Species Status Assessment Addendum

FOR

NORTH AMERICAN WOLVERINE

(*Gulo gulo luscus*)

Wolverines in southwestern Montana. *Photo credit: Mark Packila; used with permission.*

U.S. Fish and Wildlife Service

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1.0 Introduction

1.1 Background

In 2013, the U.S. Fish and Wildlife Service (USFWS, we) proposed to list the wolverine (*Gulo gulo luscus*) in the contiguous United States as a threatened distinct population segment (DPS) under the Endangered Species Act (ESA) (78 FR 7863). We withdrew that proposed rule in 2014, but it was reinstated due to a court order in 2016 (see 85 FR 64618 for more details). On October 13, 2020, we again withdrew our proposed listing rule (85 FR 64618), finding that the loss of wolverine habitat due to climate change and other stressors was not as significant as we found in our 2013 proposed rule. Our withdrawal also found that wolverines in the contiguous U.S. were not discrete from wolverines in Canada, and therefore did not qualify as a DPS under the ESA. In response to our withdrawal, conservation groups filed a lawsuit challenging our decision in the District Court of Montana. In 2022, the District Court granted us a voluntary remand to reevaluate our decision in light of new scientific information (*Center for Biological Diversity et al.,* and *WildEarth Guardians et al., v. Haaland*, *et al.*, No. 9:20-cv-00181-DWM (D. Mont. May 26, 2022). Our 2020 withdrawal was also vacated by the court, meaning that wolverines are again considered a species proposed for listing under the ESA. Therefore, we are now evaluating new information relative to our previous status review to assist in our upcoming final determination (not included here) as to whether the wolverine warrants listing under the ESA in the contiguous U.S.

This addendum evaluates new science and information that has become available following publication of our 2018 Species Status Assessment (SSA) (USFWS 2018, entire). Due to time constraints associated with our adherence to the District Court order we do not restate the contents of the 2018 SSA unless our assessment of the new information resulted in an update to our analysis or was necessary for understanding the new information. Comparing and contrasting the new information with our previous analysis will require familiarity with the content of the 2018 SSA. The information in this addendum, taken alongside the information in the 2018 SSA, together comprise our current, 2023, “Wolverine SSA”.

1.2 Addendum Scope

Our 2018 SSA evaluated the status of wolverines in North America. For this addendum, we focus specifically on the status of wolverines in the contiguous U.S. (the DPS we proposed to list in 2013). We did not include an updated assessment of wolverines in the Great Lakes, Great Plains, the Northeast, or the Upper Midwest because wolverines are presumed extirpated from these regions, had few historical verified records, and likely lack suitable habitat for recolonization by a reproducing population (Aubry et al. 2007, pp. 2152–2156; 75 FR 78034 [December 14, 2010]). While our focus in this addendum is on wolverines in the western U.S., we also provide updated information for British Columbia and Alberta given the importance of connectivity between the U.S. and Canada to wolverine conservation in the western U.S. We also cite studies from other regions of the world if relevant to our understanding of wolverine ecology.

1.3 Methods

This addendum provides an assessment of new information relevant to wolverine biology, ecology, threats, or protections published or recorded since the 2018 SSA including peer-reviewed articles and gray literature published since March 1, 2018, and new wolverine observation records within the contiguous western U.S. We identified peer-reviewed articles through searches in Web of Science, the USFWS Library catalog, Google Scholar, EBSCOHost, and indexes of open access content using the search words "*Gulo gulo*" and "wolverine." We also evaluated papers from personal libraries or those we encountered during opportunistic web searches. In addition, we solicited new information and publications relevant to our analysis from wolverine researchers, government agencies, Tribes, and the public (see 87 FR 71557, November 23, 2022). Finally, we considered information from the States of Idaho, Wyoming, and Montana received in July and August 2020, prior to the publication of our 2020 proposed rule, but after we completed our 2018 SSA.

This process resulted in the identification of over 180 publications and hundreds of new wolverine observation records. In addition to our review of the literature and new information, we updated our projections of spring snow cover in the western U.S. to include a broader geographical area and a longer time horizon than was presented in our 2018 assessment.

Based on our literature review and analysis of spring snow cover projections, we then conducted a new evaluation of known and potential stressors that may impact the physical and biological features that the species needs for survival and reproduction and prepared a revised risk assessment (see **Risk Assessment** section, below) for wolverines in the western U.S. using the conservation biology principles of resiliency, redundancy, and representation.

2.0 Physical and Ecological Requirements

In our 2018 SSA, we defined the following physical and ecological requirements of wolverine in the contiguous U.S.:

(1) large territories in relatively inaccessible landscapes; at high elevation (1,800 to 3,500 meters (5,906 to 11,483 feet));
(2) access to a variety of food resources, that varies with seasons; and
(3) physical/structural features (e.g., talus slopes, rugged terrain) linked to reproductive behavioral patterns.

We affirm these requirements and the characterization in our 2018 SSA that the wolverine is a snow-adapted, cold-climate animal in its physiology and morphology (Telfer and Kelsall 1984, p. 1830); phylogeography (historical processes that may be responsible for past and present geographic distributions of genealogical lineages); and behavior and habits (Fisher et al. 2022, p. 7). Based on substantial new information regarding wolverine habitat associations, wolverines in the contiguous U.S. also likely need habitats characterized by the presence of persistent spring snow for survival and reproduction (see **Wolverine Habitat Use** section, below).

Hypotheses for a mechanistic relationship between persistent spring snow and reproduction and survival include the importance of snow to create dens, predation avoidance, competitive advantages over other scavengers and predators in food acquisition, thermoregulation, food storage and refrigeration, or some combination of these factors. Temperature may also play a role in defining the climatic niche of wolverines, although the interplay of temperature and persistence of spring snow and the point at which temperature becomes limiting is largely unknown.

3.0 Current Condition

3.1 Distribution, Density, and Abundance

Wolverine Distribution

Western States Wolverine Conservation Project
In our 2018 SSA, we described preliminary unpublished results from the Western States Wolverine Conservation Project (WSWCP) (see *Population Abundance and Distribution* section, USFWS 2018, pp. 50–56). In 2020, a formal analysis of the results of the WSWCP's efforts was published (Lukacs et al. 2020, entire). The WSWCP used a network of camera stations placed within a sampling frame of 15 x 15 kilometer (km) (9.32 x 9.32 mile (mi)) cells (this size was selected to approximate a resident female wolverine home range) in modeled wolverine habitat to estimate the probability of wolverine occupancy in Washington, Idaho, Montana, and Wyoming (Figure 1).

As illustrated in Figure 1, wolverine occupancy varied across the wolverine's range, with the highest occupancy probability among ecosystems in the Northern Continental Divide Ecosystem in Montana (occupancy probability = 0.8–1); intermediate occupancy in the Cascade Mountains of Washington and in Central Idaho (occupancy probability = 0.4–0.6); and low occupancy in the Greater Yellowstone Ecosystem (occupancy probability = 0.1–0.3) (Lukacs et al. 2020, pp. 846–847). Occupancy probabilities were similarly variable across States with Montana having the highest occupancy, Idaho and Washington with intermediate occupancy, and Wyoming with low occupancy (Table 1).

WSWCP survey results in 2016–2017 indicated an expansion of the wolverine population into the southern Cascades of Washington and the Wind River Range in Wyoming (Lukacs et al. 2020, pp. 847–848). Spatial occupancy models revealed areas of relatively low occupancy in northern Idaho and Wyoming, although standard errors in these estimates were high in the Greater Yellowstone Ecosystem and in the Nez Perce-Clearwater National Forest in Idaho (Lukacs et al. 2020, pp. 847–848).

Wolverines are highly mobile, and the sampling frame used for the WSWCP does not align exactly with home ranges of individuals (Lukacs et al. 2020, p. 845). Due to this mismatch, the estimates derived from this effort violated the assumption of "closure" (that sampling sites are closed to changes in occupancy between surveys) necessary to make when estimating occupancy (Lukacs et al. 2020, p. 845). Consequently, the estimates of occupancy are most appropriately interpreted as the probability that a given cell (or camera station) was used by ≥1 wolverine during the survey (Lukacs et al. 2020, p. 845).

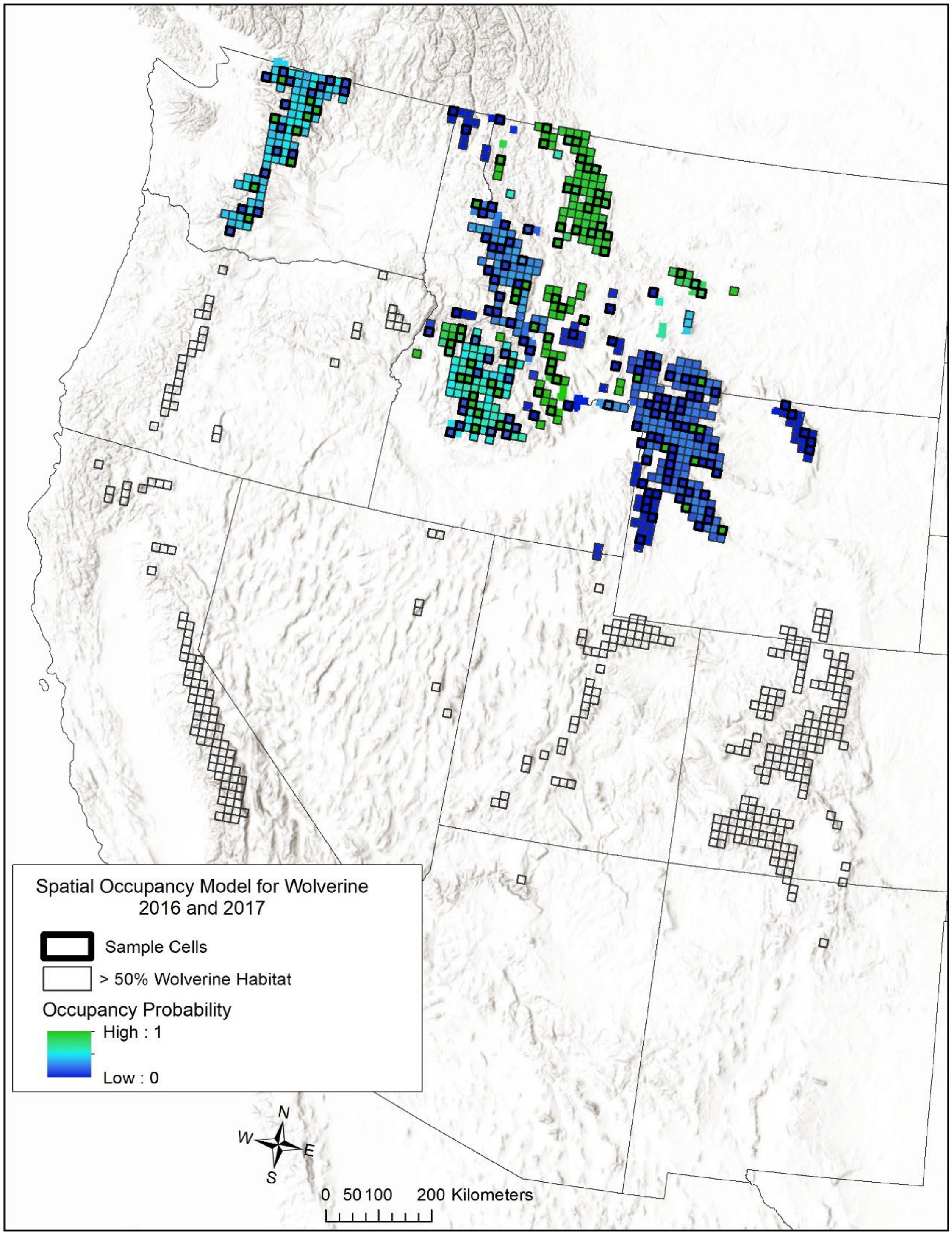

Figure 1. Western States Wolverine Conservation Project wolverine occupancy probabilities across a 4-state area, USA, in the winter of 2016/2017 (adapted from Lukacs et al. 2020, p. 846). All identified cells contained >50% modeled wolverine habitat. Cells with a dark outline are cells sampled in 2016/2017.

Table 1. Estimated number of wolverine-occupied 15 x 15 km (9.32 x 9.32 mi) grid cells and occupancy probabilities per state from the 2016–2017 Western States Wolverine Conservation Project surveys (Lukacs et al. 2020, p. 848). LCL = Lower Credible Limit; UCL = Upper Credible Limit.

		Number of Occupied cells			Occupancy probability		
State	**Cells**	**Estimate**	**LCL**	**UCL**	**Estimate**	**LCL**	**UCL**
Idaho	189	87	65	112	0.46	0.34	0.59
Montana	194	117	85	132	0.60	0.44	0.68
Washington	93	40	21	62	0.43	0.23	0.67
Wyoming	157	24	11	41	0.15	0.07	0.26
Total	633	268	182	347	0.42	0.29	0.55

The survey described in Lukacs et al. (2020, pp. 843–845) is scheduled to reoccur at 5-year intervals and was repeated during the winter of 2021–2022 in Washington, Idaho, Montana, and Wyoming with an additional 47 sample cells in portions of Oregon, Utah, and Colorado. For each sampling period, the same spatially balanced randomized and stratified sample is taken with the intent to have sufficient power to detect trends in wolverine occupancy over time (Lukacs et al. 2020, pp. 843, 849–850).

Table 2. Wolverine occupancy results (number of surveyed 15x15 km^2 cells (9.32 x 9.32 mi) and number of detections) from 2016-2017 and 2021–2022 Western States Wolverine Conservation Project surveys (from Mosby et al. 2023, p. 3). Percent detections in parentheses. NA = not applicable.

State	Cells surveyed 2016-2017	Cells surveyed 2021-2022	Detections 2016-2017	Detections 2021-2022
Idaho	59	58	20 (33.8%)	20 (34.5%)
Montana	48	47	21 (43.7%)	8 (17.0%)
Washington	26	24	9 (34.6%)	3 (12.5%)
Wyoming	52	51	6 (11.5%)	13 (25.5%)
Colorado	0	16	NA	0
Oregon	0	16	NA	0
Utah	0	15	NA	0

Within the original 4-state area (i.e., Idaho, Montana, Washington, and Wyoming), non-spatial occupancy model estimates were slightly lower in 2021-2022 (mean occupancy = 0.33; 95% credible interval 0.21–0.34) compared to 2016-2017 (mean occupancy = 0.27, 95% credible interval 0.27–0.39), but with overlapping confidence intervals (Mosby et al. 2023, p. 4; Table 2). Despite overlapping confidence intervals, Bayesian analysis revealed an 85% chance that the occupancy estimate from 2021–2022 was outside the 95% credible interval of the 2016–2017 occupancy estimate (Mosby et al. 2023, p. 4). The percentage of surveyed cells that were occupied decreased between the sampling periods in Montana (43.7% to 17.0%) and Washington (34.6% to 12.5%), increased in Wyoming (11.5% to 25.5%) and remained relatively unchanged in Idaho (33.8% to 34.5%) (Table 2). Spatial occupancy models by geographic area showed substantial differences between the sampling periods, with both lower and higher occupancy probabilities depending on the geographic area (Table 3; Mosby et al. 2023, pp. 4–7). Although no wolverines were detected during the 2021–2022 survey in the sampled cells of Oregon, Utah, or Colorado (Table 2), recent wolverine detections from other research efforts or incidental observations have been reported in Oregon, Utah, and California (see *Wolverine Observations and Dens [2009–2022]*, below).

Table 3. Per cell wolverine spatial occupancy estimates in geographic areas during the 2016–2017 and 2021–2022 surveys in Idaho, Montana, Washington, and Wyoming (from Mosby et al. 2023, p. 4)

Geographic Area	Occupancy Probability 2016-2017	Occupancy Probability 2021-2022
Northern Continental Divide	0.8–1.0	0.2–0.4
Washington Cascades	0.4–0.6	0.2–0.4
Central Mountains of Idaho	0.4–0.6	0.6–0.8
Greater Yellowstone Ecosystem	0.1–0.3	0.2–0.4
Bitterroot Mountains of Idaho and Montana	0.1–0.3	0.0–0.2

Despite differences between the sampling periods, Mosby et al. (2023, p. 7) indicate that interpretations of the relationship between the two estimates be considered cautiously, and that repeated surveys into the future will be helpful in ultimately interpreting any trends in occupancy estimates. The reasons for the observed changes in occupancy by geographic region are not yet clear, and could be sampling anomalies, a real shift in distribution, or some combination of factors (Mosby et al. 2023, p. 7).

