area: 54% of all forest and park lands are managed for multiple uses, such as recreation and timber production, and 46% are in protected wilderness. In the British Columbia portion of our analysis area, Provincial parks account for 13% (1963/15 047 km^2) of the total land base: 99% are managed for multiple uses and <1% are protected in ecological reserves.

The terrain in our analysis area consists primarily of high, rugged mountains and glaciated peaks, with elevations that range from 305 to 1500–2100 m along much of the Cascade crest, where some peaks reach 2748–3285 m in elevation. The west side of the Cascade crest has a maritime climate characterized by relatively dry, cool summers and wet, mild winters. East of the Cascade crest, dry continental conditions predominate; compared to the west side, annual precipitation is less, summers are warmer, and winters are colder. Consequently, climatic conditions are highly variable in the northern Cascade Range, depending on both location (west vs. east side of the crest) and elevation (see Wiken et al. 2011; WRCC 2021). Maximum snow depth is typically attained by mid-March and varies from 3 to 8 m in upper elevation areas, where snow typically remains on the ground until June or July on both sides of the Cascade crest. Subalpine forests on both sides of the crest include Engelmann spruce (*Picea engelmannii* Parry), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), and lodgepole pine (*Pinus contorta* Dougl.; Wiken et al. 2011). At lower elevations, forests are composed primarily of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western redcedar (*Thuja plicata* Donn.), and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) on the west side of the crest, and ponderosa pine (*Pinus ponderosa* Dougl.) and Douglas-fir on the east side.

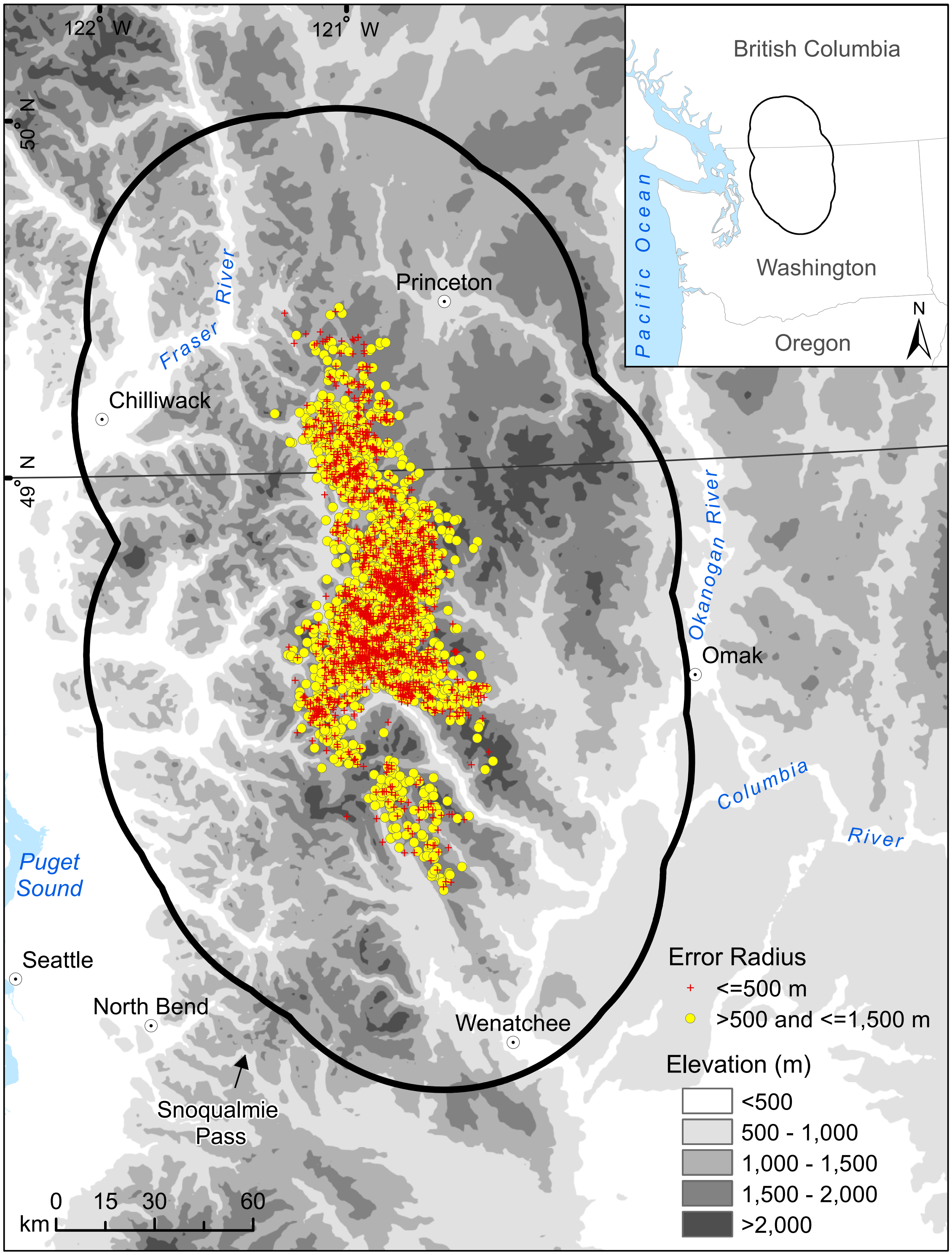
Capture and monitoring of wolverines

Each winter from 2007/2008 to 2014/2015, we operated live traps designed to capture wolverines (Copeland et al. 1995; Lofroth et al. 2008). Typically, we initiated trapping efforts in January and continued until mid-March or early April, when snow melt prevented us from accessing trap sites on snowmobiles. We built traps in situ in areas where wolverine occurrences had been documented previously and located them within about 150 m of snowmobile routes to ensure reliable access during the winter. We baited traps with parts of mule deer (*Odocoileus hemionus* (Rafinesque, 1817)), North American beaver (*Castor canadensis* Kuhl, 1820), or salmon (*Oncorhynchus* spp. Suckley, 1861) carcasses, and monitored them daily via trap-site transmitters (VHF or satellite) that indicated whether the trap lid had closed. We visited all traps twice per week to ensure they were functioning properly. We identified captured animals to species based on information presented in Kays and Wilson (2009); biological samples obtained from wolverines during our study were deposited in the Burke Museum of Natural History and Culture in Seattle, Washington.

In Washington, we immobilized captured wolverines by injecting a mixture of ketamine hydrochloride (8 mg/kg) and medetomidine hydrochloride (0.3 mg/kg) via jab stick; once processing of the study animal was completed, we injected atipamezole hydrochloride (0.2 mg/kg) to reverse the effects of the medetomidine. British Columbia field crews injected a mixture of equal parts tiletamine hydrochloride and zolazepam hydrochloride (10 mg/kg) to immobilize captured wolverines. We outfitted each study animal with a Sirtrack KiwiSat 101 or 303 telemetry collar containing both an Argos satellite transmitter and a standard VHF transmitter; the former to obtain location data and the latter to locate the dens of reproductive females or collars that were no longer moving, which indicated either a sloughed collar or wolverine mortality. The procedures we used to live-trap, handle, and collar wolverines were approved by the Washington State Department of Fish and Wildlife under a series of annual Scientific Collecting Permits, and complied with guidelines published by the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2011).

Based on the average mass of females (8.9 kg) and males (13.1 kg) captured during our study (seven females, seven males), the KiwiSat 101 collar represented about 2.4% and 1.6% of female and male body masses, respectively. During the final 2 years of our study, we outfitted two males with KiwiSat 303 collars, which were lighter (160 vs. 210 g) and had a longer battery life. During a pilot study conducted from 2006 to 2008, we experimented with different duty cycles and found that most of the higher quality Argos lo-

Fig. 1. Map of the Cascade Range in northern Washington, USA, and southern British Columbia, Canada, depicting the wolverine (*Gulo gulo*) telemetry locations (red crosses and yellow circles) we used to delineate our analysis area (heavy black line) by creating a 60 km buffer around these locations. Yellow circles represent Argos locations with error radii >500 m and ≤1500 m. The radius of the yellow circles is approximately 1500 m, which represents the maximum error radius of the wolverine locations we used to delineate our analysis area. Red crosses represent wolverine locations with error radii ≤500 m, which was the maximum error of the locations we used to model wolverine distribution. Map produced in ArcGIS Desktop 10.7.1 software by Esri (2022) using Esri provided boundary, water, and elevation layers. Map projection: WGS_1984_UTM_Zone_10 N. Geographic coordinate system: GCS_WGS_1984.



cations (those with an estimated spatial error of ≤1500 m) were acquired between the hours of 0600 and 1800 PST. Because there were no apparent differences in the areas used by wolverines during diurnal and nocturnal hours, we programmed our satellite transmitters to operate for 14 consecutive hours between 0500 and 1900 PST every other day (i.e., 14 h on, 34 h off), enabling us to monitor wolverines for up to 8 (KiwiSat 101) or 15 (KiwiSat 303) months. To account for unusual behaviors that may have resulted from capture and processing, we excluded locations obtained <24 h after releasing each collared wolverine from all data analyses.