Wolverine Observations and Dens (2009–2023)

To further evaluate the current distribution of the wolverine, we solicited information from State wildlife agencies, the U.S. Forest Service, the National Park Service, Tribes, researchers, and others regarding recent verified or confirmed wolverine observations in the western U.S. We then mapped these 2009–2023 occurrences to help visualize the wolverine's current distribution, only including those observations that were considered "confirmed," "verified," or "trusted" by credible sources using the definitions described by Aubry et al. (2007, p. 2148). We used different symbols for observations between 2009–2016 and 2017–2023 to help visualize differences since our last mapping effort for our 2018 SSA (Figure 2). To circumscribe the known breeding distribution of wolverines, we also mapped confirmed den locations over the last three wolverine generations (2000–2022). In this section, we also include a discussion of specific information on wolverine observations and distribution on a State-by-State basis.

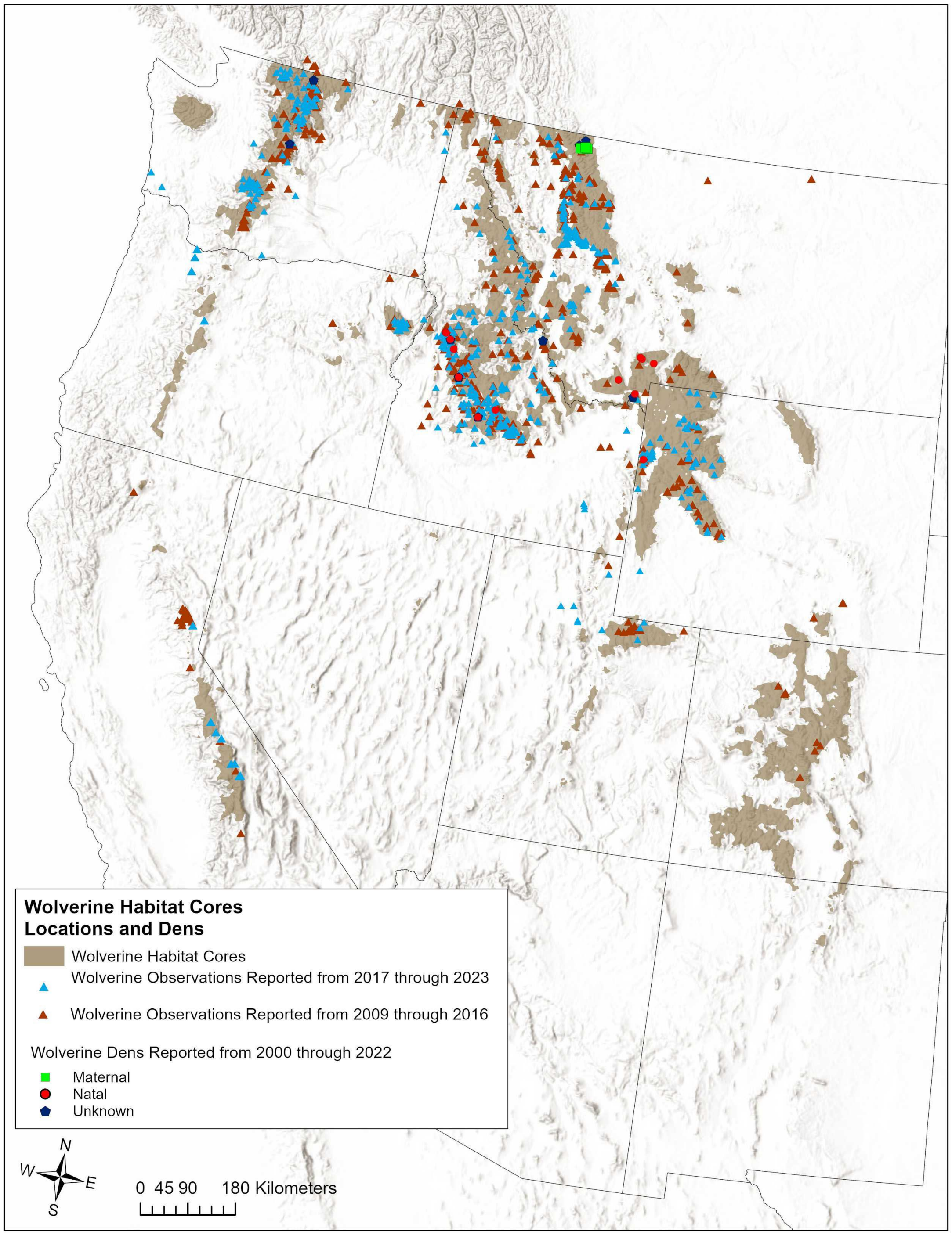

Figure 2. Wolverine observations (2009–2023) and dens (2000–2022) from various sources (State wildlife agencies, U.S. Forest Service, National Park Service, and others), and modeled wolverine habitat core areas (from Carroll et al. 2020, p. 4). Natal dens are those used during parturition, maternal dens are those used after the natal den and before weaning, and unknown den status indicates a confirmed den as either a natal or maternal den.

California

In our 2018 SSA, we included the occurrence of a resident male wolverine near Truckee, California (documented from 2008–2018), far from any other known wolverine occurrences (California Department of Fish and Wildlife [CDFW] 2020, unpaginated). Prior to that observation, wolverines had not been detected in California since the 1920s (CDFW 2023, unpaginated). Given the age of the wolverine and the lack of detections since 2018, the CDFW reported in 2000 that there may no longer be any wolverines in California (CDFW 2020, unpaginated). However, in the spring of 2023, there were several verified observations (likely of a single individual, and likely a different individual than observed from 2008–2018) in the Inyo National Forest and Yosemite National Park (CDFW 2023, unpaginated).

Colorado

Only one wolverine has been confirmed in Colorado in the last century (Packila et al. 2017, p. 400)—a subadult male wolverine that crossed atypical habitat and movement obstructions from northwestern Wyoming into Colorado; after 3 years in Colorado the animal was ultimately shot in 2016 in a cow pasture in North Dakota (Packila et al. 2017, pp. 400–402; USFWS 2018, pp. 12, 23). While a significant amount of modeled core habitat has been identified for wolverines in Colorado (Figure 2), no wolverines are currently known to occur there and there have been no verified wolverine observations in the last seven years (approximately equal to one wolverine generation).

Idaho

Since providing the last dataset to the USFWS on November 29, 2017, the Idaho Department of Fish and Game (IDFG) has assembled 537 new wolverine observation records (IDFG 2022, *in litt.*, p. 4). These records consist of observations documented during wildlife inventories or targeted surveys conducted by IDFG, other agencies and subject-matter experts (e.g., academic researchers) and incidental observations by biologists, along with high-quality observations by the public (including incidental captures by trappers). Due to the large home ranges of wolverines, these observations likely contain multiple entries pertaining to the same individuals. Therefore, the number of observations cannot be used to infer wolverine population size.

Our understanding of the broad-scale distribution of wolverines in Idaho since our 2018 SSA has not changed substantially. Statewide occupancy results from 2021–2022 show wolverines were detected in a similar percentage of 15 x 15 km (9.32 x 9.32 mi) grid cells as in 2016–2017 (Table 2). We also received new information relative to wolverine distribution and occupancy at finer spatial scales for Idaho, which we summarize below.

Salmon River Mountains: Results from a camera-trap and DNA survey in the McCall portion of the wolverine winter recreation study area (Heinemeyer et al. 2019, entire) within the Payette National Forest in central Idaho conducted in the winter of 2020–2021 found that previously documented territories appeared to be vacant (Mack and Hagen 2022, p. 13), which they consider to be supportive of a conclusion from Heinemeyer and Squires (2014, p. 7) of an incremental loss of resident wolverines from 2010 and 2011 to 2014. The 2020–2021 winter survey study results, from 9 captured animals in 2011 to just 4 animals confirmed in 2021 within the Payette National Forest study area, led the researchers to suggest "that what was considered to be a stable core subpopulation area could, in fact, be more tenuous" for this region (Mack and Hagen 2022, p. 13). The researchers noted that they were not always able to obtain high-quality DNA and/or diagnostic photographs to be positive of a wolverine's identity; thus, the final number of individual wolverines contains a level of uncertainty and could be high or low (Mack and Hagen 2022, p. 12). In contrast, surveys of wolverine activity within the Boise National Forest in central Idaho appeared stable, with some differences noted in distribution (Mack and Hagen 2022, pp. 12–13). Overall, this 2020–2021 central Idaho survey detected 7 individual wolverines (likely at least 8) across 14 camera stations through a combination of DNA analyses and photographs (Mack and Hagen 2022, p. 6). Of the DNA samples collected in which a gender and individual profile could be completed, the study reported one new male wolverine not previously recorded in the Genomics Center database (Mack and Hagen 2022, pp. 7, Table 1).

Lemhi and Lost River Mountains: Additional detections of wolverines (via camera bait stations) were confirmed in the Lost River and Lemhi Ranges in southeastern Idaho in the winter of 2017–2018 (Mack 2019, entire). Prior to this study, there was no confirmed contemporary record of a female wolverine in the Lemhi Range (Mack 2019, p. 10).

There are very few wolverine records from the Lost River Range, which may, in part, be the result of less focused effort (such as camera surveys) to detect wolverines in this range as compared with the Lemhi Range (Mack 2019, p. 11). The 2017–2018 winter camera survey represented the only systematic survey that had sampled the length of the mountain range (Mack 2019, p. 10). One wolverine (a female) was detected in the Lost River Range, and wolverine activity at this location was documented at several different times of the year (Mack 2019, p. 10). Whether this female was a resident of the area and whether she was the only animal present, was not determined (Mack 2019, p. 10). Overall, the study concluded that, based on the limited area and linear configuration of these two mountain ranges, only one male and one+ female could likely maintain territories in the Lemhi Range and possibly the Lost River Range (Mack 2019, p. 11). The study also reported, based on DNA analysis, that one female wolverine in the Lemhi Range and one female in the Lost River Range were new to the wolverine genomics database (Mack 2019, pp. 8, Table 1).

Caribou Targhee National Forest: Surveys conducted in 2019–2020 in the Caribou Targhee National Forest in both the Southeast and Upper Snake IDFG regions, and in the Boise National Forest in the Magic Valley Region detected wolverines at one location in the Magic Valley Region, and one location in the Southeast Region. No wolverines were detected in the Upper Snake Region despite this area containing a larger amount of modeled wolverine habitat and its proximity to known occupied habitat in the Greater Yellowstone Ecosystem (Mosby 2020, p. 4).

Lastly, surveys conducted by the U.S. Forest Service on the southern half of the Bitterroot National Forest from 2013–2019 genetically identified 3 female and 13 male wolverines (Paul 2021, p. 13). Genetic results for the northern half of the Forest, in Montana, are reported below.

Montana

In the northern half of the Bitterroot National Forest, a total of 13 individuals (4 females and 9 males) were genetically identified by volunteer-led surveys from 2015–2019 (Paul 2021, p. 12). When combined with the U.S. Forest Service's work on the southern half of the Forest in Idaho, 24 wolverines (7 females, 17 males) were identified in the Bitterroot National Forest between 2013–2019 (Paul 2021, p. 13). This survey also documented evidence of reproduction and confirmation of a resident population of wolverine in the Sapphire Mountains in 2018 (Paul 2021, p. 21).

Data from the 2021–2022 multi-state wolverine occupancy survey in Montana show an overall decline in wolverine detections and spatial occupancy between 2016–2017 and 2021–2022 (Table 2; Mosby et al. 2023, pp. 4–6). In addition to detections during formal surveys, another 104 verified wolverine detections, within 16 different cells that overlap wolverine habitat, were gathered from volunteers and observers during the 2021–2022 sampling period (Montana Fish, Wildlife, and Parks [MTFWP] 2022, *in litt.*, p. 2). Between January 1, 2018, and October 19, 2022, volunteers recorded 382 wolverine detections in areas across western Montana and as far east as Lewistown (MTFWP 2022, *in litt.*, p. 2). Due to the large home ranges of wolverines, these observations likely contain multiple entries for the same individuals. Therefore, the number of observations cannot be used to infer wolverine population size.

Oregon

In Oregon, there were five verified wolverine sightings between 1929 and 2010, with no verified sightings between 1992 and 2010 (Magoun et al. 2013, p. 5). Three individuals, including a subadult male, an adult male, and an adult of unknown sex (although photographs suggest this wolverine was also a male) were detected at camera stations in the Wallowa Mountains in 2011 (Magoun et al. 2013, pp. 11–12). Only the adult male wolverine detected in 2011 and 2012 has been detected since that time, with a recent detection on September 19, 2022 (Oregon Department of Fish and Wildlife [ODFW] 2022, *in litt.*, p. 36), indicating his ability to persist in the area over multiple years. There is no verified recent evidence of female wolverines in Oregon. In spring 2023, there were multiple wolverine sightings (probably of the same individual, based on the timing and trajectory of the observations), first around Portland and later in the central Cascades.

Utah

Since 2005, wolverines have been confirmed in the Bear River, Wasatch, and Uinta Ranges of northern Utah, including a young female in 2016 (Utah Division of Wildlife Resources [UDWR] 2022, *in litt.*, p. 2). However, there are no recent records of wolverine reproduction in Utah. The UDWR documented recent wolverine observations in Utah in at least 13 locations in the northern portion of the State, but we do not know if these observations represent a single individual or multiple animals. Several observations were in atypical habitat, such as the lakebed of Great Salt Lake and adjacent urban areas and are presumably of a dispersing or transient individual. The UDWR captured and radio-collared an estimated 3-year-old male wolverine in 2022. This individual was relocated to the Uinta Mountains due to depredation on domestic sheep. The wolverine was tracked for approximately one month until his tracking collar malfunctioned.

Washington

In Washington, the wolverine population in the Cascade Mountains likely consists of fewer than 50 individuals (Lewis 2022, *in litt.*, p. 1). Wolverine habitat in the North Cascades spans the U.S.–Canada border and the population is connected across this border to the Cascade Mountains in British Columbia south of Highways 1 and 3 (Aubry et al. 2023, pp. 4, 14–15). Based on a limited set of verified detections (e.g., photographs and genetic identifications) of wolverines over the last two decades, wolverines appear to have been at least intermittently present in the southern Cascades (i.e., south of I-90) since the mid-2000s, and consistently present since 2010 (Lewis et al. 2020, p. 4). The National Park Service documented recent wolverine reproduction in Mount Rainier National Park, with a single female producing two kits in 2020 and two kits in 2021 (Wolstenholme 2022, *in litt.*, p. 2). Reproduction in the William O. Douglas Wilderness just outside Mount Rainier National Park was also documented in 2022 (2 kits) and in 2023 (3 kits) (Akins 2023, *in litt*., p. 1) A wolverine (presumably a lone disperser) was also sighted in 2021 on the Long Beach Peninsula feeding on an elephant seal carcass more than 145 km (90 mi) from the nearest occupied core habitat (Washington Department of Fish and Wildlife [WDFW] 2022, *in litt.*, p. 3).

Wyoming

Based on formal survey efforts and incidental observations, wolverines appear to be distributed across several areas in the Greater Yellowstone Ecosystem in Wyoming, yet occupancy rates were low in 2016–2017 (Figure 1 and Table 1). Recent observations were rare in the southern Wyoming Range and Yellowstone National Park despite historical occupancy (Wyoming Game and Fish Department [WGFD] 2020, pp. 7–8). Notwithstanding their rarity in portions of the State, occupancy surveys in areas of suitable core habitats in Wyoming during the winter of 2021–2022 confirmed wolverines in more survey cells (13 of 51) than in 2016–2017 (6 of 52) (Mosby et al. 2023, pp. 4–6; Table 2). Observations of the persistent presence of two female wolverines in the Greater Yellowstone Ecosystem, as well as other observations of both males and females, suggest long-term residency and the potential for reproduction and continued population expansion in this ecosystem (WGFD 2020, p. i; Bjornlie et al. 2021, pp. 112–116).

Outside of the areas described above we are not aware of any further verified reports of wolverines in the western U.S. since publication of our 2018 SSA.

Population Densities

In our 2018 SSA, we reported wolverine density estimates (wolverines per 1,000 km^2 (621 mi^2)) in the contiguous U.S. collected during different timeframes ranging from 3.5 for the Greater Yellowstone Ecosystem (2001–2008), 4.5 for central Idaho (1992–1995), to 15.4 for northwestern Montana (1972–1977). Density estimates have not been reported for the Cascades in Washington.

There are no new density estimates available for any regions of the contiguous U.S.; however, new information on wolverine densities is available from southwestern Canada (Table 4). Recent wolverine density estimation in southern and central British Columbia and the Alberta Rockies has moved from traditional capture-mark-recapture (CMR) to spatially explicit capture-recapture

(SECR) models (Mowat et al. 2020, entire; Barrueto et al. 2020, entire; 2022, entire). Because CMR methods fail to fully account for animal movement off the sampling grid between surveys (closure), estimates of density obtained from SECR models tend to be lower than CMR models, and thus previous density estimates for wolverines that relied on non-spatially explicit CMR models may have been biased high (reviewed by Morehouse et al. 2020, p. 3). Likewise, population estimates extrapolated from density estimates, such as those used to estimate wolverine population size in the contiguous U.S. (Inman et al. 2013, p. 282) may have been biased high (see Population Estimates, below).

Using surveys and SECR models, wolverine densities estimates were developed for two study areas in southeastern British Columbia and the adjacent Rocky Mountains of southern Alberta (Mowat et al. 2020, entire). Wolverine population density estimates averaged 2 wolverines/1,000 km^2 (621 mi^2) across the study area, which is lower than estimates from previous studies (Mowat et al. 2020, p. 223). In southwestern Canada, wolverine densities are known to decline roughly along a north-south axis (Mowat et al. 2020, p. 220). However, recent data have revealed that wolverine densities at the northern end of that axis (approximately 70–170 miles north of the U.S.–Canada border), which includes high-quality wolverine habitat within a large national park complex, were lower than predicted (Barrueto et al. 2020, p. 293). In addition, wolverine abundance in the same study area declined by approximately 41% (from an estimated 54 individuals to an estimated 32 individuals) from 2011–2020 with an annual population growth rate of 0.924 (CI = 0.892–0.959) (Barrueto et al. 2022, pp. 4–5).

Table 4 presents wolverine density estimates for the U.S. and Canada, including recent estimates from southwestern Canada (Mowat et al. 2020, supporting information; Barrueto et al. 2022, p. 6).

Table 4. Wolverine density estimates (# per 1,000 km^2) for regions of the contiguous U.S. and southwestern Canada.

Region	Density estimate	Methods	Closure Correction	Citation
Southwestern Montana	1.4–1.8	Live-capture/radiotelemetry	No	Squires et al. (2007)
Northwestern Montana	15.4[a]	Live-capture/radiotelemetry and track counts	No	Hornocker and Hash (1981)
Northern Idaho	4–11.1	Live-capture/radiotelemetry and track counts	No	Copeland (1996)
Greater Yellowstone Ecosystem	3.5	Live-capture and genetic sampling	No	Inman et al. (2013)
Southeastern British Columbia	5.8	Live capture/photo traplines	No	Lofroth and Krebs (2007)
Southeastern British Columbia and Southwestern Alberta	0.9–4.4	DNA hair capture and mark-recapture	Yes	Mowat et al. (2020)
Rocky Mountain National Parks (Canada)	3.1	DNA hair capture and mark-recapture	Yes	Barrueto et al. (2020)

Rocky Mountain National Parks (Canada)	Decline from 3.6 (95% Bayesian Credible Interval [BCI] = 3.0–4.2) to 2.1 (95% BCI = 1.8–2.5) from 2011 to 2020	DNA hair capture and mark-recapture; remote cameras	Yes	Barrueto et al. (2022)
Unprotected areas around Rocky Mountain National Parks (Canada)	Decline from 0.9 (95% BCI = 0.7–1.2) to 0.5 (95% BCI = 0.3–0.8) from 2011 to 2020	DNA hair capture and mark-recapture; remote cameras	Yes	Barrueto et al. (2022)

[a] A substantial edge effect, because of a small (1,300 km^2 (808 mi^2)) study area and a liberal interpretation of what constituted a resident wolverine, likely biased Hornocker and Hash (1981) density estimate upward (Lofroth and Krebs 2007, p. 2166).

Population Estimates

In our 2018 SSA, we reported the total population estimates as well as total population capacity estimates for the western U.S. based on a habitat suitability model and extrapolations of wolverine densities from the Greater Yellowstone Ecosystem (Inman et al. 2013, entire). In Table 5, we provide the regional estimates of wolverine population size and capacity (Inman et al. 2013, p. 282). These estimates were based on resource selection function habitat modeling of wolverine telemetry data collected in the Yellowstone region from 2001 to 2010. Density estimates did not account for closure and, therefore, may be biased high (see Population Densities, above). As we discussed in detail in the 2018 SSA Report (USFWS 2018, p. 51), the population estimate presented in Inman et al. (2013, p. 282) for the contiguous U.S. was 318 individual wolverines (95% confidence interval [CI] 249–926). The wide confidence intervals for the population estimate and for the population capacity estimate (shown in Table 5) indicate imprecise numbers. Inman et al. (2013, p. 284) noted at the time that: “our knowledge of fundamental population characteristics such as current distribution of reproductive females and population trajectory is lacking or based on sparse data.”

Table 5. Estimates of wolverine population size and population capacity by region in the western U.S. (from Inman et al. 2013, p. 282). 95% confidence interval in parentheses.

Region	**Population Capacity Estimate**	**Population Estimate**
North Cascades	48 (37–138)	37 (29–103)
Northern Continental Divide	49 (38–138)	49 (38–138)
Salmon-Selway/Wallowa Mts	124 (97–352)	119 (93–338)
ID/MT Linkage	50 (38–173)	50 (38–172)
Greater Yellowstone Ecosystem	146 (119–412)	63 (51–175)
Southern Rockies	137 (108–390)	0
Sierra Nevada	45 (35–128)	0
Uinta	21 (17–58)	0
Bighorn	12 (10–35)	0
Great Basin	11 (6–48)	0
Oregon Cascades	1 (1–9)	0
Western United States	**644 (506–1881)**	**318 (249–926)**

In Table 6, we present a summary of new estimates of wolverine population size from southwestern Canada (Mowat et al. 2020, supporting information; Barreuto et al. 2022, p. 6). These estimates are based on density estimates that accounted for closure. No new estimates of the wolverine population in the North Cascades of British Columbia are available; the most recent estimate for this area was approximately 14 wolverines (95% CI = 8–27) (Lofroth and Ott 2007, pp. 2196–2197). A discussion of effective population size and its relevance to connectivity with Canada can be found in the **Genetics and Population Structure** section, below.

Table 6. Estimates of wolverine population size by region in southwestern Canada[a] (from Mowat et al. 2020, as updated by Barrueto et al. 2022 for Banff, Kootenay, and Yoho [BKY] National Parks[b]).

Region (Year)	Population Estimate (95% CI)
Northern Study Areas	
Banff, Kootenay, and Yoho National Parks (2013 and 2020)	49 (40–60); 20 (17–24)[b]
Mount Revelstoke and Glacier National Parks (2016)	27 (22–35)
Central Study Areas	
Central Rockies (2015)	25 (19–32)
Central Purcell (2016)	24 (20–29)
Central Selkirk (2014)	17 (13–21)
Southern Study Areas	
Southern Rockies (2016)	25 (19–32)
Southern Purcells (2013)	16 (13–20)
Southern Selkirks (2012)	5 (3–7)
Valhalla Ranges (2015)	6 (5–8)
Waterton-Westcastle (2014)	10 (8–13)
Southwestern Canada[a] (date for first listing and 2020)	204 (162–257); 175 (139–221)[b]

[a]Not including the Cascade Mountains; [b]Updated estimate based on Barrueto et al. 2022 in BK

Key Areas of Uncertainty for Wolverine Distribution, Density, and Abundance

Estimated wolverine population sizes in the contiguous U.S. are largely extrapolations from habitat models and density estimates in the Greater Yellowstone Ecosystem. Systematic surveys to obtain population estimates have not been attempted in the contiguous U.S. given the difficulty of surveying a species that is highly mobile and occurs across large areas that are difficult to access. Therefore, the true population size in the contiguous U.S. is unknown, as is the effective population size; best available estimates suggest populations are relatively small (~300 in the western U.S.).

Population trends and rates of change in the contiguous U.S. are also unknown. One study of population trends in southwestern Canada found an approximately 41% decline in wolverine abundance between 2011 and 2020, likely from one or more of the following causes: trapping, backcountry recreation, human development, and food availability (Barrueto et al. 2022, pp. 4, 6–8). This study occurred approximately 113– 274 km (70-170 mi) from the contiguous U.S. The rate of change outside their study area in other parts of southern British Columbia or Alberta (e.g., closer to the international border) remains unknown as does the extent to which this decline may have impacted dispersal of wolverines between Canada and the U.S.

3.2 Wolverine Habitat Use

Habitat selection occurs across a continuum from a species' range or distribution (first-order selection) to an individual or social group's home range (second-order selection), to use of various habitats within a home-range (third-order selection), to selection among specific resources at a site within the home-range (fourth-order selection) (Johnson 1980, p. 69). Research published since our 2018 SSA confirms that broad-level habitat selection (first- and second-order selection) at the southern edge of the wolverines' distribution can be accurately predicted using a small number of high-elevation variables and terrain features (Carroll et al. 2021a, pp. 1470–1471; Aubry et al. 2023, p. 7). New evidence from around the world reinforces that snow—especially persistent spring snow—is an important predictor of broad-scale wolverine distribution and density in most ecological domains (Aubry et al. 2023, pp. 15–16; Carroll et al. 2020, p. 8; Fisher et al. 2022, p. 10; Glass et al. 2021, entire; Mowat et al. 2020, p. 220); but persistent spring snow is apparently not a limiting factor in all ecological domains (see Persson et al. 2023, entire). At higher orders of selection (third- and fourth-order selection), the precise nature of the relationship between wolverine space-use and snow is complex, involving multiple snow characteristics (e.g., density, depth, and melt), various phases of the wolverine lifecycle (e.g., denning, feeding and food caching, within-territory movements, and dispersal) and sex-specific habitat selection (Carroll et al. 2021, p. 1469; Glass et al. 2021, entire; Heinemeyer et al. 2019, p. 16). While wolverines appear capable of occupying and reproducing in areas without persistent spring snow in some ecological contexts, wolverine dens outside of areas with persistent spring snow have thus far only been documented to occur in colder boreal or arctic environments in Canada and Scandinavia (Aronsson and Persson 2017, p. 266; Copeland et al. 2010, pp. 240–242; Fisher et al. 2022, p. 8; Jokinen et al. 2019, pp. 6–8; Webb et al. 2016, pp. 1466–1467; Persson et al. 2023, entire). Although persistent spring snow may not be limiting the distribution of wolverines in all areas, it could be limiting in some regions where there are differences in habitat features such as the abundance of alternative den site structures, competitors, or food resources (Persson et al. 2023, p. 9).

In the 2018 SSA we discussed the following confounding factors for understanding wolverine habitat: spatial and temporal scales of analyses, environmental variables evaluated in model selection, and correlations among habitat variables. Researchers attempt to address these confounding factors in various ways, including the use of multiple spatial and temporal scales, the removal of correlated variables, and the use of model selection techniques. Below, we describe new wolverine habitat studies and models that have been published since our 2018 SSA, organized by: (1) Habitat studies and models that are not specific to denning or burrowing (but some of which included denning animals); (2) habitat studies specific to denning or resting burrows; and (3) habitat studies that evaluated food-caching behavior – which has implications for year-round habitat selection.

Habitat Studies and Models

Numerous new habitat studies and models associate wolverine presence, movements, or density with various habitat features. Below, we review these new studies and discuss their relevance to our understanding of wolverine ecology and conservation. Because wolverine space-use can vary across the species' Holarctic range, we organized our review geographically, with new research from the contiguous U.S. (Table 7), Canada (Table 8), and Alaska and Scandinavia (Table 9). We also include a separate discussion of habitat studies specific to denning habitat given its central importance to wolverine reproductive success. Finally, we evaluate new research on food caching behavior and cache site selection because of its potential significance to wolverine reproduction and survival.

Roads, human development, recreation, and other factors can influence wolverine habitat selection, movement, and mortality risk (Scrafford et al. 2018, entire; Heinemeyer et al. 2019a, entire, 2019b, entire; Balkenhol et al. 2020, entire). These factors, and their impact on wolverine distribution, population dynamics, effective dispersal, and population connectivity are discussed in greater detail in our **Stressors** section, below.

Contiguous United States

In the Greater Yellowstone Ecosystem, distance to high-elevation talus, snow water equivalent (a surrogate for snow depth), and latitude-adjusted elevation were the most important environmental factors explaining selection of home ranges and habitats within home ranges. The importance of these environmental predictors of wolverine habitat selection varied by scale and sex (Carroll et al. 2021a, pp. 1468–1471). These habitat variables are also known to be important in defining the wolverine's distribution (first-order habitat selection) (Inman et al. 2013, p. 278). Third-order habitat selection models (within a home range) performed poorly compared to second-order selection models (home range selection) models suggesting that other factors not included in the third-order model may be important at this scale, or that finer-scale covariate data are needed to understand wolverine habitat selection within wolverine home ranges (Carroll et al. 2021a, pp. 1469–1471).

Table 7. Wolverine habitat studies and models in the contiguous U.S. (2018–present).

Study Location	Wolverine Data	Model Type	Source
Northern Rocky Mountains and Cascades	Camera traps and DNA	Occupancy model (winter)	Lukacs et al. (2020)
Western U.S.	Radio telemetry and GPS (from Inman et al. 2012)	Resource selection functions (core areas); landscape resistance models (dispersal/connectivity)	Carroll et al. (2020)
Greater Yellowstone Ecosystem	Radio telemetry and GPS (from Inman et al. 2012)	Random forests	Carroll et al. (2021a)
U.S. Northern Rocky Mountains	DNA samples from harvested animals and research projects (previously analyzed by Schwartz et al. 2009)	Landscape genetics model (dispersal/connectivity)	Balkenhol et al. (2020)
Central Idaho and Greater Yellowstone Ecosystem	GPS	General linear mixed-effects model	Heinemeyer et al. (2019a)
North Cascades Ecosystem (including the U.S. and B.C.)	GPS/ARGOS satellite tags	Mixed effects logistic regression	Aubry et al. (2023)

A multivariate, multiscale landscape genetics approach was used to detect environmental predictors of genetic structure (the amount and distribution of genetic variation within and among populations) at several scales within the Northern Rocky Mountain Region of the U.S (Balkenhol et al. 2020, p. 791). Results from dispersal suitability models developed for wolverines indicate that isolation by landscape resistance (areas that individuals are less likely to traverse due to high energy, mortality, or other biological costs) explained more of the variation in wolverine genetic differences than did isolation by distance (Balkenhol et al. 2020, pp. 795–797). This means that wolverines are moving non-randomly across the landscape in association with specific landscape features. Snow depth (average 1-year snow depth at 1 km^2 (0.62 $mi.^2$) resolution); terrain ruggedness (measure of how jagged or flat the terrain is on average); and housing density best predicted gene flow in wolverines, and the relative importance of variables was scale dependent (Balkenhol et al. 2020, pp. 795–797). Models that incorporated landscape features explained more of the variation at scales relevant to gene flow within wolverine habitat complexes (79% of the variation explained) than at scales reflecting long-distance dispersal across areas not typically inhabited by wolverines (65% of the variation explained) (Balkenhol et al. 2020, p. 790). Snow depth was the most important variable for predicting genetic structure overall, and at scales relevant to individual habitat complexes, where it explained 43% of the variance (Balkenhol et al. 2020, p. 790). The study noted that, had they only analyzed the all-scale model, they would have concluded that snow depth is the best variable for predicting genetic structure, and while that finding would not be incorrect, it provides an incomplete picture, because deep snow in the region occurs only within typical wolverine habitat, where most gene flow occurs across usual dispersal and mating distances (Balkenhol et al. 2020, p. 799). At broad spatial scales, housing density and terrain ruggedness were the most important factors, explaining 55% and 25% of variation, respectively (Balkenhol et al. 2020, p. 790).

Lukacs et al. (2020, entire) describe an occupancy model for wolverines across the Northern Rocky Mountains and Cascade Mountains, where they evaluated the relationship between several covariates and wolverine occupancy. Although they found no association between wolverine occupancy and vegetative productivity, human disturbance, or habitat patch size, testing habitat relationships was not a primary focus of their research. The scale of the study design (15 x 15 km (9.32 x 9.32 mi) sampling cells) and restriction of the sampling frame to high-elevation forest also predisposed this study to have low statistical power to detect wolverine-habitat relationships (Lukacs et al. 2020, p. 849). Therefore, this study was not particularly informative for assessing wolverine-habitat relationships.