Argos satellite telemetry data

Argos estimates an error radius and an error ellipse for each location, and then assigns it to a location class based on the estimated error radius and the number of messages received from the transmitter (Argos User's Manual 2016). Bolis (2013) investigated sources of error for Argos satellite locations obtained in our study area using collars that were the same model, configuration, and duty cycle as those we attached to wolverines, and concluded that the error radius was a more reliable predictor of spatial error than the error ellipse. Consequently, to account for the inherent spatial error of Argos telemetry data, we converted each wolverine location to a circular area based on its error radius to create our wolverine use polygons. We filtered our Argos data by excluding all locations with error radii of >1500 m, as well as all locations that were based on fewer than three messages, regardless of their associated error radius (Supplementary Table S1).

For each study animal, we used ArcMap to evaluate the locations obtained during each 14 h on-cycle to determine if straight-line distances moved between sequential locations were plausible. Based on several detections of known individuals at different camera stations during the same day, the greatest movement rate we documented was 3.8 km/h. If the distance between sequential locations exceeded this movement rate by a factor of 2 or more, the locations were flagged and further evaluated to determine if one of the locations was unreliable and should be removed. Typically, the location with the larger error estimate was removed. This filtering process resulted in 3601 Argos telemetry locations obtained on 10 resident wolverines (six females, four males) from 2008 to 2016. On average, there were three locations per study animal during each 14 h duty cycle, with a mean time and Euclidean distance between successive locations of 3.2 h and 3.7 km. Accordingly, we considered successive locations obtained during each 14 h sampling period to be independent and suitable for use in modeling the wolverine's first-order habitat selection.

Modeling wolverine distribution in the Cascade Range

Use and availability data

Because this is a first-order analysis, we estimated the geographic area that was available to our study animals by measuring the distance between the two farthest locations (based on the above screening) obtained on each wolverine during a given monitoring year. The mean maximum distance moved among our study animals was 59.8 km (females: 51.5 km; males: 68.1 km). Accordingly, to delineate the area within which to sample available locations for modeling the wolverine's first-order habitat selection (i.e., our analysis area), we buffered our final data set of wolverine locations by 60 km (Fig. 1).

To create a data set for randomly sampling environmental conditions available to wolverines within our analysis area, and for comparability with our wolverine use polygons, we generated circles of varying radii that replicated the distribution of spatial errors in our use data set to create our availability polygons. We then conducted exploratory analyses to determine if the varying accuracy of our wolverine locations affected the predictive power of environmental covariates to distinguish between used and available locations. The area under the receiver operator curve (AUC; Hanley and McNeil 1982) increased as the spatial error of wolverine use polygons decreased, and the overall mean difference between use and availability increased as the spatial error of the use polygons decreased (Supplementary Table S2). Consequently, we only used wolverine telemetry locations with spatial errors ≤500 m (n = 1404) to generate resource selection functions. Although this decreased our sample size by almost 40%, both the spatial pattern of these locations (Fig. 1) and the proportion of locations contributed by each wolverine were comparable to those in the full data set. We obtained our final data set of 1404 wolverine locations ($\bar{X}$ = 140, range = 29 to 358 per study animal) throughout the year, but our sample sizes during the months of November, December, and January were relatively sparse (<50 locations). Following Hebblewhite and Merrill (2008), we randomly selected availability locations at a density of 1 per km^2 (n = 43 988). Exploratory analyses on one of our snow covariates showed that increases in sampling density did not change the mean of our sample, indicating that we were sampling the full range of variation in our analysis area (see Northrup et al. 2013). We buffered each availability location with an error radius drawn randomly from the distribution of error radii in our final use data set ($\bar{X}$ = 342.8 m, SD = 92.0 m).

Environmental covariates

To avoid the arbitrary selection of covariates, we identified environmental covariates to include in our modeling based on a literature review of studies that investigated environmental constraints on the wolverine's geographic distribution (i.e., their first-order habitat selection) in southwestern North America. Because animals may select different habitat components at different orders of selection (Mayor et al. 2009) and mixing selection orders can weaken resulting models (Meyer and Thuiller 2006), we did not include covariates in our modeling that were only reported to be important to wolverines at higher orders of selection (e.g., selection of home ranges within areas of occupancy (second order) or selection of habitat components within home ranges (third order); Johnson 1980). We identified nine studies that either modeled first-order habitat selection by wolverines based on statistical comparisons of used vs. available locations, or that were sufficiently lengthy and intensive to generate plausible hypotheses about the environmental factors that may constrain the wolverine's distribution. In addition, we included covariates that were not evaluated in previous studies if we had reason to think they could be useful for predicting wolverine distribution in the Cascade Range. Covariates that were either included in published distribution models or identified by the authors as being important to wolverines at the first order of selection were limited to five major habitat categories: climate, topography, human disturbance, food, and land cover (Table 1).

We excluded covariates from consideration in our modeling that represented features or environmental conditions that did not occur in our study area (e.g., industrial linear features; Heim et al. 2017), which lacked a clear and compelling relation to wolverine distribution (e.g., proximity to streams; Copeland et al. 2007), which required ecological data that were unavailable in our study area (e.g., avoidance of coyotes (*Canis latrans* Say, 1823) and red foxes (*Vulpes vulpes* (L., 1758)); Heim et al. 2017), or that represented conditions that were so prevalent in our study area that they were unlikely to constrain the distribution of wolverines (e.g., protected areas; Kortello et al. 2019). Although elevation and latitude-adjusted elevation were reported as significant predictors in two studies (Copeland et al. 2007 and Inman et al. 2013, respectively), we did not include elevation in our modeling because we do not consider it to be a primary driver of the wolverine's distribution. Rather, we contend that in montane regions, elevation is correlated with many of the environmental resources that are thought to limit wolverine distribution in southwestern North America (e.g., late-spring snow cover, cool summer temperatures, terrain ruggedness). We used Google Earth Engine (GEE; Gorelick et al. 2017) to produce all covariates from input data that we obtained from the GEE data catalogue, unless noted otherwise below.

Climatic covariates

Copeland et al.'s (2010) late-spring snow coverage simply tallied the number of years out of seven (2000–2006) during which each MODIS (Moderate Resolution Imaging Spectroradiometer) pixel was classified as snow from 24 April to 15 May. We reasoned, however, that a continuous snow-cover index would be more likely to reveal important relations with our wolverine occurrence data than a categorical one. Accordingly, we created an Improved Late-spring Snow Cover Index using Normalized Difference Snow Index (NDSI) values from version 6 of the MODIS Terra Snow Cover Daily L3 Global 500 m gridded data set (Hall et al. 2016) from 24 April to 15 May averaged across the 11-year period (2007–2017) that encompassed the years of our wolverine telemetry study (2008–2016). We used the "NDSI_Snow_Cover_Basic_QA" bitmask included with the MODIS snow cover imagery to remove clouds and other artifacts, keeping only the highest quality pixels in each image.

We evaluated a late-spring snow depth covariate (Snow Depth on 1 May), which is near the mid-point of the date range used by Copeland et al. (2010), using the 1 km resolution Snow Data Assimilation System (SNODAS) snow depth product (NOHRSC 2004) for the same 11-year period we used to evaluate late-spring snow cover (2007–2017). We also included a 30-year normal (1981–2010) mean Annual Precipitation as Snow covariate, generated using ClimateNA ver. 6.21 (Wang et al. 2016).

We included two covariates that estimated the distance to areas of relatively deep spring snowfall. We derived the first covariate by calculating the distance to the nearest pixel that had a snow depth of ≥1 m on 1 May according to the mean SNODAS snow depth value averaged across the 11-year analysis period (Distance to Snow >1 m Deep on 1 May–SNODAS). In addition, we generated an alternative version of this covariate by calculating the distance to the nearest pixel in which annual precipitation as snow was ≥500 mm (Distance to Snow >1 m Deep on May 1–PAS), which corresponds to a snow depth ≥1 m on 1 May, based on a regression between SNODAS snow depth and precipitation as snow (not shown). We also included four climatic covariates that reflect exposure to high temperatures based on mean values for 30-yr normal ClimateNA data from 1981 to 2010: Degree Days >18 °C, 30-year Maximum Annual Temperature, Mean Warmest Month Temperature, and Number of Frost-free Days per Year.

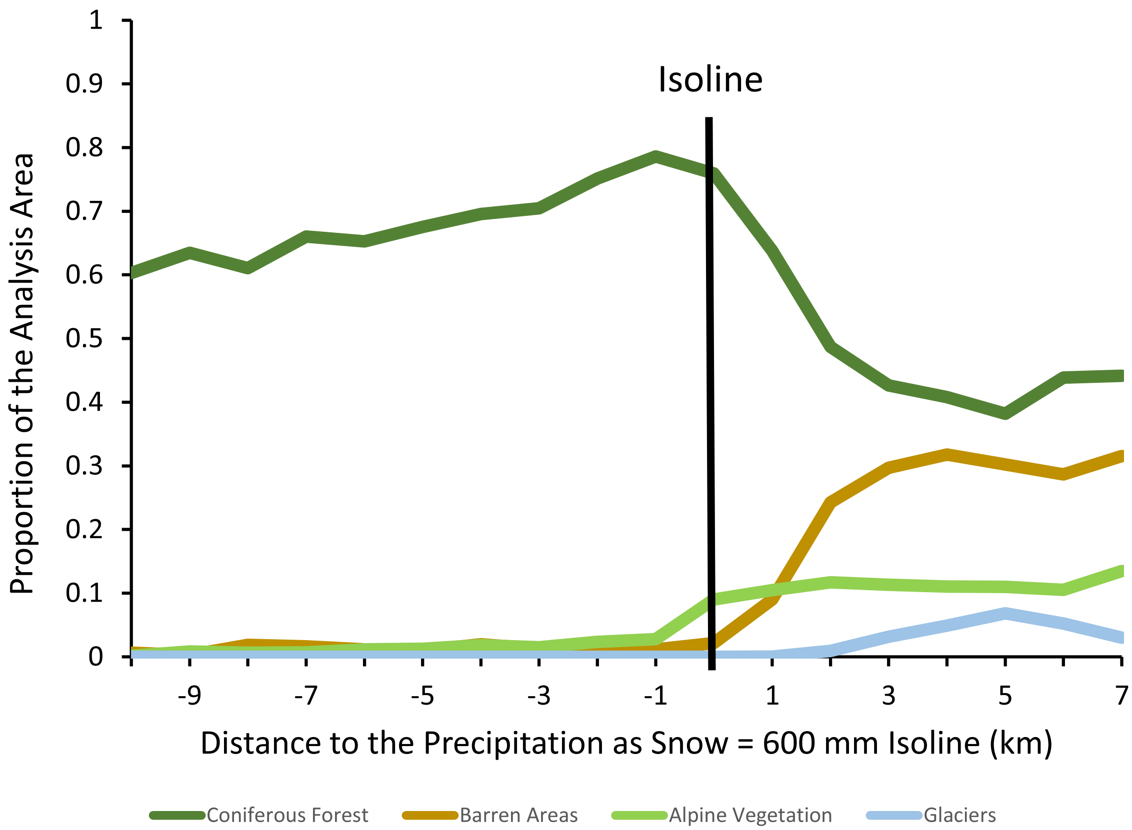
We also included a covariate that had not been rigorously evaluated in previous studies of the wolverine's distribution but had been reported by wolverine biologists both historically and recently. Several authors have described the wolverine as occurring primarily near alpine tree line in southwestern North America (Grinnell et al. 1937; Dalquest 1948; Inman et al. 2012*a*). Accordingly, we developed a covariate to investigate the wolverine's potential association with the environmental conditions that occur near alpine tree line. In the Cascades, there is rarely a continuous and clearly defined tree line; rather, it is a transitional zone that contains a mosaic of open forests and meadows (the subalpine parklands) that lie between the upper edge of dense conifer forests and the lower edge of alpine grasslands and shrublands where trees cannot persist. This transition from montane conifer forests to alpine vegetation at upper elevations in the Cascade Range appears to be determined primarily by the presence of deep snowpacks that do not melt until the late spring or summer (Franklin and Dyrness 1988). Consequently, we sought to describe this transitional zone as a function of variation in snowfall by correlating a forest cover-based estimate of alpine tree line (Supplementary Fig. S1) with a series of annual precipitation-as-snow isolines ranging from 400 to 1000 mm in 100 mm increments (Supplementary Fig. S2). The best fit with the forest cover-based estimate of alpine tree line was the precipitation as snow = 600 mm isoline (Pearson correlation = 0.95); thus, we included distance to the precipitation as snow = 600 mm isoline as a covariate in our modeling. We calculated this covariate by measuring the Euclidean distance from each use and availability polygon to this isoline and assigning a sign to each distance—we gave a negative sign to polygons with mean precipitation-as-snow values <600 mm,

Table 1. Environmental covariates reported to be important predictors in previous studies of first-order habitat selection by wolverines (*Gulo gulo*) in southwestern North America, the major habitat category each belongs to, its literature sources, its presumed relations with the wolverine" geographic distribution, and the covariates we included in our modeling of first-order habitat selection by wolverines in the Cascade Range of northern Washington, USA, and southern British Columbia, Canada.

Covariates reported to be useful predictors of wolverine distribution[a], arranged by major habitat categories	Literature sources	Presumed relations with wolverine distribution	Covariates included in our modeling
Climate			
Late-spring snow cover (+)	Copeland et al. 2010; Webb et al. 2016; Heim et al. 2017; Kortello et al. 2019	Preference for areas with adequate snow cover for reproductive denning, and cold climatic conditions	Improved Late-spring Snow Cover Index[b]
Snow depth on 1 April (∗)	Inman et al. 2013		Snow depth on 1 May[c], Annual Precipitation as Snow[d]
Distance to 1 April snow >2.5 cm deep (+)	Inman et al. 2013		Distance to Snow >1 m Deep on 1 May–SNODAS[c], Distance to Snow >1 m deep on 1 May–PAS[d]
Average maximum August temperature >22 °C (–), Movement to higher elevations during summer	Copeland et al. 2010; Hornocker and Hash 1981	Avoidance of areas with high temperatures	Degree days >18 °C[e], 30-year Maximum Annual Temperature[e], Mean Warmest Month Temperature[e], Number of Frost-free Days per Year[e]
Based on field observations and elevational analyses, not habitat modeling	Merriam 1892; Grinnell et al. 1937; Dalquest 1948; Inman et al. 2012*a*	Preference for the environmental conditions near alpine tree line that provide reproductive denning habitat, food resources, and security cover	Proximity to the Transitional Zone Near Alpine Tree Line; positive distances indicate annual precipitation as snow >600 mm, whereas negative distances indicate annual precipitation as snow <600 mm.
Topography			
Terrain ruggedness (∗, +)	Inman et al. 2013; Fisher et al. 2013	Preference for areas with escape cover from larger predators, avalanche chutes for ungulate carrion, denning and (or) food caching sites	Terrain Ruggedness Index, Topographic Position Index
Slope (+)	Copeland et al. 2007		Slope
Human disturbance			
Human activities or density (–)	Inman et al. 2013; Stewart et al. 2016	Avoidance of areas with human activities	Distance to Nearest Trail
Road density (–)	Inman et al. 2013; Kortello et al. 2019		Road Density[f], Distance to Nearest Road
Food			
Marmot habitat (+)	Inman et al. 2013; Kortello et al. 2019	Preference for areas with access to marmots and other prey associated with alpine meadows or avalanche chutes	Proportion of Alpine Vegetation[f]
Mountain goat habitat (+)	Kortello et al. 2019	Preference for areas with access to ungulate carrion	Distance to Mountain Goat Escape Terrain[g]
Land cover			
Rock/barren areas (–)	Copeland et al. 2007	Avoidance of areas where both food and security cover are scarce	Proportion of Barren Areas[f], Normalized Difference Vegetation Index[h]
Proximity to tree cover (+)	Inman et al. 2013	Preference for areas with security cover, proximity to reproductive denning sites	Proportion of Forest Cover[f]

Note: Presumed relations may overlap among covariates; thus, they are not intended to represent competing hypotheses. Covariates that we excluded from consideration for various reasons are not shown.
[a]Nature of habitat association: (+), preference; (–), avoidance; (∗), quadratic.
[b]Based on a continuous index of MODIS snow-cover data from 24 April to 15 May for the years 2007–2017; range = 1 to 100.
[c]Based on an 11-year average from 2007 to 2017 using SNODAS.
[d]Based on a 30-year average from 1981 to 2010 using annual precipitation as snow (PAS) from ClimateNA data.
[e]Based on a 30-year average from 1981 to 2010 using ClimateNA data.
[f]Calculated within a 1-km-radius circular moving window.
[g]Defined as slopes >40°.
[h]Range = −1.0 to 1.0.

Fig. 2. Proportion of the analysis area in the Cascade Range of northern Washington, USA, and southern British Columbia, Canada, that contained coniferous forest, barren areas (rock, talus, scree, and areas of sparse vegetation), alpine vegetation, or glaciers at varying distances from the precipitation as snow = 600 mm isoline. Positive distances represent areas that receive >600 mm of precipitation as snow annually, whereas negative values represent areas that receive <600 mm.



and a positive sign to those with mean precipitation-as-snow values >600 mm (Distance to the Transitional Zone Near Alpine Tree Line). Examination of covariate values in relation to various landcover classes (Fig. 2) confirmed that the precipitation as snow = 600 mm isoline provides a reliable representation of the transitional zone near alpine tree line where coniferous forests are decreasing in prevalence, and alpine vegetation, barren areas, and glaciers are increasing in prevalence.

Topographic covariates

We evaluated three topographic covariates: Slope, Terrain Ruggedness Index, and Topographic Position Index, all of which were derived from the Shuttle Radar Topography Mission (Farr et al. 2007) 30 m digital elevation model. We calculated Slope using the ee.Terrain.slope () function in Google Earth Engine. We calculated Terrain Ruggedness as the standard deviation of elevation within a 1 km circular moving window. This window size was chosen to reflect a typical ridge-to-valley bottom distance in our analysis area. We calculated Topographic Position as the difference between the pixel elevation and the mean elevation within a 1 km circle around each pixel.