A species distribution model for the Cascade Range in southern British Columbia and Washington using Argos satellite location data on 10 resident adult wolverines from 2008–2016 showed that three climatic variables explained the most variation in wolverine location data: proximity to the transitional zone near the alpine tree line, number of frost-free days per year, and annual precipitation as snow (Aubry et al. 2023, p. 10). Model validation provided evidence that wolverine distribution (first-order habitat selection) in the Cascades is constrained by climatic conditions and that snowy cold environments delimit the areas that are "overwhelmingly associated with resident wolverines" (Aubry et al. 2023, p. 16). High variation in frost-free days associated with maritime influences on the western side of the Cascades precluded wolverine use in some areas (Aubry et al. 2023, p. 13). The highest-use areas were on the eastern side of the Cascades where alpine habitats had fewer frost-free days (Aubry et al. 2023, p. 15). These findings were consistent with other models of first-order habitat selection, indicating that wolverines are restricted primarily to the transitional zone between treeline, below which environmental conditions become too warm, and upper elevations of permanent ice and snow where there is insufficient food and cover to support wolverines (Aubry et al. 2023, pp. 13–14).

Carroll et al. (2020, entire) updated Inman et al.'s (2013, entire) analysis of second-order wolverine habitat selection (home range selection) across the western U.S. by identifying landscape variables most correlated with wolverine home ranges using GPS location data on 38 wolverines from 2001 to 2010. The top resource selection function model included landform (e.g., ridges and peaks), vegetation classification, distance to high-elevation talus, latitude-adjusted elevation, average monthly snow water equivalent, and human modification (Carroll et al. 2020, p. 8). Carroll et al. (2020, pp. 3–8) then used the results of the resource selection function model to identify core areas and assessed the connectivity between these core areas using a landscape resistance model, validated with GPS location data from dispersing wolverines (Figure 3). Their results showed that resident wolverines in core habitats are far more sensitive to low-quality habitat than are dispersing individuals, but that dispersers still follow lower-resistance pathways that connect higher-quality core habitats (Carroll et al. 2020, p. 9). Nevertheless, there is still some threshold beyond which wolverine movement appears to be constrained that warrants further investigation (Carroll et al. 2020, p. 9; Fisher et al. 2022, p. 11).

Heinemeyer et al. (2019a, entire) modeled third-order (within home range) wolverine habitat selection in areas of the Northern Rocky Mountains with high amounts of winter backcountry recreation. They found significant differences in male and female habitat selection (Heinemeyer et al. 2019a, p. 9). The best model for male wolverines uniquely included distance to roads and proportion of lower-elevation grass and shrub cover, while the best model for female wolverines uniquely included talus, persistent spring snow cover (defined in the cited studies as snow cover present between 24 April and 15 May) and forest edge:area covariates (Heinemeyer et al. 2019a, p. 9). Best models for both sexes included covariates for topographic position index, quadratic form of slope, distance to forest edge, solar insulation and percentage cover of forest, riparian, and montane open cover types. Models indicated that wolverines avoided areas of both motorized and non-motorized winter recreation with off-road recreation eliciting a stronger response than road-based recreation (Heinemeyer et al. 2019a, pp. 11–13). Female wolverines exhibited stronger avoidance of off-road motorized recreation and experienced higher indirect habitat loss than did male wolverines (Heinemeyer et al. 2019a, pp. 16–17). Models further indicated that wolverines showed negative functional responses to the level of recreation exposure within home ranges, with female wolverines showing the strongest functional response to motorized winter recreation (Heinemeyer et al. 2019a, pp. 13–14; 17–18).

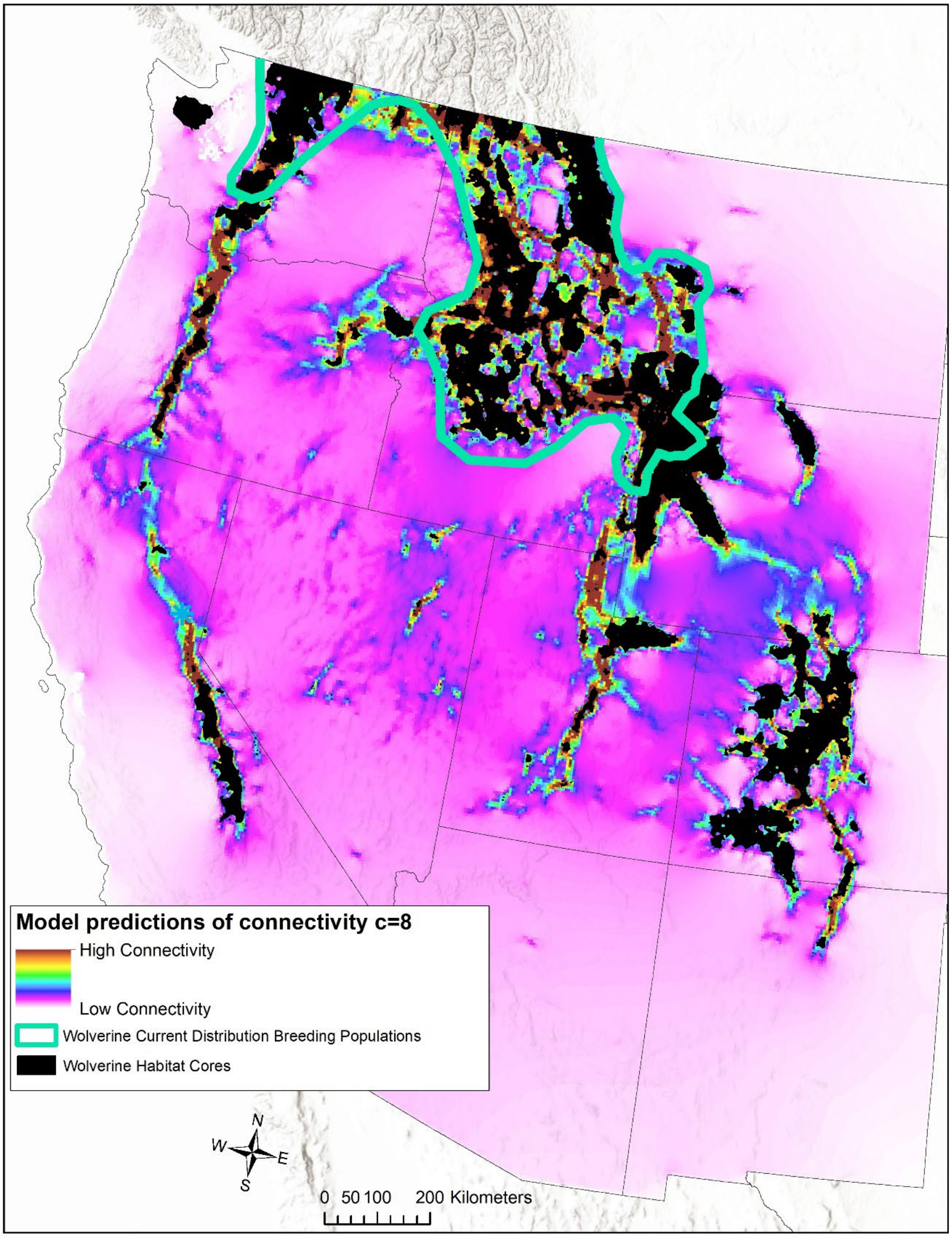

Figure 3. Model of wolverine landscape connectivity from Carroll et al. 2020. Areas with higher connectivity values are shown in yellow/orange/red and areas with lower connectivity values are shown in white/pink/purple. C=8 represents the modeled relationship value for habitat quality and resistance determined to best describe observed wolverine dispersal.

Canada

Wolverine density in and around the national park complex in the southern Canadian Rocky Mountains was three times higher within national parks, increased with spring snow cover, and decreased with increasing night light intensity (a measure of human development) (Barrueto et al. 2022, p. 4). Along the Front Range of the Canadian Rocky Mountains, wolverines selected areas with natural land-cover and high snow cover and avoided anthropogenic features and heterospecific competitors (Heim et al. 2019, pp. 2499–2502). The authors hypothesize that competition from other carnivores that more readily exploit anthropogenic change may exacerbate the habitat loss and displacement impacts of such changes on wolverines, although given their small sample size they called for more studies of this phenomenon to confirm their preliminary findings (Heim et al. 2019, pp. 2503–2504).

Using existing camera trap data from two previous studies (Fisher et al. 2013, entire; Heim et al. 2019, entire) in the Rocky Mountains of Alberta, Chow-Fraser et al. (2022, pp. 4–5) found that wolverine occurrence in space and time was best explained by coyote (*Canis latrans*) occurrence and the density of linear disturbance features (e.g., roads, pipelines, seismic lines, motorized and non-motorized recreational trails), with both of these factors decreasing the likelihood of wolverine occurrence. However, interaction among these variables existed, with wolverines and coyotes more likely to co-occur as linear disturbance densities increased (Chow-Fraser et al. 2022, p. 6). Declining wolverine occurrence in that area (Fisher et al. 2013, p. 713; Heim et al. 2017, pp. 8908–8910) and the success of coyotes there (Heim et al. 2019, pp. 2499–2502) suggests that coyotes are more tolerant of anthropogenic disturbance, more able to exploit linear features, and may be outcompeting wolverines (exploitation competition, which means indirect competition for common resources like food or territories) and excluding them from part of their former range (Chow-Fraser et al. 2022, p. 6).

In the southern Canadian Rockies, wolverine density was found to be positively correlated with the number of years of persistent spring snow cover and negatively correlated with road density (Clevenger 2019, p. 62; Mowat et al. 2020, pp. 218–219). Female densities in areas with more cumulative years of persistent spring snow were higher than male densities which suggests there may be some association with the preference for snowy areas when denning. However, the researchers acknowledge that their various hypotheses did not specifically test for why females preferred snow more than males and suggest the difference could be due to the smaller home ranges of females which may allow them to locate their ranges in relatively better habitat conditions (Mowat et al. 2020, pp. 221, 224).

A separate study, also in the Canadian Rockies, found that food availability and human disturbance were major drivers of wolverine distribution in winter (Kortello et al. 2019, p. 7). Persistent spring snow was inversely correlated with forestry roads in their study area, making it difficult to discern the true driver of wolverine distribution in winter, likely because their forestry roads variable incorporated information on both climate and disturbance (Kortello et al. 2019, p. 8). Removal of the forestry roads variable from their models resulted in persistent spring snow being an important factor in explaining the variation in female wolverine distribution in winter and overall wolverine distribution at coarse scales (using a 10-km (6.2 mi.) buffer from sampling sites) (Kortello et al. 2019, p. 8). The researchers concluded that their results "do not reject the hypothesis that wolverine occurrence is constrained by an obligate association with persistent spring snow (Aubry et al. 2007, p. 2154; Copeland et al. 2010, p. 244), but do suggest the alternative explanation that the relationship between spring snow and wolverine distribution could be functionally related to the distribution of food, disturbance or mortality risk." (Kortello et al. 2019, p. 8).

Table 8. Wolverine habitat studies and models in Canada (2018–present).

Study Location	Wolverine Data	Model Type	Source
Canadian Rocky Mountains	Hair samples (DNA) from Heim et al. (2017), Kortello et al. (2019), Mowat et al. (2020), and Barrueto et al. (2020); camera traps from Barrueto et al. 2022	Ensemble species distribution model	Schepens et al. (2023)
Canadian Rocky Mountains	Camera traps, Hair samples (DNA)	Integrated Bayesian spatial capture-recapture models	Barrueto et al. (2022)
Front Range of the Canadian Rockies	Camera traps	Species distribution models and redundancy analysis	Heim et al. (2019)
Front Range of the Canadian Rockies	Camera traps (from Fisher et al. 2013 and Heim et al. 2019)	Generalized linear mixed models	Chow-Fraser et al. (2022)
Southern Canadian Rocky Mountains	Hair and scat samples (DNA), camera surveys, and trapping mortality data	Spatially explicit capture-recapture model	Clevenger (2019); Mowat et al. (2020)
Canadian Rocky Mountains	Hair samples (DNA)	Occupancy models (Female distribution in winter)	Kortello et al. (2019)
Northern Ontario, Canada	Aerial track surveys	Hierarchical Bayesian occupancy models	Ray et al. (2018)
Northern Alberta, Canada	GPS	Descriptive study of dens	Jokinen et al. (2019)

A synthesis of four wolverine habitat models in the southern Canadian Rocky Mountains found that persistent spring snow was the most strongly correlated variable with wolverine habitat (r=0.82), followed by a negative relationship with resource road (typically one- or two-lane gravel road) density (r=-0.60) (Schepens et al. 2023, p. 8). As with other habitat models in the Rocky Mountains, this study could not disentangle the inverse relationship of snow cover and human disturbance (Schepens et al. 2023, p. 11). Snow forecasts within the British Columbia portion of the study area projected a 44% decline in spring snow cover by 2080 under RCP 8.5 (Schepens et al. 2023, p. 10–11).

Analysis of wolverine tracks from aerial surveys in the Hudson Bay Lowlands and the Boreal Shield in Ontario from 2003–2012 showed that wolverine occupancy was most influenced by geographic location (wolverines were concentrated in the northwestern portion of the study area) and thawing degree days (number of days per year with mean temperature greater than 0° C) (Ray et al. 2018, pp. 1484–1486). However, the authors cautioned that the influence of the number of thawing degree days on their results should not be considered proof that the persistence of spring snow is driving wolverine distribution, as thawing degree days was likely correlated with other variables such as summer temperature, soil temperature and moisture, forest cover types and human development, all of which could influence the occurrence and relative abundance of wolverines and their food resources (Ray et al. 2018, p. 1487).

Alaska

A habitat selection study of 21 adult, non-denning wolverines (11 female, 10 male) fitted with GPS collars in the Alaskan arctic found that wolverines generally selected more rugged areas closer to streams, rivers, and lakes (Glass et al. 2021a, p. 893). This study also showed that snow characteristics are important to wolverines for reasons other than solely creating reproductive dens. Specifically, they found that non-denning wolverines select deeper, denser snow, but only when that snow is not undergoing melt (Glass et al. 2021a, pp. 894–895). Wolverine movement rate was negatively influenced by snow depth but positively influenced by snow density (Glass et al. 2021a, p. 895), although the width of the confidence bands of model coefficient estimates revealed a measure of uncertainty in these relationships. The wolverine's observed preference for denser snow might be a function of both ease of movement across the surface, as well as the ability of denser snow to maintain snow cavities and tunnels (Glass et al. 2021a, p. 895).

Table 9. Wolverine studies and models in Alaska and Scandinavia (2018–present).

Study Location	Wolverine Data	Model Type	Source
Alaska Northern Alaska	GPS with accelerometers and light/temperature loggers	Regression and resource selection functions	Glass et al. (2021a, b)
Alaska Northern Alaska	GPS, direct observations, den excavation	Descriptive studies of dens and resting burrows	Glass et al. (2021b, 2022)
Scandinavia Northern Sweden	Snow-track surveys	Generalized linear models, structural equation modeling, and non-metric multidimensional scaling ordination	Stoessel et al. (2019)
Scandinavia Northern Sweden	GPS	Cox proportional hazards models (dens)	Heeres (2020)
Scandinavia Norway and Sweden	GPS	Conditional logistic regression (food caches)	van der Veen et al. (2020)
Scandinavia Norway and Sweden	GPS, opportunistic sampling, genetic	Spatial capture-recapture models	Moqanaki et al. (2023)

Scandinavia

In a 12-year study of wolverine tracks in the Scandinavian mountain-tundra community, Stoessel et al. (2019, entire) created models that largely failed to explain the abundance and distribution of wolverines, and showed only a few weak relationships. They speculated that the wolverine's ability to cope with unpredictable food resources, and their food caching behavior, might explain the lack of clear patterns in their data.

Using spatial capture-recapture models and a data set of 742 genetically identified wolverines collected over 0.5 million km^2 across their entire range in Norway and Sweden, researchers identified landscape-level factors explaining the current population density of wolverines in the Scandinavian Peninsula (Moqanaki et al. 2023, entire). Distance from the relict range along the Swedish–Norwegian border, where the wolverine population survived a long history of persecution, along with regional differences in management and environmental conditions were found to play the primary roles in shaping spatial patterns of present-day wolverine density. Slower recolonization was also documented in areas that had set lower wolverine population goals in terms of the desired number of annual reproductions (Moqanaki et al. 2023, p. 10).