Human disturbance covariates

We evaluated the effects of vehicle traffic on roads, as well as outdoor recreation in proximity to the region's network of roads and trails. We did this in two ways: the Euclidean Distance to the Nearest Road and Road Density within a 1 km radius circular moving window. We obtained road data from Open Street Maps (OpenStreetMap Contributors 2020), including all road-related "ways" labeled as motorway, trunk, primary, secondary, tertiary, residential, service, or track roads. We estimated Distance to the Nearest Trail based on the Euclidean distance to the nearest Open Street Map "way" labeled as path, cycleway, footway, bridleway, or pedestrian.

Food covariates

Alpine meadows represent the primary habitat of various wolverine prey species, such as marmots and ground squirrels, and avalanche chutes may provide sources of ungulate carrion. To investigate the wolverine's potential association with these environmental features, we delineated alpine meadow habitat and avalanche chutes based on the grass and shrub land cover classes in a regional 30 m land cover model produced annually. We used the most frequently occurring land cover class in each pixel during the 11-year study period to identify grass and shrub land cover types, and then required that those classes be in areas of deep snow (defined as mean annual precipitation as snow >400 mm) and have a near-infrared reflectance of vegetation (NIRv) >1.5, which corresponds to lush alpine vegetation. We calculated NIRv from annual Landsat cloud-free summer (July–September) composite images averaged across the 11-year study period as the product of the near-infrared band and the normalized difference vegetation index (NDVI; Tucker 1979). We then calculated the proportion of a 1 km moving window that contained alpine meadow and shrub habitat (Proportion of Alpine Vegetation).

Mountain goats (*Oreamnos americanus* (de Blainville, 1816)) occur in the diets of wolverines in this portion of their range (Lofroth et al. 2007), and several studies conducted in the northern Cascade Range showed that proximity to escape terrain (slopes >40°) was a robust predictor of mountain goat occurrence (Johnson 1983; Wells et al. 2011, 2014). We speculated that steep terrain may contribute to goat mortalities and provide carrion for wolverines. Consequently, we calculated the Euclidean Distance to Mountain Goat Escape Terrain, based on the 30 m digital elevation model used for the topographic covariates described above.

Land cover covariates

We evaluated several covariates related to land cover, including the potential avoidance of barren areas (e.g., rock, talus, areas of sparse vegetation) that lack food and security cover, as well as a preference for areas near tree cover that may provide security cover and reproductive denning sites. We used the 30 m resolution regional land cover model described above to evaluate the proportion of a 1 km circular moving window that was either barren (Proportion of Barren Areas) or forested (Proportion of Forest Cover). In addition, we calculated the mean Normalized Difference Vegetation Index; areas with low values lack vegetation, whereas areas with high values are forested or otherwise contain high amounts of vegetative cover.

Analytical approach

Environmental covariates associated with cold climatic conditions were reported most often in previous studies of the wolverine's geographic distribution in southwestern North America; otherwise, there were few consistent patterns (Table 1). Terrain ruggedness, human activities, road density, and marmot (*Marmota* spp. Blumenbach, 1779) habitat were each reported to be important to wolverines in two of these studies; but all other covariates were reported only once. Thus, although we predicted that climatic conditions would be important influences on wolverine distribution in the Cascade Range based on the results of previous studies (Table 1; Aubry et al. 2007), there was little basis from those studies to develop a set of plausible hypotheses to evaluate in an information-theoretic framework. Our primary goal was to generate a predictive model of the wolverine's geographic distribution in the Cascade Range to help inform management and conservation activities, but we also sought to improve our understanding of the environmental conditions that limit their distribution in this portion of their range. Accordingly, we modeled the wolverine's first-order habitat selection in the Cascade Range based on the suite of covariates that were reported previously to be important predictors of the wolverine's distribution in southwestern North America (Table 1), and selected our final model using measures of fit and parsimony.

Our modeling approach involved two steps. The first was exploratory, whereby our goal was to remove from further consideration any covariate that had a weak univariate association with wolverine occurrences, as well as to selectively remove highly correlated covariates to protect against multicollinearity. We used the lme4 package (Bates et al. 2015) in R (R Core Team 2020) to fit univariate mixed-effects logistic regression models with each covariate as the explanatory variable and use-availability as the response variable. The covariates were calculated as the mean value of each use or availability polygon. We included a random intercept for the individual wolverine linked to each observation. For some of our covariates (e.g., those related to precipitation and temperature), we predicted that wolverine use may be highest at intermediate levels, whereby areas that are extremely cold and snowy and those that are much warmer and receive little snow are less suitable for wolverines. Accordingly, for all climatic, topographic, and land cover covariates, we also included a quadratic term in the model to evaluate whether relations with these covariates were nonlinear. To account for the much smaller sample of use polygons compared to availability polygons in our data, we weighted use polygons greater than availability polygons during model fitting based on the inverse of the prevalence of use polygons in the data. This approach balances the influence of use and availability data in the model and has been shown to produce the most accurate species distribution models (Barbet-Massin et al. 2012). From the fitted models, we calculated AUC as a measure of effect size. We only retained covariates for use in multi-covariate model fitting if they had AUC of ≥0.70 and a significant association with wolverine occurrences in the fitted model ($P \leq 0.05$). If two covariates meeting those criteria had a Pearson correlation of >0.70, we retained the covariate with the lower AIC value, a more robust approach than choosing covariates based on higher AUC (Lobo et al. 2008).

In the second step, our goal was to combine the remaining covariates into a multi-covariate model while maximizing parsimony. We fitted a mixed-effect logistic regression model with the same response, quadratic terms, random effect, and weights as above, but included all covariates identified in step 1 as explanatory variables in a multi-covariate model. We then sought to find a more parsimonious multi-covariate model by removing any covariates that were not significant ($P > 0.05$) in the fitted multi-covariate model, and by omitting each covariate iteratively and assessing model AIC (Akaike 1973). Any omitted covariate with a ΔAIC of <10 was removed from the multi-covariate model. We assessed the performance of our final multi-covariate model in several ways, including AUC, sensitivity, specificity, and percentage correctly classified (PCC; based on thresholding the model where model sensitivity equaled specificity).

We used two different independent data sets to validate our final multi-covariate model within the analysis area (Supplementary Fig. S3). The first validation was based on wolverine telemetry data in location classes 3 (error ≤250 m) and 2 (error >250 and ≤500 m) that we obtained from three resident wolverines (two females, one male) during 2007 (n = 122). We had excluded those data from resource selection modeling because they were collected during a pilot study when we were still experimenting with duty cycles; in addition, they lacked estimates of the error radius associated with each telemetry location because Argos did not provide such data to the user until 2008. Accordingly, for model validation, we used the maximum error associated with each location class to delineate the error polygon for each location. The second and third validations were based on an independent data set of verifiable wolverine detections (i.e., those associated with physical evidence, such as remote-camera photos, genetic identifications, and road kills) obtained in the Cascade Range of Washington and southern British Columbia from 1996 to 2020; these detections represent point locations with no error polygons associated with them. For the second validation, we used only detections obtained within our analysis area (n = 159), whereas for the third validation, we used detections obtained anywhere in the Cascade Range (n = 207; Supplementary Fig. S3). For each validation polygon or point location, we extracted the intensity of use index from the multi-covariate model, and then compared the distribution of those indices to the distribution of indices for the use and availability polygons that we used to generate our final multi-covariate model (n = 1404 and 43 509, respectively). For a clear and compelling validation of our model, we expected the median value of each wolverine data set to be significantly different from the median value of our availability data set (i.e., that the 95% confidence intervals (CI) around each median would not overlap).

To investigate the contribution of each covariate to our final model, we generated multi-covariate response curves whereby each covariate was plotted against the final model values while holding all other covariates at their mean values for the wolverine use data with which we generated our final model. In addition, we created maps depicting geographic variation among the values for each covariate in our final model throughout the Cascade Range to investigate the potential influence of physiographic features on the behavior of our final model.

Results

Univariate models

Among the 21 environmental covariates we evaluated, 12 met the criteria of being strong univariate predictors of wolverine occurrence in our analysis area based on AUC ≥ 0.70 and P ≤ 0.05 (Table 2). These included all 10 of the climatic covariates we evaluated, as well as one human disturbance covariate (Distance to Nearest Road) and one land cover covariate (Proportion of Barren Areas). After removing highly correlated covariates (Supplementary Table S3), only four covariates remained for potential inclusion in a multi-covariate model: Proximity to the Transitional Zone Near Alpine Tree Line, Number of Frost-free Days per Year, Annual Precipitation as Snow, and Distance to Nearest Road. Quadratic terms for the three climatic covariates were also included.

Multi-covariate model

The three climatic covariates, their associated quadratic terms, and the road covariate were significant in a multi-covariate model; however, we eliminated Distance to Nearest Road from our final model because removing it resulted in a ΔAIC < 2. In contrast, removing each of the remaining three covariates and their quadratic terms iteratively from the multi-covariate model produced substantial increases in AIC (Table 3). Thus, our final model was limited to three climatic covariates (Proximity to the Transitional Zone Near Alpine Tree Line, Number of Frost-free Days per Year, and Annual Precipitation as Snow, in decreasing order of importance in the model) and their quadratic terms, and showed strong model fit (AUC = 0.8916, PCC = 81.7) with high sensitivity (0.8184) and specificity (0.8173).

Model validation

Validation analyses demonstrated that our model was robust and could identify areas of potential wolverine distribution in the Cascade Range with high specificity (Fig. 3). The wolverine locations we used to generate the model had a median intensity of use of 0.808 (95% CI = 0.801–0.815). By comparison, the median intensity of use associated with availability locations was 0.046 (95% CI = 0.041–0.050). Telemetry polygons obtained within our analysis area in 2007 had a median intensity of use of 0.790 (95% CI = 0.766–0.814), and verifiable detections obtained within our analysis area from 1996 to 2020 had a median index of 0.753 (95% CI = 0.723–0.783). Importantly, when we projected our model throughout the Cascade Range and used verifiable detections obtained anywhere in the Cascades from 1996 to 2020 to validate our model (Supplementary Fig. S3) the results were similar, whereby the median intensity of use was 0.730 (95% CI: 0.697–0.762). Thus, for each of the three validations we conducted, the 95% CI for the median probability of use does not overlap with the 95% CI for the median value of our availability data (Fig. 3), indicating that these distributions are significantly different.

Model interpretation

Examination of ΔAIC values and multi-covariate and univariate response curves for Proximity to the Transitional Zone Near Alpine Tree Line and the Number of Frost-free Days per Year (Table 3, Fig. 4) shows that a preference for the transitional zone near alpine tree line and an avoidance of landscapes associated with relatively warm temperatures are the primary drivers in our model. Within our analysis area, the multi-covariate and univariate response curves for Proximity to the Transitional Zone Near Alpine Tree Line are similar (Figs. 4A, 4D), indicating that regardless of how values for the other two covariates in the model change, this co-

 Can. J. Zool. **101:** 95–113 (2023) | dx.doi.org/10.1139/cjz-2022-0005

Table 2. Results of univariate logistic regressions for 21 environmental covariates we identified as having potential effects on first-order habitat selection by wolverines (*Gulo gulo*) in the Cascade Range of northern Washington, USA, and southern British Columbia, Canada.

Environmental covariate[a]	Mean of use polygons[b]	Mean of availability polygons[c]	*P* value	AUC	AIC	ΔAIC
Proximity to the Transitional Zone Near Alpine Tree Line (km)[1]	3.43	−4.51	0.0000	0.832	82 776	0
Number of Frost-free Days per Year[2]	148.6	180.5	0.0000	0.806	87 554	4778
Annual Precipitation as Snow (mm)[3,5]	814.7	529.5	0.0000	0.787	90 065	7289
Snow Depth on 1 May (m)[3]	2.45	1.47	0.0000	0.780	91 071	8295
Distance to Snow >1 m Deep on 1 May—PAS (m)[1]	72.7	2841.2	0.0000	0.757	92 611	9835
Degree Days >18 °C[2,4]	718.9	1076.6	0.0000	0.776	94 170	11 393
Mean Warmest Month Temperature (°C)[2,4]	11.5	13.5	0.0000	0.779	94 536	11 760
Improved Late-spring Snow Cover Index[5,6]	13.2	6.0	0.0000	0.779	96 293	13 517
Distance to Snow >1 m Deep on 1 May—SNODAS (m)[1]	36.1	2224.0	0.0000	0.724	97 144	14 368
30-year Maximum Annual Temperature (°C)[3,4]	28.8	31.0	0.0000	0.749	100 372	17 595
Proportion of Barren Areas[6]	0.2	0.1	0.0000	0.718	110 818	28 042
Distance to Mountain Goat Escape Terrain (km)	2.51	4.56	0.0000	0.645	112 139	29 362
Distance to Nearest Road (km)[7]	4.61	2.75	0.0000	0.708	112 730	29 954
Slope (°)	23.3	19.3	0.0000	0.635	112 954	30 178
Distance to Nearest Trail (km)	1.49	2.51	0.0000	0.620	113 950	31 174
Proportion of Alpine Vegetation	0.1	0.0	0.0000	0.699	114 070	31 294
Terrain Ruggedness Index (m)	6.5	5.1	0.0000	0.638	114 204	31 428
Road Density	0.0	0.1	0.0000	0.581	114 283	31 507
Proportion of Forest Cover	0.5	0.6	0.0000	0.596	117 962	35 186
Topographic Position Index (m)	2.4	−0.2	0.2004	0.577	120 073	37 297
Normalized Difference Vegetation Index	0.5	0.6	0.0001	0.528	120 311	37 534

Note: Covariates were retained for multi-covariate model fitting if they had $P \leq 0.05$ and an area under the receiver operator curve (AUC) ≥ 0.70; if two covariates meeting these criteria were correlated (Pearson correlation >0.70), the covariate with the lower AIC value was retained.
[a]Covariates sharing the same superscript number have Pearson correlation coefficients >0.70; results are presented only for covariates that have univariate logistic regressions with $P \leq 0.05$ and AUC ≥ 0.70.
[b]$n = 1404$.
[c]$n = 43\,988$.

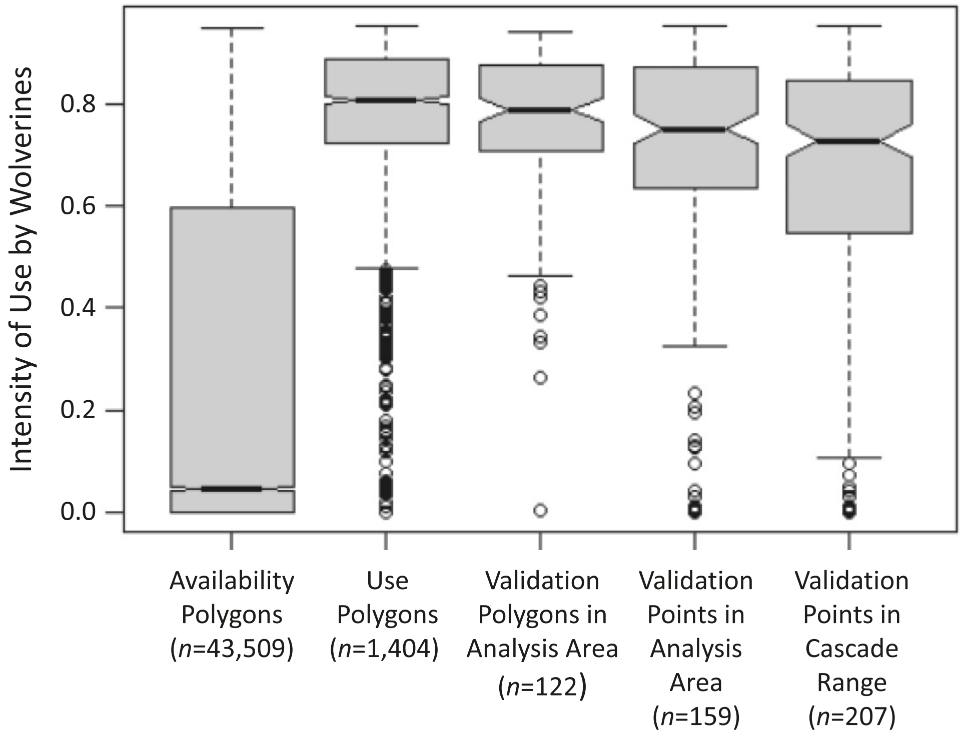
Table 3. Final multi-covariate logistic regression model of first-order habitat selection by wolverines (*Gulo gulo*) in the Cascade Range of northern Washington, USA, and southern British Columbia, Canada.

Term	*β*	*β* (SE)	*Z* score	*P* value	ΔAIC
Intercept	− 3.462	0.170	− 20.35	0.0000	36
Proximity to the Transitional Zone Near Alpine Tree Line	7.824	0.139	56.25	0.0000	10 005
Quadratic term	− 2.833	0.065	− 43.85	0.0000	2609
Number of Frost-free Days per Year	− 3.867	0.054	− 71.26	0.0000	13 727
Quadratic term	− 2.229	0.039	− 56.71	0.0000	4612
Annual Precipitation as Snow	− 1.345	0.036	− 31.39	0.0000	2804
Quadratic term	0.132	0.008	16.01	0.0000	222

Note: ΔAIC values represent the change in model fit when each term is removed iteratively from the model.

variate has a strong effect on the intensity of use by wolverines. In the areas where precipitation as snow is <600 mm, there is a threshold located about 5 km below the 600 mm isoline where increasing precipitation as snow results in a sharp increase in wolverine use (Fig. 4A). In the areas where precipitation as snow is >600 mm, intensity of use continues to increase until about 5 km above the 600 mm isoline, at which point use by wolverines begins to decrease. Wolverine use is highest in the areas that receive >600 mm in precipitation as snow annually (Fig. 4A), which correspond to the areas where conifer trees are decreasing in prevalence, and barren areas, alpine vegetation, and glaciers are increasing in prevalence (Fig. 2). The multi-covariate and univariate response curves for Number of Frost-free Days per Year are also similar (Figs. 4B, 4E). The intensity of use peaks near the mean of our wolverine use data (∼150 days), but with increasingly warm conditions, use by wolverines decreases sharply until about 220 frost-free days per year, at which point such areas become unsuitably warm for wolverines. In contrast, differences in the shapes of the multi-covariate and univariate response curves for Annual Precipitation as Snow (Figs. 4C, 4F) indicate that this covariate functions largely to constrain

Fig. 3. Box and whisker plots (notches depict the 95% confidence intervals) showing the results of validations we conducted on our first-order habitat selection model for wolverines (*Gulo gulo*) in the Cascade Range of Washington, USA, and British Columbia, Canada. We generated the model using Argos telemetry data for 10 resident wolverines obtained from 2008 to 2016 (use polygons) and polygons located randomly within our analysis area (availability polygons). Validation polygons represent Argos telemetry data obtained on three resident wolverines in 2007, whereas validation points represent the precise locations of verifiable wolverine detections obtained from 1996 to 2020 in our analysis area and throughout the Cascade Range in Washington and British Columbia. The geographic locations of the polygons and points used in our validation analyses are shown in Supplementary Fig. S3.