Habitat Studies Specific to Resting Burrows and Reproductive Dens

Denning habitat has been a focus for wolverine conservation because wolverines have naturally low reproductive rates. Impacts to denning habitat could thus have important consequences for demographic rates (Fisher et al. 2022, p. 8). In addition, there is growing evidence that wolverines rely on subnivean space (the environment between snow and terrain) for thermoregulation, to escape predation risk, and/or to cache food (van der Veen et al. 2020, pp. 8–10; Fisher et al. 2022, p. 10). Although wolverines have been documented to den in areas without persistent spring snow (e.g., Jokinen et al. 2019, pp. 4–9; Persson et al. 2023, entire), this phenomenon has thus far only been observed in cold, high-latitude boreal or arctic regions. In the alpine habitats of the contiguous U.S., there is no evidence that wolverines have denned in areas without persistent spring snow. As noted by Persson et al. (2023, p. 9), the importance of persistent spring snow for denning "may vary among areas with abundance of alternative den site structures, competitors, and food resources….In areas with steep altitudinal gradient, such as the US Rocky Mountains (Inman et al. 2013), it could be difficult to determine the importance of spring snow cover as it may covary with terrain ruggedness, vegetation, abundance of competitors, and human development."

In a study of den-shifting behavior in the arctic of northern Sweden, Heeres (2020, p. 11) hypothesized that wolverines would use more dens during a single breeding season in forest habitats than in alpine habitats because forests have less reliable snow cover and earlier snowmelt. Den-shifting behavior represents a tradeoff between moving and risking potential energy loss and vulnerability of offspring during den shifts versus staying in the original den site and risking exposure to disturbance or changed conditions that might make the original den site unsuitable. Studying 18 adult female wolverines fitted with GPS collars over an 11-year period occupying 271 den sites, Heeres (2020, p. 15) determined that, on average, a female used 12 den sites during 1 denning season (range: 4–28; median: 10). As predicted, female wolverines had a higher probability of shifting den sites in forested habitats, as compared to alpine habitats, likely as a result of earlier snow melt in forests which may make den sites uninhabitable early in the season (Heeres 2020, p. 20), although snow cover was a non-significant variable for both habitat types, possibly as a result of the coarse scale of the snow cover data (Heeres 2020, pp. 21–22). Other factors related to den shifting behavior included the level of denning experience which was quantified as the number of previous reproductive attempts by an individual (lower den-shift probability), temperature (higher den-shift probability in the warmer forested habitats; non-significant den-shift probability in alpine habitat), food resource availability (higher den-shift probability, which could be related to accessing food or increased human presence), and cub age (more shifting as cubs mature and are able to move to food resources) (Heeres 2020, pp. 20–22).

In a more extensive study of den shifting behavior in Sweden, investigating 245 den sites, researchers found the mean number of den sites per female in a single denning season was 8.8± 8.5 (range: 1–28; median: 6) (Aronsson et al. 2023, p. 6). Den site changes, inter-den movement distances, and the daily distance between den sites increased as the denning season progressed (Aronsson et al. 2023, pp. 6–8). These results highlight that increased female movement over the course of the denning season cannot necessarily be used as an indication of a non-reproducing female, nor that reproduction failed (Aronsson et al. 2023, p. 8).

In certain ecological contexts, individual wolverines and reproductive dens can exist in areas without substantial spring snowpack (Jokinen et al. 2019, pp. 4–9; Persson et al. 2023, pp. 4–9). For example, Jokinen et al. (2019, pp. 6, 10) observed seven of eight wolverine dens (three primary and five secondary dens) in hollows of uprooted trees and not in snow; however, the researchers acknowledged that sample sizes were small and limited their ability to draw robust conclusions. Jokinen et al. (2019, p. 12) speculated that wolverines, in the absence of spring snow in Alberta, were able to meet their needs through locally available features such as the cavity created by partially uplifted root masses, the thermal properties of thick moss, and the caching opportunities provided by deep peat accumulations. Wolverines are resourceful and may be more flexible in their denning requirements than documented by studies in other landscapes (Jokinen et al. 2019, p. 12; Glass et al. 2021b, entire); however, it is also apparent that boreal forest communities have a series of unique properties conducive to wolverine denning including cold spring temperatures and dense peat layers that might aid in insulating the den (Jokinen et al. 2019, p. 12). In a more extensive study of wolverine denning in Sweden from 2000-2018, examining 1,589 validated reproductive events, Persson et al. (2023, pp. 6–7) found that wolverines recolonizing the boreal forest outside of alpine habitats were increasingly using areas without spring snow cover. Whether the alpine ecosystems in the conterminous U.S. contain environmental conditions that would allow wolverines to switch denning behavior or use smaller or shallower patches of snow in response to changes in future snow under a changing climate, is an open question. Even if they were able to make this shift, snow may be important to wolverines for more than just denning (see **Physical and Ecological Requirements**, above).

Habitat Studies Specific to Food Caching

Wolverines are physiologically and behaviorally adapted to caching perishable food in snow, boulders, and peat bogs for short- or long-term storage (van der Veen et al. 2020, pp. 2–3). Through tracking 38 GPS-collared wolverines across 4 study areas in Scandinavia, van der Veen et al. (2020, pp. 6–8) found that wolverines cached food all year from scavenging and predation events, with the locations of food caches widely distributed across their home range. When caching, wolverines selected for steep and rugged terrain in unproductive habitat types or in forest, indicating a preference for less-exposed sites that can provide cold storage or protection against pilferage. The observed year-round investment in caching by wolverines suggests that food predictability is important for their survival and reproductive success. Increasing temperatures caused by climate change may provide new challenges for wolverines in at least two ways: (1) by decreasing the shelf-life of cached food, and (2) and by increasing competition from pilferers that benefit from a warmer climate (van der Veen et al. 2020, pp. 8–10). However, significant uncertainties remain, particularly the consequence of climate changes on behavior and demography of the wolverine (van der Veen et al. 2020, pp. 8–10).

Key Areas of Uncertainty for Wolverine Habitat Use

The precise causal mechanism(s) for the apparent association of wolverine distribution and persistent spring snow are not yet clear. Hypotheses for this association include the importance of snow to create dens, the advantages of snow for catching prey within a wolverine's metabolic limits, competitive advantages over other scavengers and predators in snow-covered areas, thermoregulation, food storage and refrigeration, or some combination of these factors. The interplay of temperature and persistence of spring snow and the point at which temperature becomes limiting is also largely unknown.

While wolverines rely primarily on the presence of snow to create reproductive dens, there are instances where they have used other structures for denning in the absence of substantial spring snow; however, these instances so far appear to be limited to boreal and arctic ecosystems. Whether wolverines in the alpine environments of the contiguous U.S. would be able to successfully switch to den sites outside of snow-covered areas, or use smaller or shallower patches of snow, remains unknown.

New research has shown that resident wolverines in core habitats are far more sensitive to low-quality habitat than are dispersing individuals, but that dispersers still follow lower-resistance pathways that connect higher-quality core habitats (Carroll et al. 2020, p. 9). There is presumably some limit at which wolverines will not cross certain habitats or traverse certain barriers, but that threshold is not known. Understanding this threshold for females is particularly important because they often disperse shorter distances than males and appear to be more affected by potential barriers to movement, such as highways (e.g., Sawaya et al. 2019, pp. 621–623).

Recent studies from Canada and Alaska have shown that apex predators and sympatric mesocarnivores (small to mid-sized carnivores that occur in the same area) can influence wolverine space use (e.g., (Heim et al. 2019, pp. 2499–2504; Frey et al. 2020, pp. 1133–1137; Bell 2021, pp. 46–47; Klauder et al. 2021, p. 569; Chow-Fraser et al. 2022, p. 4). In addition, it is possible that competitors such as coyotes that thrive within human-dominated landscapes could potentially displace wolverines in areas with substantial anthropogenic disturbance (Chow-Fraser et al. 2022, pp. 4–5). However, the influence of apex predators and intraguild competition on wolverine distribution, abundance, and dispersal in the contiguous U.S. remains unstudied.

3.3 Genetics and Population Structure

Since our 2018 SSA, genetic analyses have been used to address questions about the North American wolverine's evolutionary history and phylogeography (Krejsa et al. 2021, entire); habitat connectivity (Sawaya et al. 2019, entire; Balkenhol et al. 2020, entire); population size and distribution (Kortello et al. 2019, entire; Mowat et al. 2020, entire); population structure and genetic diversity (Krejsa et al. 2021, entire); taxonomy (Hessels et al. 2021, entire); as well as their adaptive capacity and susceptibility to disease (Lok et al. 2022, pp. 19–20). Below we assess new information on genetics relevant to our status assessment of wolverines in the contiguous U.S., inclusive of: phylogeography, estimates of effective population size, and measures of gene flow and population connectivity.

Phylogeography

New genetic studies largely support and augment our understanding of the wolverine's phylogeographic history in North America. In a recent genomic analysis, divergence time estimates across the mustelid family were largely in agreement with previous findings, placing the split between the *Mustela* and *Guloninae* subfamilies at 11.2 million years ago (Ma) (highest posterior density interval [HPDI] between 13.1 and 9.5 Ma), and the split between the *Eira* genus and the *Gulo–Martes* group at 7.5 Ma (HPDI between 9 and 6.1 Ma) (Derežanin et al. 2022, p. 2904). The split between the *Gulo* and *Martes* genera was dated at 5.9 Ma (HPDI between 7.4 and 4.7 Ma) (Derežanin et al. 2022, p. 2904). Additional evidence from mitochondrial DNA and microsatellites supports previous research showing a post-glacial colonization of wolverines in North America from a single refugium in Beringia (Russia, Northwest Alaska, and Alaska) north of the Brooks Range (Krejsa et al. 2021, p. 902). Following their expansion, wolverines of far northwestern North America showed relatively high levels of historical connectivity with the possible exceptions of the Southeastern Alaska and Kenai Peninsula populations (Krejsa et al. 2021, p. 903). The wolverine's evolutionary and phylogeographic history suggest a species adapted to cold and snowy climate conditions (Fisher et al. 2022, p. 7).

Effective Population Size in the Contiguous U.S.

As reported in our SSA (USFWS 2018, pp. 46-47), effective population sizes (N_e) are typically smaller than census population sizes. N_e is the number of individuals in a population that would result in the same loss of genetic diversity, inbreeding, and genetic drift, if they behaved in the manner of an idealized population (equal sex ratio, random mating, all adults producing offspring, equal numbers of offspring per parent, and a constant number of breeding individuals across generations) (Frankham 1995, p. 96). The concept of effective population size relates to population viability because, as a general rule, closed populations with random mating that have effective population sizes below 50 are at higher risk of inbreeding depression, and below 500 are more likely to lose genetic variation important to maintaining long-term evolutionary potential. Some have argued, though, to avoid risk of inbreeding depression or lose genetic variation, these values should be closer to the range of 100 and 1,000, respectively (Frankham et al. 2014, entire). Fragmentation can further exacerbate inbreeding depression and genetic loss, while connectivity to larger source populations can alleviate the adverse effects of small effective population sizes (Frankham et al. 2014, p. 60). In addition, small, isolated populations are more vulnerable to extinction through interactions between environmental, genetic, and demographic factors (Caughley 1994, pp. 221–227).

The only available estimate of effective population size in wolverines in the contiguous U.S. is from the Northern Rocky Mountains (inclusive of the Greater Yellowstone Ecosystem, Idaho, and Montana). This is where the bulk of the wolverine population in the contiguous U.S. resides

(Table 5). In 2009, the N_e estimate for the Northern Rocky Mountains was 35 (credible interval = 28–52) and N_e did not change significantly from 1989–2006 (Schwartz et al. 2009, p. 3226).

In our 2018 SSA, we acknowledged gaps in the distribution of genetic samples in the Northern Rocky Mountains, which could have been interpreted as criticism of Schwartz et al.'s (2009, entire) effective population size estimate. New information provided by Schwartz (2022, *in litt.*, pp. 2-3) explained that Schwartz et al. (2009, entire) used scientific best practices to estimate N_e in the Northern Rocky Mountains, and that excluding certain samples was necessary to avoid biasing estimators. Simulations of the N_e estimate's sensitivity to removing samples and subsampling demonstrated that the N_e estimate was not significantly affected by these changes (Schwartz 2022, *in litt.*, pp. 2-3). We are not aware of any new estimates of effective population size for wolverines in the contiguous U.S.; therefore, the N_e estimate of wolverine population in the Northern Rocky Mountains provided by Schwartz et al. (2009) represents the best available scientific information regarding effective population sizes in the U.S. portion of the Northern Rocky Mountains (see Population Estimates, above).

There are no published estimates of effective population size for wolverines in the North Cascades. Therefore, we estimated the effective population size of wolverines in the North Cascades by: (1) obtaining an N_e:N ratio from Schwartz et al.'s (2009, p. 3226) best estimate of N_e (35) and Inman et al's (2013, p. 282) best estimate of wolverine population size in the Northern Rocky Mountains (see Table 5; n = 318); and (2) applying that N_e:N ratio (0.11:1) to the best estimate of wolverine population size for the North Cascades from Inman et al. (2013, p. 282) (i.e., 37 wolverines). This resulted in an estimate of N_e=4 for the North Cascades. These estimates are consistent with an observed ratio N_e:N of about 10–20% on average in a meta-analysis across many species and populations (Palstra and Fraser 2012, p. 2360; Frankham et al. 2014, p. 60). This range of observed N_e:N ratios is also in agreement with theoretical expectations when fluctuations in population size are considered (Vucetich et al. 1997, pp. 2017–2020; Wang et al. 2016, p. 203).

Overall, the effective population size estimates of wolverines in the contiguous U.S. are small compared to conservation rules-of-thumb. Therefore, they appear to be vulnerable to inbreeding and loss of genetic diversity when considered in isolation. However, only one or two migrants per generation are likely needed to achieve genetic population connectivity (Cegelski et al. 2006, p. 13; see Gene Flow between the U.S. and Canada section, below). If populations were connected, with a sufficient level of gene flow to offset the random loss of genetic variation in small populations, it would be more appropriate to evaluate the effective population size of the transboundary, interconnected population for the purposes of using conservation genetic rules-of-thumb.

Gene Flow between the U.S. and Canada

In the contiguous U.S., small, isolated wolverine populations are likely dependent on gene flow from Canada for population persistence (Cegelski et al. 2006, pp. 208–209; McKelvey et al. 2014, entire). Based on simulation analyses of gene loss, a census population of approximately 2,400 adult wolverines in the Northern Rocky Mountains and Greater Yellowstone Ecosystem would be needed to maintain 95% of the genetic variation over 100 wolverine generations

(Cegelski et al. 2006, pp. 12–13). Because there is not likely sufficient habitat for that number of wolverines in the entire contiguous U.S. (Inman et al. 2013, p. 282), gene flow (on the order of one or two wolverines per generation) from Canada is critical to maintaining genetic diversity in wolverines in the contiguous U.S. (Cegelski et al. 2006, p. 13).

In the Northern Rocky Mountains, the best available genetic data indicate genetic structuring (the amount and distribution of genetic variation within and among populations) of populations despite some dispersal (Cegelski et al. 2006, pp. 204–205, 208; Sawaya et al. 2023, pp. 12–14). Given the relatively recent recolonization of wolverines in the contiguous U.S. from Canada (within the last 60–70 years), nuclear genetic diversity was lower in the southern periphery of the species' range in the south (Sawaya et al. 2023, pp. 9–11). Nuclear DNA analyses indicated differences in allele frequencies between the U.S. and Canada along the Rocky Mountains, with some areas of overlap in wolverine populations straddling the border due to male-mediated gene flow. Females appear to be segregated near the international border due to their higher rates of philopatry than males and their apparently greater tendencies to avoid crossing major roadways, including the Trans-Canada Highway (Highway 1) and the Crowsnest Highway (Highway 3) in southern British Columbia (Saya et al. 2023, pp. 12, 17). Both highways were opened in the 1960s (British Columbia Ministry of Transportation and Highways 2001, pp. 16, 20). Since then, they have been widened in many areas and traffic volumes have substantially increased (British Columbia Ministry of Transportation and Highways 2001, pp. 7–11, 16–21). Mitochondrial DNA patterns in the Rocky Mountains showed no unique contemporary maternal lineages detected south of the international border, which is consistent with observational data indicating that wolverines recolonized the contiguous U.S. from Canada within the last 60–70 years (Sawaya et al. 2023, pp. 2, 16–17). Substantially lower mitochondrial DNA diversity in the U.S., as compared to mitochondrial DNA diversity in Canada, is consistent with the nuclear DNA signals of limited contemporary female gene flow between the countries along the Northern Rocky Mountain range and the wolverine's relatively recent recolonization at the southern edge of their range (Sawaya et al. 2023, p. 17).