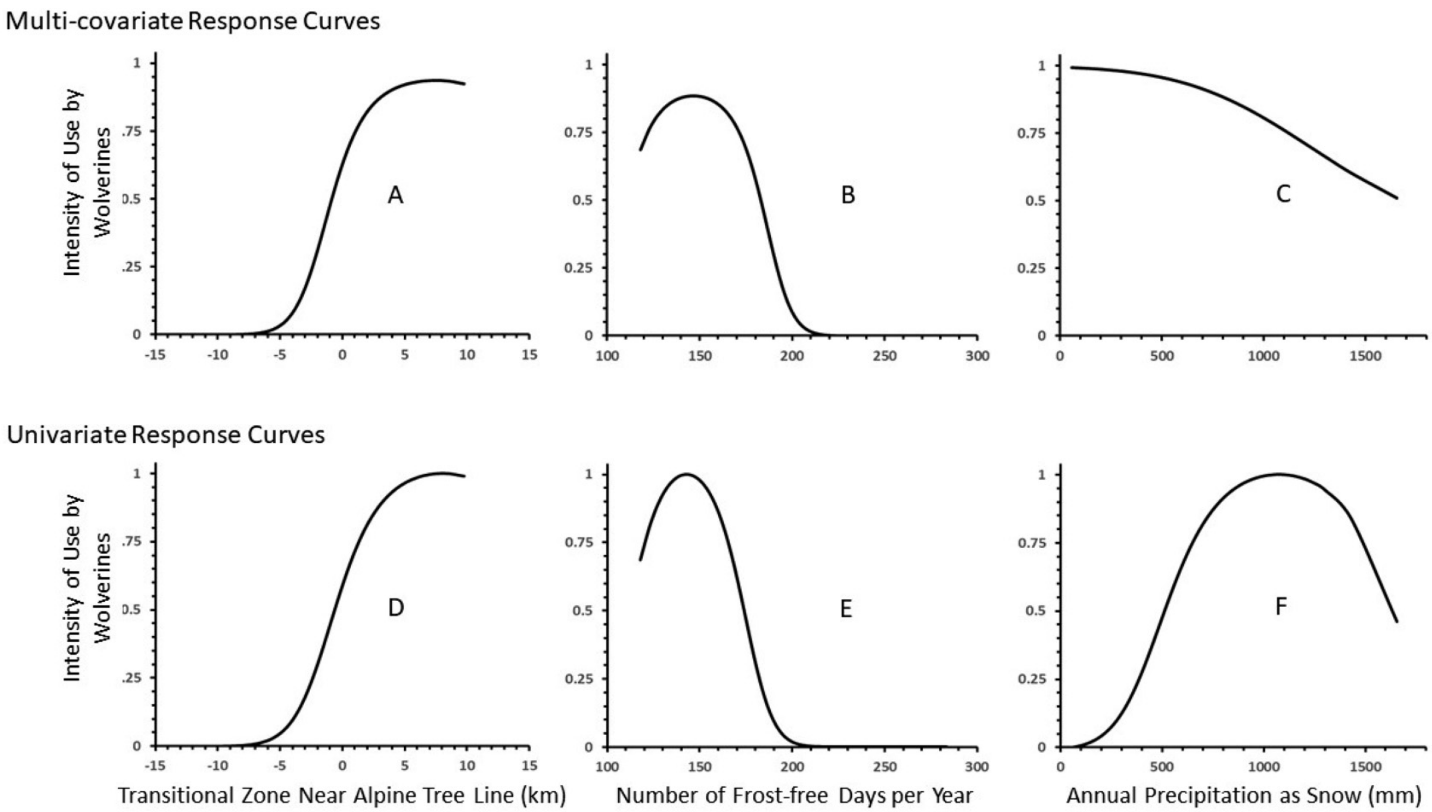
the effects of the other two covariates in areas where average annual snowfall becomes too great and average annual temperatures become too cold (i.e., at the highest elevations where vegetation becomes increasingly sparse or disappears). The univariate response curve for Annual Precipitation as Snow (Fig. 4F) shows that wolverine use is greatest at values of ∼1000 mm and decreases sharply both below and above this value. However, the multi-covariate response curve (Fig. 4C) indicates that when Proximity to the Transitional Zone near Alpine Tree Line and the Number of Frost-free Days per Year are at their respective mean values where use by wolverines is relatively high (3.43 km and 148.6 days, respectively), increasing amounts of annual snowfall decrease wolverine use sharply.

When our final multi-covariate model is projected across western Washington and southwestern British Columbia (Fig. 5), it depicts a species that primarily occupies habitat conditions occurring near the crest of the Cascade Range; however, high-use areas are generally more extensive east of the Cascade crest, especially in the central and southern Cascades. The geographic location of the 600 mm isoline in Fig. 6A (i.e., the boundary between negative and positive values) and variation in Annual Precipitation as Snow (Fig. 6C) are similar on the west and east sides of the Cascade crest; i.e., they are closely linked to high-elevation habitats on either side of the crest. However, the west side has many more frost-free days than the east side (Fig. 6B), indicating that maritime influences create warmer conditions on the west side of the Cascade crest that decrease use by wolverines compared to similar elevations on the east side.

The largest contiguous areas of high-use wolverine habitat in the Cascade Range occur within our analysis area in northern Washington and southern British Columbia (Fig. 5). Patterns in the intensity of use by wolverines indicate that the primary areas of habitat connectivity for wolverines in this region are located near the Cascade crest. However, high-use wolverine habitat in the southern Cascade Range in Washington is disjunct from similar habitat conditions in the northern Cascades, due to a zone of unsuitable habitat in the vicinity of Snoqualmie Pass (Fig. 5), where connectivity among Cascade wolverines is likely to be most limited. The strong maritime signal on the west side of the Cascade crest is reflected in the geographic distribution of high-use wolverine habitat in the Cascade Range, especially in the central and southern Cascades where most of the highest use areas occur east of the Cascade crest (Fig. 5).

Maritime influences on the intensity of use by wolverines are particularly evident on Mt. Baker, the westernmost vol-

Fig. 4. Response curves for the environmental covariates included in our final multi-covariate logistic regression model of first-order habitat selection by wolverines (*Gulo gulo*) in the Cascade Range of northern Washington, USA, and southern British Columbia, Canada. The multi-covariate plots (A–C) show the effects of each covariate on the intensity of wolverine use while holding the other two covariates in the model at the mean values for our wolverine use data (Proximity to the Transitional Zone Near Alpine Tree Line = 3.43 km, Number of Frost-free Days per Year = 148.6 days, and Annual Precipitation as Snow = 814.7 mm; n = 1404). The univariate plots (D–F) show the effects of each covariate on the intensity of wolverine use independent of the other covariates in the model.