In the North Cascades, GPS tracking data show that wolverines in western Washington and southern British Columbia form a small transboundary population (Aubry et al. 2023, p. 4). Preliminary results from a large transboundary population genetics study show that wolverines in the North Cascades are isolated from other wolverine populations in the U.S. and Canada and likely went through a genetic bottleneck with few founders (M. Sawaya, pers. comm. 2023). The population has low heterozygosity (<0.5) and is likely experiencing some level of inbreeding (M. Sawaya, pers. comm. 2023). However, there are no indications that individuals or population dynamics are being adversely affected by inbreeding depression (M. Sawaya, pers. comm. 2023).

Population Structure and Gene Flow within Canada

In our 2018 SSA, we stated that wolverines in Canada are considered to occur as a single large group because they are easily able to move between areas of good habitat and because wolverine habitat is relatively contiguous. New scientific information now shows that certain anthropogenic features (e.g., multi-lane highways) limit gene flow in southwestern Canada and supports previous research showing a pattern of decreasing genetic diversity in wolverines from north to south (e.g., Sawaya et al. 2019, pp. 621–623; Sawaya et al. 2023, pp. 11–14). Human infrastructure and other anthropogenic and natural barriers also have the potential to impede dispersal and affect wolverine population distribution and gene flow in Canada (Lofroth and Ott, 2007, pp. 2194–2195). These impediments are more prevalent in the southern portions of Canada (e.g., Lofroth and Ott 2007, p. 2194). Additionally, the best available genetic data indicate substantial female population substructure in wolverines (McKelvey et al. 2014, pp. 328–332; Schwartz et al. 2009, app. A; Zigouris et al. 2012, pp. 1520–1522; Sawaya et al. 2023, p. 12), with the possibility that the Trans-Canada Highway represents a “continental barrier to female wolverine movement” (Sawaya et al. 2019, p. 623). There is also new information that Highway 3 in southern British Columbia likely limits female wolverine gene flow (Sawaya et al. 2023, p. 17). Therefore, wolverine populations in southern British Columbia and Alberta near the transboundary interface have more genetic substructure than we found in our 2018 SSA.

Gene Flow within the Contiguous U.S.

Previous studies found wolverines have a strong association with areas that have persistent spring snow cover (Copeland et al. 2010, entire). Snow depth was the most important variable for predicting genetic structure overall in a new landscape genetics study in the Northern Rockies and at smaller spatial scales (up to ~230 (143 mi.) between genetic samples); however, at broad spatial scales (>430 km (267 mi.) between genetic samples) housing density and terrain ruggedness explained the most variability in wolverine population genetic structure (Balkenhol et al. 2020, p. 799). These data highlight the importance of maintaining dispersal corridors for wolverines outside of core habitats, as they represent critical pathways for gene flow across broad spatial scales (Balkenhol et al. 2020, p. 799).

As part of the multi-state wolverine occupancy surveys in 2016–2017, researchers obtained 240 wolverine DNA samples (Lukacs et al. 2020, p. 846). These samples represented 26 unique females and 24 unique males (Lukacs et al. 2020, p. 846). Analyses of the mitochondrial DNA control region revealed regional structuring, with all of the samples in Idaho, Montana, and Wyoming assigned to Haplotype Wilson A (the most abundant haplotype in North America) and all of the samples in Washington assigned to Haplotype Wilson C (Lukacs et al. 2020, p. 846). These results are consistent with the latest genetic analysis from a large transboundary study (Sawaya et al. 2023, entire) and previous mitochondrial DNA studies showing that the Northern Rocky Mountains and North Cascades do not appear to share any contemporary haplotypes (McKelvey et al. 2014, p. 328). New information also suggests that wolverines in the Greater Yellowstone Ecosystem have relatively low genetic diversity and high genetic distance from other wolverine populations in Idaho and Montana (Sawaya et al. 2023, pp. 8–9, 15–16).

Genomics

Genomics (the study of an organism’s entire set of DNA) is a new research frontier for wolverines in North America. Based on a single individual reference genome from a male wolverine collected 30 years ago in northern Canada, preliminary results suggest a relatively diverse gene pool in the Canadian arctic (Lok et al. 2022, p. 19). We can expect that further application of genomics research to wolverines will improve estimates of gene flow, inbreeding, relatedness, parentage, effective population size, and the timing of past extirpation and recolonization events in their southern range (Lok et al. 2022, p. 20). Identifying genes under selection (the process by which certain traits become more prevalent in a species than other traits due to the advantages a trait may have in promoting survival or reproduction) using genomics could also provide insights to local and future adaptive potential or vulnerability across the wolverine's North American range (Lok et al. 2022, p. 20).

Key Areas of Uncertainty for Genetics and Population Structure

The most recent estimate of wolverine effective population size in the contiguous U.S. was from over a decade ago (Schwartz et al. 2009, p. 3226) and did not include wolverines in the North Cascades. It is not clear whether there have been changes in the wolverine's effective population size since that time.

Our knowledge of the rates of wolverine gene flow within Canada, between the contiguous U.S. and Canada, and within the contiguous U.S. is improving, but gaps remain. Ongoing population genetic and genomic studies are likely to provide additional insights into wolverine population structure and gene flow.

3.4 Stressors

Effects from Roads

In our 2018 SSA, we concluded that "Roads present a low stressor to wolverines at the individual and population level in most of its current contiguous United States range." New information on the effects of roads on wolverine distribution, density, and reproduction, as well as connectivity and gene flow, are presented below.

Mortality

Since 2018, we are aware of four wolverine mortalities from collisions with vehicles in the contiguous U.S.

Idaho:

- July 14, 2020: A wolverine was killed by a vehicle collision on Highway 21, milepost 101.0, Boise County, ID (IDFG 2022, *in litt.*, p. 5)

Washington:

- April 17, 2021: An approximately 28-pound male wolverine was recovered on the Yakima Canyon Road (State Route 821) between Ellensburg and Yakima, WA.
- June 7, 2018: An approximately 37-pound male wolverine was recovered near mile marker 43 on interstate 90 between North Bend and Snoqualmie Pass, WA. (WDFW 2022, *in litt.*, p. 3).

Montana

- March 31, 2021: An adult male wolverine was killed by a vehicle collision on Highway 1, west of Anaconda, MT (N. Kluge, Montana FWP, pers. comm. 2023).

Young, inexperienced male wolverines have greater risk of road mortality during dispersal compared to adults and immature females that are less prone to long-distance dispersal (e.g., Krebs et al. 2004, pp. 497–498). The small number of mortalities observed since 2018, especially if they are biased toward dispersing males, are unlikely to have substantial impacts to the resilience of the wolverine population when viewed in isolation. However, wolverine mortalities from anthropogenic causes can accumulate with other stressors to affect population growth in localized areas. Wolverine mortalities that are biased toward dispersing individuals can also negatively impact gene flow.

Effects on Distribution and Density

In our 2018 SSA, we reported that "based on modeling results… wolverines avoided or increased their speed near roads and wolverine movement (speed), but not avoidance, increased with greater traffic volume" (Scrafford et al. 2018, p. 540). The research study authors hypothesized that the reason for this lack of increased avoidance at higher traffic volumes likely indicates that "avoidance behavior occurs at a course scale relative to speed and does not necessarily adjust to passing vehicles but instead to the general risk of roads." They concluded that "… roads generally reduce the quality of wolverine habitats" (Scrafford et al. 2018, p. 541).

New studies in southwestern Canada and the western U.S. have found that wolverine distribution and density are negatively related to road density. In southwestern Canada, consistency of spring snow and road density are the two most important variables correlated with wolverine density (Clevenger 2019, p. 52; Mowat et al. 2020, p. 220). Wolverine population estimates derived from models based on snow and road density predicted that wolverine abundance would be 44% higher without the depressing effect of the road covariate (Clevenger 2019, p. 52; Mowat et al. 2020, p. 220). As most roads are concentrated in areas of human development at lower elevations with less snow, correlations between wolverine distribution and road density can be confounded by other collinear variables (Copeland et al. 2007, pp. 2210–2211). However, in southeastern British Columbia, the density of forestry roads that extended into high-elevation wolverine habitat was a strong negative predictor of wolverine distribution in winter, especially for females (Kortello et al. 2019, p. 10). The most likely explanation for this negative relationship is the use of these high-elevation forestry roads by snowmobilers, rather than predator avoidance or trapping pressure (Kortello et al. 2019, p. 10). Other possible explanations are increased trapping access or less abundant food resources near roads (Mowat et al. 2020, p. 224). While the statistical significance of the relationship between roads and wolverine densities has been demonstrated in some areas, the mechanisms behind this relationship are unclear and require further study (Mowat et al. 2020, p. 224).

Effects on Reproduction

There is little new information on the impacts of roads on wolverine denning and reproduction. Based on a study of eight wolverine dens in a remote boreal region of Alberta, wolverines appeared to select den sites far from roads (range = 0.4–12 km (2.5-7.5 mi.) (median = 6 km (3.7 mi.)); however, this may have been simply a function of the available habitat (Jokinen et al. 2019, pp. 8–9). Despite the lack of a clear causal relationship, these findings are consistent with previous research which found wolverines selecting den sites away from roads at the home range and landscape scales in south-central Norway (May et al. 2012, p. 202).

Effects on Connectivity and Gene Flow

Large transportation corridors (e.g., multi-lane highways with substantial traffic volumes) can have a significant impact on wolverine population connectivity and gene flow. The mechanisms for reducing connectivity and gene flow are road mortality and reduced habitat permeability (i.e., fewer individuals crossing major highways). Mitochondrial and nuclear DNA measures of genetic population structure found that the Trans-Canada Highway corridor in the Canadian Rockies, alongside other natural and anthropogenic barriers to movement, fragmented the wolverine population by restricting female movements (Sawaya et al. 2019, pp. 621–622). This restricted movement resulted in male-biased dispersal and gene flow (Sawaya et al. 2019, pp. 621–622). This highway is approximately 150 miles north of the U.S.–Canada border and the study area for analyzing wolverine movement across the Trans-Canada Highway was in the lower Bow River Valley, which is a human-dominated landscape containing the Trans-Canada Highway, a town with approximately 10,000 residents, a golf course, 3 ski areas, the Canadian Pacific Railway, and a secondary highway. This transportation corridor was not an absolute barrier to female movement (4 of 20 female wolverines crossed the road during the study); however, females traversing the transportation corridor did not translate to gene flow (Sawaya et al. 2019, p. 622). The differences between male and female dispersal across this highway were likely due to the exacerbating effects of linear anthropogenic barriers on the strong natural tendencies for female wolverine philopatry (tendency to return to or remain near a particular area or site) (Sawaya et al. 2019, p. 623).

Wildlife crossing structures spanning the Trans-Canada Highway along the crest of the Continental Divide may improve wolverine connectivity across this highway. Evidence suggests that female wolverines may be starting to use wildlife crossings to cross the Trans-Canada Highway. A female wolverine may have been the wolverine photo-detected traveling northward at Castle Underpass on February 16, 2011. She was detected by hair sampling just 2 days prior at a nearby hair trap south of the underpass and on April 25, 2011, she was detected at a hair trap north of the Trans-Canada Highway (Sawaya et al. 2019, p. 624). However, the efficacy of these structures in restoring gene flow has not yet been measured (Sawaya et al. 2019, p. 623). There are few wildlife crossing structures spanning major highways in the contiguous U.S.; a series of three under-crossings and one dedicated wildlife overpass on I-90 in the Washington Cascades (connecting the northern and southern Cascades) were completed in 2019 (Sugiarto 2022, p. 9). To date, however, no wolverines have been detected using these relatively new crossings.

Habitats in the contiguous U.S. outside of the known breeding distribution of wolverines, including the Sierra Nevada in California and the central Rocky Mountains in Colorado, are separated from occupied habitats by large expanses of high-resistance habitats, anthropogenic features, and highways (e.g., Carroll et al. 2020, pp. 9–10; Bjornlie et al. 2021, pp. 116–117). While highways are not an absolute barrier to movement (wolverines have been documented crossing multi-lane highways), they can apparently limit female wolverine gene flow in some situations (e.g., Sawaya et al. 2019, pp. 621–622). The wolverine's capacity to traverse large expanses of high-resistance habitats, anthropogenic features, and highways and naturally recolonize and establish a population in some relatively isolated habitats in the contiguous U.S. (e.g., Oregon Cascades, Sierra Nevada, and central Rocky Mountains) remains unclear.

Disturbance from Winter Recreation Activity

In our 2018 SSA, we concluded that, "the effect of winter recreational activity represents a low stressor to wolverines in the contiguous United States at the individual and population level[s]." New information on winter recreation impacts on wolverines is presented below.

Functional responses of wolverine space use to various levels of backcountry winter recreation (motorized and non-motorized) in four study areas in Idaho, Montana, and Wyoming has been tested (Heinemeyer et al. 2019a, p. 8). Although the study design precluded the ability to directly assess demographic or fitness effects on wolverines (Heinemeyer et al. 2019a, p. 17), within home ranges, wolverine avoided all forms of winter recreation (motorized and non-motorized) and increasingly avoided areas as the amount of off-road winter recreation increased, resulting in indirect habitat loss or functional degradation of moderate- or high-quality habitats in winter (Heinemeyer et al. 2019a, p. 16). Wolverines did demonstrate the ability maintain multi-year home ranges in areas with winter recreation activity. Some resident animals had over 40% of their home range within the footprint of winter recreation; suggesting that at some scale, wolverines tolerate winter recreation (Heinemeyer et al. 2019a, p. 16).

Dispersed or off-road winter recreation appears to elicit a stronger avoidance response than recreation along roads and groomed routes with females showing more sensitivity than males (Heinemeyer et al. 2019a, p. 15). Females exhibited the strongest negative response to motorized recreation, which occurred at higher intensity across a larger footprint than did non-motorized recreation.

In a study evaluating the strength of aerial survey metrics in predicting wolverine responses to motorized and non-motorized backcountry winter recreation, higher recreation intensity classes showed stronger avoidance coefficients and were the most important modelled predictors of female wolverine presence (Heinemeyer et al. 2019b, pp. 18–20). Given the likelihood that, under climate change, both wolverines and backcountry winter recreation will be impacted by declining snow extent and depth and an abbreviated snow season, there is the potential for increased overlap between winter recreation and wolverine distribution (Heinemeyer et al. 2019a, p. 18).

The impacts of motorized and non-motorized backcountry winter recreation on wolverines in the Nez Perce-Clearwater, Sawtooth National Recreation Area, and Salmon-Challis National Forests of Idaho were evaluated by Regan et al. (2020, entire) using aerial survey methods of Heinemeyer et al. (2019b, pp. 6–10). Preliminary results showed that recreational impacts, in both area and intensity, are increasing over time. In the Sawtooth-Boulder White Cloud Mountains, researchers compared current extents of winter recreation with known historical wolverine home ranges and found that most of these home ranges contained little or no backcountry recreation (Regan et al. 2020, p. 4).

Camera-trap and DNA surveys on the Payette National Forest in central Idaho revisited a portion of a previous winter recreation study and affirmed that there had been an incremental loss of resident wolverines from 2010–2011 to 2014, and that previously documented territories appeared to be vacant (Mack and Hagen 2022, p. 13). The authors suggest that "what was considered to be a stable core subpopulation area could, in fact, be more tenuous" and "that the change in wolverine abundance in this area might be attributed to changes in habitat quality from direct or indirect influences" including dispersed recreation, although the precise cause for the apparent decline in wolverine abundance requires further study (Mack and Hagen 2022, p. 13).

As described above in Effects from Roads, forestry roads that are used by snowmobilers appear to have a strong negative correlation with wolverine distribution (Kortello 2019, p. 10). Non-motorized recreation can also impact wolverines. Remote camera-based surveys from 2011–2020 in protected and non-protected habitat in southwestern Canada found that wolverine detection probability was strongly and negatively correlated with the amount of non-motorized human recreation (Barrueto et al. 2022, pp. 4–8). This pattern held for both winter and summer and was consistent with the findings of Heinemeyer et al. (2019a, p. 18). Data from winter occupancy surveys showed that 95% of all wolverine detections occurred during 2-week periods with three or fewer recreational user groups detected on remote cameras (Barrueto et al. 2022, p. 4). While this study also documented declines in density and occupancy of wolverine, further research is necessary to determine the specific causal mechanisms most responsible for these declines (Barrueto et al. 2022, p. 8).

Other Human Disturbance

In our 2018 SSA, we concluded that human infrastructure may "affect individual wolverine behavior (e.g., avoidance) or loss or modification of wolverine habitat... but these effects are small or narrow in scope and scale and appear to represent a trade-off between foraging opportunities in areas that provide minimal risk of predation and avoidance of open areas and/or higher predation risk" (USFWS 2018, p. 62). Below, we discuss new information related to the impacts of human infrastructure on wolverine populations.

Wolverine density and detection probability in the Canadian Rocky Mountains declined with increased night light intensity, which is a measure for actively used human developments (Barrueto et al. 2022, p. 8). This pattern is consistent with telemetry-based findings that wolverines avoid infrastructure (May et al. 2006, entire; Moqanaki et al. 2023, pp. 11-12; Scrafford et al. 2018, entire). Connectivity among wolverine habitats appears to be particularly sensitive to housing developments and other human impacts in rugged areas located between typical wolverine habitats (Balkenhol et al. 2020, p. 799). As the study population was small, habitat fragmentation and decreased population connectivity would increase the effects of demographic stochasticity (Barrueto et al. 2022, p. 8). As discussed in the **Genetics and Population Structure** section, above, housing density was found to be an important predictor of long-distance wolverine dispersal and population structure in the Northern Rocky Mountains, explaining approximately 55% of the variation in the data (Balkenhol et al. 2020, p. 799). Therefore, even if areas between wolverine primary alpine habitats are not typically inhabited by wolverines, they may be used during dispersal and can therefore offer crucial pathways for gene flow across broad spatial scales (Balkenhol et al. 2020, p. 799).

The extent of the impacts of human presence and actions on the landscape have been collectively called "the human footprint" (Janzen 1998, entire). In an analysis of the human footprint in the western U.S., Leu et al. (2008, p. 1125) found that the physical effect area of the 14 anthropogenic features they analyzed (human habitation, interstate highways, Federal and State highways, secondary roads, railroads, irrigation canals, powerlines, linear feature densities, agricultural land, campgrounds, highway rest stops, landfills, oil and gas development, and human induced fires) covered 13% of the land area in the western U.S, with agricultural land being the most dominant (9.8%) human use. Accounting for the indirect effects radiating out from the direct human footprint, Leu et al. (2008, p. 1125) categorized 52% of the western U.S. as having medium- or high-intensity impacts from the human footprint (both direct and indirect impacts), while low-intensity impact areas covered the remaining 48% of the landscape (Leu et al. 2008, pp. 1125–1127). We overlaid modeled wolverine core areas across the western U.S. with the human footprint map and found that less than 1% was in the high-intensity category, 12% was in the medium intensity category, and 88% was in the low-intensity category. We also overlaid the current breeding distribution of the wolverine with the human footprint map and found that only 1% of current breeding range was within the high-intensity category, 31% was in the medium-intensity category and 68% was in the low-intensity category (Figure 4). As expected, wolverine core areas are concentrated in high-elevation areas with little human infrastructure (Figure 4). However, within their current breeding distribution, wolverines must navigate across areas with greater amounts of human infrastructure to disperse from one habitat core to another (Figure 4).

In addition to effects on wolverine density and connectivity, human infrastructure can also affect wolverines through shifts in community dynamics that precipitate from changes in the behavior and temporal use of habitats by apex predators. Wolverines and other carnivores may shift their daily behavior patterns in response to the presence of human landscape disturbance (Frey et al. 2020, pp. 1133–1138). By modeling the effects of human landscape features, linear (roads, rail, trails, seismic lines, transmission lines and pipelines) and polygonal (harvest cut-blocks, residential land, well-sites), researchers sought to determine if carnivore species change behavior in response to these disturbances, creating a potential shift in temporal niche portioning and leading to a potential increased interspecific competition in the Rocky Mountains of Alberta, Canada (Frey et al. 2020, entire). In response to increased human disturbance (proportion of linear and polygonal features) wolves (*Canis lupus*) showed a shift toward nocturnal activity while coyotes shifted toward cathemeral (i.e., sporadic and random intervals of activity at any time of the day or night) and marten (*Martes americana*) shifted toward diurnal activity (Frey et al. 2020, pp. 1133–1138). Although forest cover was shown to have a stronger influence on marten-wolverine activity overlap than did human infrastructure-associated landscape change (overlap decreased significantly with increasing forest cover) the results suggest that a shift in apex predator activity can lead to cascading shifts in mesocarnivores, in turn leading to increasing competition over resources and potential displacement of species (Frey et al. 2020, pp. 1133–1138).

Indirect effects to wolverines can also be caused by range expansion of other carnivores into wolverine habitat facilitated by human infrastructure. While wolverine and coyotes are generally segregated, the probability of co-occurrence increases with the proportion of linear disturbance features (Chow-Fraser et al. 2022, p. 4). Using the same study area in Alberta as Frey et al. (2020, p. 1130), the authors found that while wolverines favored areas of low disturbance (low proportion of linear features) and coyotes favored areas of high disturbance (high proportion of linear features), co-occurrence probability increased 3x for each increase of linear feature unit (Chow-Fraser et al. 2022, p. 4). Modeling showed that competition exhibited the strongest effect on wolverine distribution with wolverine occurrence best explained by coyote occurrence at the same sites (Chow-Fraser et al. 2022, p. 4). These results suggest that anthropogenic disturbance and resulting coyote range expansion may be contributing to wolverine population declines in the Canadian Rocky Mountains (Chow-Fraser et al. 2022, p. 6).

Generalized linear models (GLMs) and variation partitioning were used to estimate the independent and cumulative effects of landscape features, human disturbance, or prey availability on wolverines and other large carnivore occurrences in Fennoscandia (Milanesi et al. 2022, entire). Contrary to the other carnivores they evaluated, variation in the "permanent" occurrence of wolverines was best explained by human disturbance and the shared effect between landscape attributes and human disturbance. This same relationship was observed for "sporadic" wolverine occurrences, but with a considerably lower level of explained variance. The researchers concluded that, "the wolverine showed higher sensitivity to human disturbance compared to the other large carnivores, and spatial segregation patterns between wolverines and humans were found, as large carnivore home ranges are usually at high elevation (often covered by snow), far from the lowlands where density of human settlements and roads is high." It appears that wolverines select den sites mainly away from infrastructure, indicating that successful reproduction may be influenced by human activities. However, they also appear to be able to cross artificial barriers to some degree. Therefore, wolverines appear to have a relatively low tolerance of human disturbance, with an ability to exhibit more flexible behavior during dispersal in some circumstances.

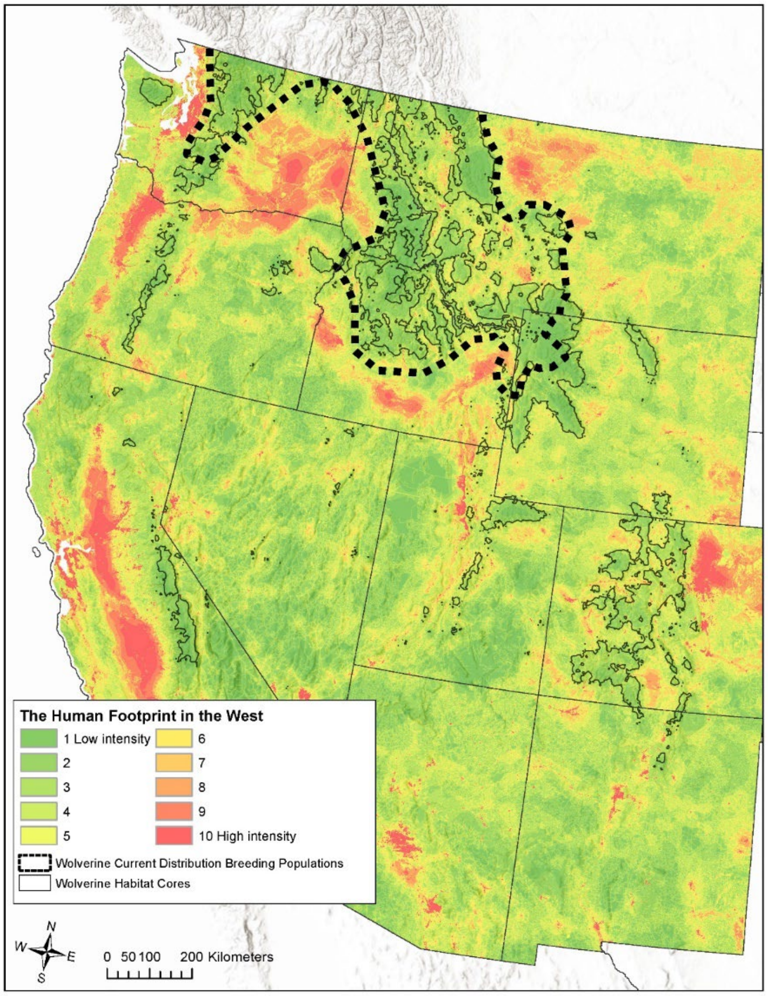

Figure 4. Human footprint in the western U.S. (Leu et al. 2008) and wolverine habitat core areas (Carroll et al. 2020).

Disease and Predation

In our 2018 SSA, we found that disease or predation were neither population- nor species-level stressors to wolverine in the contiguous U.S. Our assessment of these stressors has not changed.

There has been some new research on diseases and parasites in wolverines since the 2018 SSA was published; however, we lack data on the specific effects to wolverine populations. It is conceivable that disease-induced mortality could contribute to population declines but this remains understudied south of the Arctic (Fisher et al. 2022, p. 9). The types of bacteria or parasites that could lead to disease in wolverines are still unknown (Watson 2020, pp. 62, 65). Many authors have discovered new viruses in the U.S. and Canada, some of which were previously unrecognized species of parasites (Sharma et al. 2020, p. 277; 2021, p. 1; Watson et al. 2020, p. 43; Bandoo et al. 2021, p. 1). This new information pertains to how wolverines act as primary hosts for some parasites, such as *Trichinella* spp., and how those parasites could increase infection risk to humans and other vertebrates (Sharma et al. 2021, pp. 1, 7). Considering the global coronavirus pandemic in recent years and instances of human-animal cross-infections, researchers are beginning to use genomic data to evaluate the wolverine's susceptibility to these pathogens (Lok et al. 2022, pp. 16–18). Although no coronavirus cases have been reported in wolverines and an initial evaluation of the wolverine's genome to determine susceptibility to coronaviruses was inconclusive, there is potential risk of infection from their prey or from researchers handling captured wolverines that they release back into the wild (Lok et al. 2022, pp. 16, 18, 20).

Since our 2018 SSA, we found no substantive new information on predation. In North America, there was one new report of two wolverines being predated upon in the boreal ecosystem of Canada. One was the result of wolf predation, and the other was the result of an unknown predator (Scrafford et al. 2021, p. 9).

Overutilization for Commercial, Recreational, Scientific or Educational Purposes

In our 2018 SSA, we concluded that "overutilization does not currently represent a stressor to the wolverine in the contiguous United States at the individual, population, or species level." We also concluded that "Trapping in Montana, Alaska, and Canada has been and appears to be sustainable. Trapping or harvesting of wolverines along the contiguous U.S.–Canada border does not represent a stressor to wolverines migrating into the contiguous United States at the individual or population level." Further, we concluded that "trapping effort along the U.S.–Canada border does not represent a barrier to wolverine movement and dispersal along the international border" (USFWS 2018, p. 71). Below, we present new information on incidental captures of wolverines in the contiguous U.S. where regulated wolverine trapping remains closed (USFWS 2018, pp. 70–72), and new information on the effects of trapping mortality on wolverine populations in southwestern Canada. New information suggests that wolverine trapping in southwestern Canada likely reduced populations in the Rocky Mountains, which may have impacted connectivity across the international border.

Shooting

A small number of wolverines have been shot by hunters or others in the contiguous U.S. Since publication of the 2018 SSA, we are aware of one male wolverine shot by a landowner in Centerville, Washington when it was discovered inside a chicken coop (WDFW 2022, *in litt.* p. 3).

Incidental Trapping in the Contiguous U.S.

Wolverines are occasionally inadvertently captured in traps set for other animals. We have reports of incidental captures of wolverines in Montana and Idaho. In our 2018 SSA, we did not report any incidentally trapped wolverines in Montana since new wolverine trapping regulations were implemented in 2012. New published information shows that since 2012, there have been 10 non-target wolverine captures (average < 1/year) in Montana resulting in three mortalities; the remainder were released alive (MTFWP 2023, in litt., p.1). In Idaho, our 2018 SSA reported three wolverines incidentally trapped due to wolf control activities since 1995, with two released and one killed. Between November 2017 and August 2022, IDFG reported nine non-target captures, with two resulting in mortalities (IDFG 2022, *in litt.*, pp. 5, 16–22). We are not aware of any recent incidental captures of wolverines in other western States.

New wolf trapping laws in Montana and Idaho may have the potential to increase the amount of incidental capture of wolverines. In Montana, trapping laws are intended to reduce the wolf population through, among other things: (1) authorizing the use of snares to take wolves by licensed trappers (MCA 87-1-901 (2)(b)); (2) allowing the Montana Fish, Wildlife, and Parks (MTFWP) Commission authority to extend trapping season dates (MCA 87-1-304 (8)); and, (3) allowing the reimbursement of costs incurred to harvest a wolf or wolves in Montana (MCA 87-6-214 (1)(d)).

In Idaho, legislation revised Idaho Codes in 2021 to: (1) authorize a year-round trapping season for wolves on private property (IC 36-201(3)); (2) authorize additional methods of take previously prohibited (inclusive of the use of snares in 97 out of 99 management units) (IC 36-201(2)); (3) remove any limit to the number of wolf tags an individual may purchase (IC 36-408(1)); (4) allow a livestock or domestic animal owner to use a private contractor to kill wolves (IC 36-1107(c)); (5) allow the Idaho Wolf Depredation Control Board to enter into agreements with private contractors, in addition to State and Federal agencies, to implement the provisions of SB 1211; and (6) direct wolf control assessments ($110,000 annually) collected from the Idaho livestock industry to be combined with $300,000 the State would transfer from the IDFG fund annually beginning on July 1, 2021.

These regulation changes may increase the amount of wolf trapping and the risk of incidental trapping of wolverines because of the use of snares, extended trapping seasons, and financial incentives. The realized impact of these changes cannot yet be meaningfully measured due to the limited amount of time they have been in effect.

Because wolverines differ from wolves in size, distribution, and behavior, trappers use pan tension, site selection, and snare height to reduce the likelihood of incidental capture. Below, we report information we received from the States on their efforts to reduce incidental trapping of wolverines.

California

Recreational and commercial trapping of fur-bearing and nongame animals has not been legal in California since 2019 (CDFW 2023, in litt. p. 2). And while furbearers and nongame species can be trapped for other reasons (e.g., protection of property), existing regulations likely preclude the serious injury or mortality of incidentally captured wolverines (CDFW 2023, in litt. p. 2). The use of snares, conibear-type traps, and deadfall traps is prohibited in large areas of the state, including the most-recently estimated historical range of the wolverine (CDFW 2023, in litt. p. 2). The use of steel-jawed leghold traps is prohibited throughout the state (CDFW 2023, in litt. p. 2). All traps must be checked daily, and all captured animals that are not legal to trap should be immediately released (CDFW 2023, in litt. p. 2).

Colorado

Recreational trapping of wildlife in Colorado is limited to live cage traps (CPW 2023, in litt. p. 1) and any wolverines incidentally trapped should be released unharmed. However, there are currently no wolverines present in Colorado and therefore no incidental trapping of wolverines occurs (CPW 2023, in litt. p. 1).

Idaho

IDFG has multiple voluntary guidelines that are shared with the trapping community to reduce the non-target capture of wolverine (IDFG 2023, in litt.; IDFG 2022, p. 40). The guidelines include recommendations on the types of traps used, trap tension, trap placement, avoiding areas with wolverine tracks observed, selecting habitats less likely to have wolverines, and contacting IDFG or a local sheriff's office to assist with the safe release of wolverines incidentally trapped (IDFG 2023, in litt). In addition, year-round wolf trapping season in Idaho are limited to private lands, where there is very little core wolverine habitat.

Montana

Montana FWP has multiple trapping regulations that help mitigate the non-target capture of wolverines by recreational trappers (MTFWP 2023, in litt. p. 1). The regulations include requirements for trappers to take an education course, check wolf traps every 48 hours, and to set wolf trap tension and snare height to limit wolverine capture (MTFWP 2023, in litt. p. 1). There are also several regulations required to mitigate the non-target capture of the Federally listed lynx which are also applicable to wolverines, including the prohibition of wolf snares on public lands in lynx protected zones which overlap much of the wolverine's habitat in Montana (MTFWP 2023, in litt. p. 5).