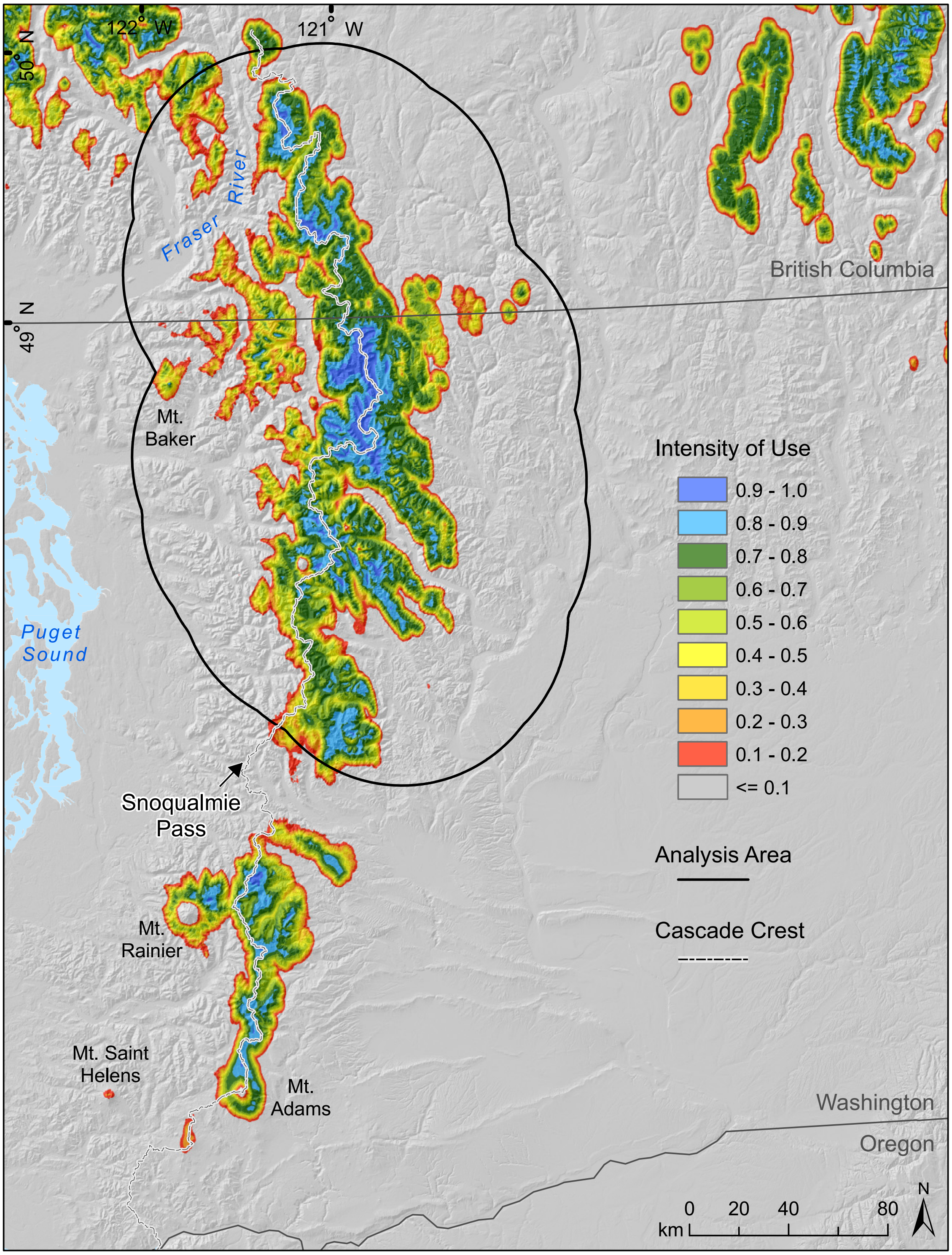
cano in the northern Cascade Range (Fig. 5), which is 3286 m high and contains an extensive alpine zone (Fig. 6A), but relatively little high-use wolverine habitat. Thus, our model may help explain why there are no reliable historical records of wolverine occurrence on Mt. Baker (Aubry et al. 2007). Both the gap in wolverine use near Snoqualmie Pass and the lower prevalence of high-use areas west of the crest are driven primarily by variation in the Number of Frost-free Days per Year (Figs. 5, 6). In both cases, geographic patterns in the intensity of use by wolverines (Fig. 5) are similar to those for this covariate (Fig. 6B), whereby warm average annual temperatures along the west side of the Cascades and in Snoqualmie Pass result in covariate values that generally exceed 195 days per year, creating unsuitable habitat conditions for wolverines.

Discussion

The species distribution model we generated indicates that the wolverine's first-order habitat selection in the Cascade Range is constrained by climatic conditions. Our model shows that there is a relatively narrow belt of suitable habitat conditions for wolverines in the Cascade Range that lies primarily between the upper limit of dense coniferous forests and the lower limit of permanent ice and snow. We propose that in the Cascade Range, wolverines are restricted primarily to the transitional zone near alpine tree line because at higher elevations where alpine vegetation is sparse or can no longer become established, there is insufficient food and cover to support wolverines, whereas at lower elevations environmental conditions become too warm. Although our model indicates that Cascade wolverines are primarily inhabitants of the transitional zone near alpine tree line, we also documented our study animals using the coniferous forests below tree line and the alpine meadows and shrublands above tree line. Our findings indicate, however, that intensity of use by Cascade wolverines is greatest above alpine tree line where snowfalls are greater (Figs. 2, 4), environmental conditions are colder, and trees are sparser (Figs. 2, 4A, 4B, 4D, 4E).

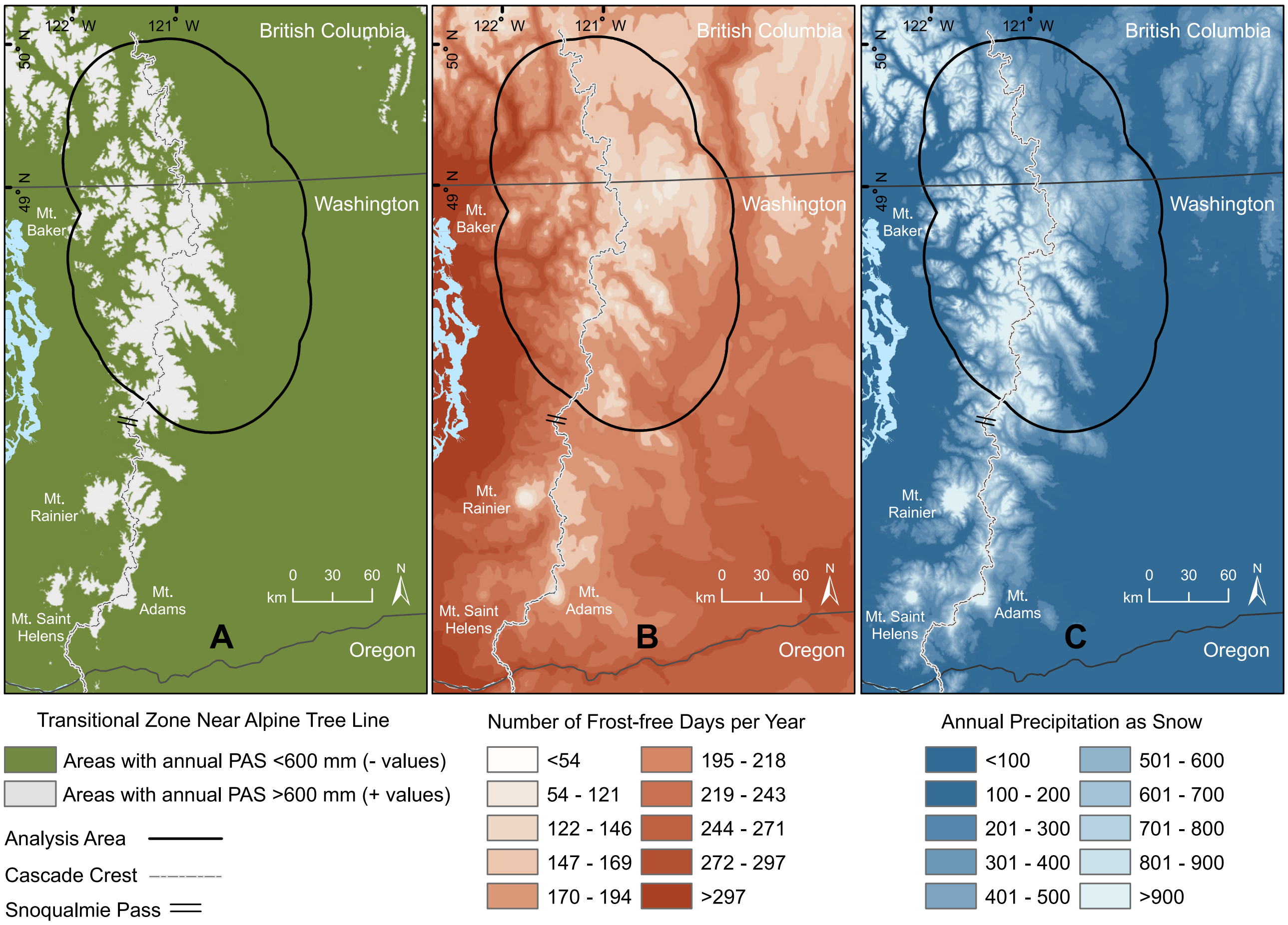
Results from previous studies of first-order habitat selection by wolverines in southwestern North America (Table 1) support the importance of climatic conditions for delineating their geographic distribution. Climatic covariates were the most common constituents of previously published distribution models, including selection for areas with late-spring snow cover and relatively cold climatic conditions (Copeland

Fig. 5. Spatial extent of our final multi-covariate logistic regression model of first-order habitat selection by wolverines (*Gulo gulo*) in the Cascade Range of Washington, USA, and southern British Columbia, Canada. Map produced in ArcGIS Desktop 10.7.1 software by Esri (2022) using Esri provided boundary, water, and elevation layers. Map projection: WGS_1984_UTM_Zone_10 N. Geographic coordinate system: GCS_WGS_1984.



et al. 2010; Inman et al. 2013; Webb et al. 2016; Heim et al. 2017; Kortello et al. 2019), and avoidance of areas with high summer temperatures (Hornocker and Hash 1981; Copeland et al. 2010). In high-elevation montane regions, there are many landscape attributes that correlate with snowy and cold environments: such areas tend to be high in elevation, steep, rocky, largely open due to snow parks and avalanche chutes, far from urban areas, lightly roaded, federally protected as wilderness or parks, and contain potential wolverine prey (e.g., mountain goats, marmots, ground squirrels).

Fig. 6. Geographic variation in values for each of the three covariates included in our final multi-covariate logistic regression model of first-order habitat selection by wolverines (*Gulo gulo*) in the Cascade Range of Washington, USA, and southern British Columbia, Canada. Map produced in ArcGIS Desktop 10.7.1 software by Esri (2022) using Esri provided boundary and water layers. Map projection: WGS_1984_UTM_Zone_10 N. Geographic coordinate system: GCS_WGS_1984.



Other wolverine distribution models developed in southwestern North America contain many of those attributes (Table 1). However, concordance between Inman et al.'s (2013) wolverine distribution model that contains eight covariates in multiple habitat categories and Copeland et al.'s (2010) univariate snow-cover map supports the primacy of climatic conditions for delineating the wolverine's geographic distribution. Moreover, there are strong commonalities between the environmental covariates in our model and Copeland et al.'s (2010) findings, both of which reveal the importance of snowy areas and cold environmental conditions for delineating the wolverine's range. Thus, our model provides additional support for the patterns in wolverine distribution and habitat relations reported previously by Copeland et al. (2010).

In many ways, our findings confirm descriptions provided by early naturalists who studied wolverines in the Cascade Range and Sierra Nevada prior to their extirpation. Merriam (1892), Grinnell et al. (1937), and Dalquest (1948) all described the wolverine as occurring primarily within the Hudsonian Life Zone (see Merriam 1898). In southwestern North America, this zone is restricted to a relatively narrow belt of habitat conditions that occurs only on the highest mountain peaks near alpine tree line (Bailey 1936; Grinnell et al. 1937; Dalquest 1948; Jewett et al. 1953). Grinnell et al. (1937) noted that in the Sierra Nevada of California, "Probably, the wolverine has always been a relatively scarce animal in this state. The territory of cold climate to which it closely restricts itself is of small extent".

The wolverine's geographic distribution in the Cascade Range is constrained by climatic conditions that are often correlated with other potentially important environmental features that occur near alpine tree line where snow cover persists into the late spring and climatic conditions are relatively cold (Table 1). However, as might be expected of a first-order habitat selection model, inferences are primarily to the factors that best describe where wolverines are found but say little about why. It could be that cold and snowy conditions provide the limiting factors (e.g., denning requirements (Magoun and Copeland 1998) or refrigerated food caching (Inman et al. 2012b)), but there are likely additional attributes that were either not measured or were masked by the scale of our analysis. For example, studies of moose (*Alces americanus* (Clinton, 1822)), another boreal species whose distribution can be strongly related to temperature (Lenarz et al. 2009), have found that the likely mechanisms of limitation are complex and may involve changes in food quality, parasite loading, and predation in addition to thermal limits (Weiskopf et al. 2019). It is important to note that Johnson (1980) assumed that such relations would emerge in higher order analyses that employed different methods and covariates.

Few studies have investigated habitat selection by wolverines at the second or third orders in southwestern North America (i.e., selection of home ranges and selection of habitat components within home ranges, respectively; Johnson 1980). Carroll et al. (2021) modeled second- and third-order habitat selection by wolverines in the Greater Yellowstone Ecosystem with the same data that Inman et al. (2013) used previously to model the wolverine's first-order habitat selection. Distance to high-elevation talus and measures of snow depth (i.e., linear and quadratic snow-water equivalent) best explained the selection of home ranges by wolverines. These covariates were also reported to be important at the first order of selection (Inman et al. 2013) and align well with our findings about the wolverine's association with alpine tree line, cold temperatures, and precipitation as snow in the Cascade Range. Additional studies will be needed to better understand the environmental constraints on selection of home ranges by wolverines in southwestern North America, but Carroll et al.'s (2021) findings suggest that there may not be strong differences in habitat selection by wolverines at the first and second orders of selection in this portion of their range. Models of third-order habitat selection presented by Carroll et al. (2021) performed poorly compared to their second-order models, likely reflecting the need for finer scale covariate data and more nuanced analyses to investigate the selection of habitat components within wolverine home ranges (Carroll et al. 2021).

Heinemeyer et al. (2019) modeled third-order habitat selection by wolverines in four study areas in Idaho, Montana, and Wyoming that were used heavily by winter backcountry recreationists. Both sexes responded negatively to increasing intensity of winter recreation within home ranges, but females were more sensitive than males. Both sexes showed strong selection for drainage-bottom topography, riparian areas, and areas near forest edges, and avoided steep slopes and higher elevation shrub and grass cover types; additionally, males selected fir-dominated forests and areas close to secondary roads, and avoided lower elevation shrub and grass habitats, whereas females selected talus, higher patch edge:area ratios (i.e., smaller forest patches), and areas with persistent spring snow cover. The latter covariates may confer fitness benefits to reproducing females because talus boulders often provide structure for reproductive snow dens (Magoun and Copeland 1998), forest edges may provide a greater diversity or abundance of potential prey, and persistent spring snow cover may provide the snow conditions needed by denning females (Magoun and Copeland 1998; Copeland et al. 2010). Research focused at higher orders of habitat selection by wolverines in southwestern North America is extremely scanty, and further research will be needed to gain a reliable understanding of the wolverine's second- and third-order habitat selection in this region.

Our wolverine distribution model shows that snowy and cold environments define the geographic areas that are overwhelmingly associated with resident wolverines in the Cascade Range. It remains unclear whether the wolverine's observed associations with snowy and cold environments at the first-order of selection are driven by reproductive denning needs, other ecological requirements, or physiological constraints. However, if climatic conditions warm and alpine tree line moves up in elevation and shrinks in size, both the geographic extent and connectivity of suitable habitat for wolverines (i.e., the Hudsonian zone) will be diminished. Our wolverine distribution model is based on climate data that are continuously and methodically collected, processed, and made available to potential users through various established sources (e.g., Wang et al. 2016). Consequently, it enables resource managers to monitor the direct effects of climate change on wolverine habitat in the Cascade Range easily and reliably, and to predict the extent to which climate change may impact wolverine populations under various scenarios.

Acknowledgements

The capture, immobilization, and collaring of wolverines in the Cascade Range would not have been possible without the dedication and commitment of John Rohrer of the Methow Valley Ranger District on the Okanogan-Wenatchee National Forest, Scott Fitkin of the Washington Department of Fish and Wildlife, Eric Lofroth and Rich Weir of the British Columbia Ministry of Environment, and Cliff Nietvelt of the British Columbia Ministry of Forests, Lands, and Natural Resource Operations, all of whom also contributed funding or in-kind contributions to the study. Bob Naney, Regional Carnivore Biologist (retired) for the Pacific Northwest Region of the US Forest Service (USFS) helped secure funding and institutional support for our study. Pat Cunningham of the USFS Pacific Northwest Research Station provided advice on statistical analyses, and Kim Heinemeyer and Audrey Magoun provided helpful suggestions on a previous draft of this manuscript. Additional funding and support for work conducted in Washington was provided by Seattle City Light; the USFS and Bureau of Land Management's Interagency Special Status/Sensitive Species Program (ISSSSP); the USFS National Carnivore Program in Missoula, Montana; the US Fish and Wildlife Service; the Wolverine Foundation; the Seattle Foundation/Tom and Sonya Campion Fund; and the USFS Pacific Northwest Research Station. Funding and support for work conducted in British Columbia was provided by the Habitat Conservation Trust Fund, the Skagit Environmental Endowment Commission, the British Columbia Ministry of Environment, and the British Columbia Conservation Foundation. The following individuals assisted with winter trapping operations: Bruce Akker, Mo Kelly-Akker, Chase Bolyard, David Bowden, Kat Dees, Travis Desy, Andre Dulac, Mila Dunbar-Irwin, Justin Ewer, Sherrie Farmer, Teresa Fish, Lee Ann Grubbs, Dan Guertin, Brent Gurd, Mike Harmon, Dan Harrington, Morgan Hartsock, Evan Haug, Jeff Heinlen, John Jakubowski, Adam Kehoe, Gary Koehler, Michael Liu, Alexis Monetta, Andrew Myhra, Bob Naney, Joyce Neilson, Nate Redetzke, Matt Rochetta, Kim Romain-Bondi, Dan Russell, Heidi Schindler, Brandon Sheeley, Bryan Smith, Gabe Spence, Ann Sprague, Blake Stokes, Dylan Taylor, Michael Taylor, Chris Vennum, Katie Weber, Lindsay Welfelt, Steph Williams, Zack Winters, and Aja Woodrow. Marvin Streubal and others with APHIS Wildlife Services in Washington provided beaver carcasses for baiting livetraps.

Article information

History dates

Received: 3 January 2022
Accepted: 9 August 2022
Version of record online: 17 November 2022

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Data availability

The primary research data that support the findings of this study are being stored at the Pacific Northwest Research Station of the US Forest Service in Olympia, Washington, and can be accessed upon request to the senior author.

Author information

Author ORCIDs

Keith B. Aubry https://orcid.org/0000-0003-1844-2424

Author contributions

Conceptualization: KBA, CMR, AJS, KSM, JPC
Data curation: KBA, CMR
Formal analysis: KBA, CMR, AJS, KSM, JPC
Funding acquisition: KBA, CMR
Investigation: KBA, CMR
Methodology: KBA, CMR, AJS, KSM, JPC
Project administration: KBA, CMR
Writing – original draft: KBA, CMR, AJS, KSM, JPC
Writing – review & editing: KBA, CMR, AJS, KSM, JPC

Competing interests

The authors declare that there are no competing interests.

Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjz-2022-0005.

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