Oregon

There is no open season for wolverine (and other protected species) and any incidental capture or other take must be reported to ODFW within 48 hours (ODFW 2020, p. 1). Regulations that also reduce any incidental captures or take include a 48-hour trap check (limits the ability for traps to be set in wolverine range and allows for prompt trap set modification or removal if sign is detected) and medium-sized and larger body-grip traps (such as the conibear trap) are prohibited from setting on land (ODFW 2023, in litt. p. 4). In practice, other traps successfully deployed for the capture of wolverine simply aren't used by Oregon trappers (ODFW 2023, in litt. p. 4). For example, foothold traps (#4 coil springs, MB 750s) used for wolverine in Canada and Alaska are too large for targeted Oregon species like bobcats and coyotes (ODFW 2023, in litt. p. 4). No wolverines have been incidentally captured by licensed furtakers in Oregon over the last half century (ODFW 2023, in litt. p. 4).

Utah

There are no regulations specific to wolverines in Utah, but the UDWR regulates trapping and the use of trapping devices to reduce the capture of non-targeted protected species (UDWR 2023, in litt. p. 2). Any protected wildlife found alive in a trapping device must be immediately released unharmed (UDWR 2023, in litt. p. 2). UDWR also provides trappers with multiple recommendations that can help avoid catching nontarget species in traps set for bobcats and other furbearers including recommendations on the type of traps used, placement of traps, and baits used (UDWR 2023, in litt. p. 2).

Washington

Information on wolverine is in Washington's trapping education manual and all trappers must pass a trapper education test (or a similar one in another state) prior to obtaining their first license (WDFW 2023, in litt. p. 2). Due to Washington's trap type regulations banning body gripping traps, the likelihood of accidental capture of a wolverine is very unlikely, and injury or death from these traps even more unlikely (WDFW 2023, in litt. p. 2). In Washington, the most commonly trapped animal in habitats that wolverine occupy are marten, but marten traps are too small for wolverine (even young wolverines) to be captured (WDFW 2023, in litt. p. 2). Larger cage traps that are used for bobcat and other larger animals could potentially capture a wolverine, but these are not commonly set in areas that wolverine occupy, and if a wolverine were incidentally captured, they could be released from the trap unharmed (WDFW 2023, in litt. p. 3). The past several years of trapper reports (2017-2022) do not show any records of wolverine being trapped in Washington.

Wyoming

The WGFD addresses the incidental capture of animals classified as protected, like wolverines, in their Furbearing Animal Hunting or Trapping Seasons Brochure (WGFD 2023, in litt. p. 4). All protected animals that are trapped shall be released unharmed and mortalities reported to the WGFD (WGFD 2023, p. 14). Large areas of Wyoming within the distribution of wolverines are closed to trapping, including Yellowstone National Park and Grand Teton National Park.

The WGFD is not aware of any wolverines trapped incidentally in Wyoming in recent history (WGFD 2023, in litt. p. 1). Trap types with the potential to capture wolverines are largely restricted to private lands, be partially submerged in water (where there would be low likelihood of wolverine capture) or are required to have break-away devices to limit bycatch (WGFD 2023, in litt. p. 2). Trapping that occurs in areas that overlap with wolverine habitat in Wyoming is primarily by marten trappers that use smaller cubby trap sets and it is unlikely these would capture a wolverine (WGFD 2023, in litt. p. 2).

Trapping in Southwestern Canada

Since our 2018 SSA, there is substantial evidence demonstrating that trapping has impacted wolverine densities in southern British Columbia and Alberta over the last decade (e.g., Kortello et al. 2019, pp. 1, 10; Mowat et al. 2020, entire; Barrueto et al. 2020, p. 296; Barrueto et al. 2022, entire). In addition, there appear to be edge effects from trapping, with impacts to wolverine densities extending into protected areas in southern Canada (Barrueto et al. 2020, p. 296; Barrueto et al. 2022, p. 4). In the most expansive study of wolverine trapping and density to date—and encompassing southern British Columbia and Alberta's zone of connectivity with the Northern Rocky Mountains of the U.S.—wolverine trapping mortality was found to be unsustainably high at approximately 8.4% per year (Mowat et al. 2020, p. 221). Kill rates were higher in the southern British Columbia portion of the study area, with the best estimate of trapping mortality there approaching 10% per year (Mowat et al. 2020, p. 223). This contrasts with the maximum sustainable harvest of approximately 8% after accounting for the influence of higher trap vulnerability of juveniles and males and stochasticity in juvenile recruitment rates

(Mowat et al. 2020, p. 221). Uncertainties in the stochasticity of reproduction, however, had large effects on the estimates of maximum sustainable harvest, causing it to vary between 0 and 8.1% (Mowat et al. 2020, p. 221). Based on their analyses, Mowat et al. (2020, p. 224) recommended reducing trapping mortality to no more than 4% per year (and perhaps even lower than that for an interim period) across their study area to promote wolverine population recovery.

In response to the emerging information that trapping rates were unsustainable in southern British Columbia, the B.C. Ministry of Forests, Lands, Natural Resource Operations and Rural Development closed a portion of the Province along the U.S.-Canada border to wolverine trapping in 2020 (see Changes in Regulatory Mechanisms and Voluntary Conservation Measures, below). New research published since that closure has confirmed population declines of approximately 40% in the wolverine population in a portion of the Canadian Rocky Mountains over the decade before the closure (Barrueto et al. 2022, p. 6).

Changes in Regulatory Mechanisms and Voluntary Conservation Measures

Federal Regulatory Mechanisms

Management of the wolverine and its habitat on Federal lands is crucial to their conservation as Federal lands make up approximately 96% of modeled wolverine habitat, the majority of which are U.S. Forest Service lands (USFWS 2018, p. 103). The U.S. Forest Service manages the National Forest System lands in accordance with local Land Management Plans (Forest Plans). In 2012, the U.S. Forest Service published rules for revising Forest Plans (36 CFR Part 219). The 2012 planning rule adopts a complementary ecosystem (coarse filter) and species-specific (fine filter) approach to maintaining the diversity of plant and animal communities and the persistence of native species in the plan area, within U.S. Forest Service authority and consistent with the inherent capability of the plan area (§ 219.9). This complimentary approach includes ecosystem and species-specific plan components. Ecosystem plan components are developed to maintain or restore:

(1) The ecological integrity of terrestrial and aquatic ecosystems and watersheds in the plan area, by addressing structure, function, composition, and connectivity.

(2) The diversity of ecosystems and habitat types throughout the plan area, by addressing key characteristics of ecosystem types, rare plant and animal communities, and the diversity of native tree species. The planning rule specifies that if the ecosystem plan components developed for a plan area are insufficient to provide the ecological conditions necessary to conserve proposed and candidate species, then additional, species-specific plan components must also be developed.

If ecosystem plan components would not provide the ecological conditions to conserve sensitive, candidate, proposed, or listed species, then species-specific plan components must be included.

In our 2018 SSA, we identified Forest Plans as important "federal mechanisms" that, in combination with State Wildlife Action Plans, "will alleviate effects associated with potential impacts related to stressors discussed in this report." However, in our 2018 SSA, we reviewed only four Forest Plans and did not identify in those plans any specific standards (mandatory constraints on project and activity decision-making) for wolverines. We did identify a few goals, desired conditions, proposed or possible actions, and monitoring components that could provide some benefits to wolverines.

For this addendum we conducted a more comprehensive review of the latest Forest Plans for 20 Forests within the current breeding range of the wolverine. We found a complex array of plan components aimed at achieving the 2012 planning rule's complementary ecosystem and species-specific approach, while balancing the U.S. Forest Service's multiple-use mandate. Some plans provided wolverine-specific guidelines, objectives, and direction to minimize effects of roads, winter recreation, other sources of human disturbance, but we did not identify any wolverine-specific standards and overall, there was a lack of consistency across plans. This was most apparent in the ecosystem plan components that were designed for the benefit of the many ecosystems that the wolverine and other native species depend upon. The focus of wolverine-specific plan components, when they were included, was most often limited to protection of known den sites and maternal habitat during the denning season.

Course-filter protections of habitat-types and ecosystems will undoubtably provide some conservation benefits to wolverines. For example, wolverines will benefit from wilderness area protections (calculated as 18% of the extent of wolverine occurrence and 41% of core wolverine habitats in the western U.S. [USFWS 2018, p. 103]); limitations on development and road construction; limitations on road densities in certain areas for the grizzly bear or other species; and restrictions on over-snow travel. However, quantifying these benefits outside of wilderness areas is challenging given the variability in Forest Plan standards and conservation measures across the range of the wolverine.

U.S. Forest Service regulations require Forests to designate roads, trails, and off-road areas that are open and closed to motor vehicle use (36 CFR Part 212.5). In 2015, the U.S. Forest Service published a final rule indicating that it would also designate roads, trails, and areas open or closed to over-snow motor vehicle use (80 FR 4500). These designations are done on a Forest-by-Forest basis, resulting in variability in the amount of wolverine habitat impacted by these designations. For example, a recent draft Environmental Assessment for the Idaho Panhandle National Forests proposed to increase the area available to motorized over-snow use resulting in projected increased impacts to primary wolverine habitat (from 39% currently to 52% under the proposed action) and maternal denning habitat (from 44% currently to 52% under the proposed action) (U.S. Forest Service 2023, p. 67). Conversely, the Gallatin National Forest reduced the amount of area open to over-snow use from 42% of denning habitat on the Forest to 25% (U.S. Forest Service 2006, Chapter 3–623). This variability, and the lack of a range-wide assessment that overlays the areas of U.S. Forest Service over-snow vehicle use closures and wolverine habitat, make it difficult to characterize the effects of over-snow travel management planning on wolverines in the contiguous U.S.

Several large National Parks contain core habitats for wolverines, including Yellowstone, Grand Teton, Glacier, North Cascades, and Mount Rainer National Parks. These areas are largely protected from development, although they may be impacted by winter recreation to varying degrees.

Although the Bureau of Land Management (BLM) manages relatively little land within wolverine core habitats, they do manage some of the valley bottoms between these core habitats. The wolverine is listed as a special status species by the following BLM offices: Montana/Dakotas (revision 2020), Idaho (revision 2022), and Oregon/Washington (revision 2021). The objectives of the BLM's special-status species policy are: (1) to conserve and/or recover ESA-listed species and the ecosystems on which they depend so that ESA protections are no longer needed for these species; and (2) to initiate proactive conservation measures that reduce or eliminate threats to BLM sensitive species to minimize the likelihood of and need for listing of these species under the ESA.

State and Provincial Regulatory Mechanisms

Wolverine trapping remains closed throughout the western U.S. and wolverines have retained various protected status designations in these States (Table 10). Therefore, legal trapping is no longer an active direct stressor on wolverines in the contiguous U.S. Nevertheless, incidental trapping and the legacy effects of recent overharvest in southern Canada remain potential stressors (see Overutilization for Commercial, Recreational, Scientific or Educational Purposes, above).

Table 10. State regulatory designations for the wolverine in the western U.S. (See Appendix G of the 2018 SSA for more information).

State	Regulatory designation(s)
California	State Threatened and Fully Protected Species
Colorado	State Endangered
Idaho	Protected Nongame Species
Montana	Furbearer (Currently Closed to Trapping) and Species of Concern
Oregon	State Threatened
Utah	Species of Greatest Conservation Need
Washington	Candidate for State Listing
Wyoming	Nongame Wildlife and Protected Animal

In response to studies showing that wolverine harvest was unsustainable in southeastern British Columbia (Mowat et al. 2020, entire), the Provincial government closed Resource Management Region 4 (Kootenay) in the southeastern portion of British Columbia to wolverine trapping and imposed a more intensive mortality recording system in that region in the fall of 2020 (British Columbia 2022, p. 76). Regions 2 (Lower Mainland) and 8 (Okanagan) remain closed to wolverine trapping; therefore, the entire area along the U.S.-Canada border is now closed to wolverine trapping (British Columbia 2022, p. 76; Figure 5). Wolverine trapping remains open seasonally in British Columbia Resource Management Units 3, 5, 7A, 7B, and portions of Unit 6 (British Columbia 2022, p. 76; Figure 5), as well as in the Rocky Mountain region of southwestern Alberta (Alberta Environment and Parks 2022, pp. 14–15).

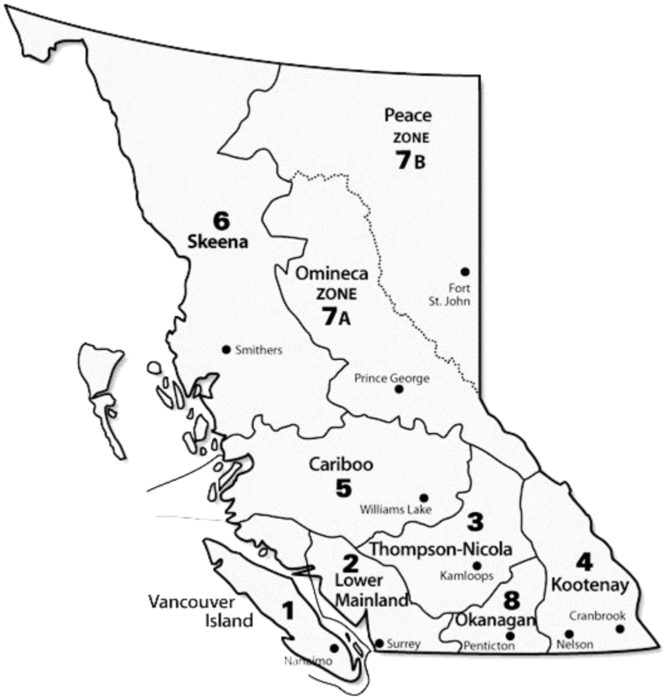

Figure 5. British Columbia Resource Management Zones used in Provincial furbearer trapping regulations (British Columbia 2022).

Resource management units in southern British Columbia remain open to trapping for several other furbearers, and incidental trapping of at least two wolverines has been documented following the closure in the Kootenay Resource Management Unit to wolverine trapping (Vander Vennen 2022, *in litt.*, p. 1). Given the likelihood that there is some non-compliance with reporting incidental captures, the precise number of wolverines incidentally trapped is not known (Vander Vennen 2022, *in litt.*, p. 1).

Aside from regulated taking of wolverines, regulatory mechanisms available to States for conserving wolverines are largely relegated to maintaining habitat conditions that support wolverine connectivity. This is because the majority of the primary habitat cores for wolverines in the contiguous U.S. are on lands managed by the U.S. Forest Service. We are not aware of any other State regulatory mechanisms specific to wolverines that limit development, winter recreation, or other human disturbances in areas important to wolverine connectivity in the contiguous U.S. Several States and other organizations, however, are implementing a number of voluntary monitoring or conservation measures for wolverines (see below).

Voluntary Conservation Measures

Western States continue to invest in monitoring wolverine occupancy. A notable effort includes that of the Western Association of Fish and Wildlife Agencies (WAFWA) Western States Wolverine Working Group, now referred to as the Forest Carnivore Sub-Committee. The purpose of this subcommittee is to "develop a statistically defensible multi-state monitoring plan for states where wolverine populations exist (WY, MT, ID, WA); seek funding to implement the monitoring plan; coordinate development of individual state wolverine conservation plans for states with suitable wolverine habitat; and coordinate and prioritize research efforts" (WAFWA 2022).

In 2020, the Wyoming Game and Fish Department (WGFD) developed a wolverine management plan for the State of Wyoming. The plan includes chapters summarizing wolverine ecology, distribution and occupancy, threats and risk factors, and management and conservation strategies in Wyoming. Its goals are to: (1) promote long-term wolverine viability, (2) support expansion of wolverines into suitable habitat, (3) support multi-state monitoring efforts, and (4) support management of the wolverine as a protected animal (WGFD 2020, p. 2).

Since 2018, Montana Fish, Wildlife and Parks has completed 10 habitat conservation projects in wolverine habitat that conserve 59,725 acres through fee title acquisition or perpetual conservation easement. A spatial toolset is now available for western Montana to help prioritize these types of acquisitions and easements (Carroll et al. 2021b, entire). Other tools such as the Crucial Areas Planning System (CAPS), a web-based landscape-scale planning tool, have also been put in place to help guide future developments that can impact wolverine habitat (MTFWP 2022, *in litt.*, p. 6).

In January 2023, the Idaho Fish and Game Commission adopted a revised *Management Plan for the Conservation of Fisher, Wolverine, and Canada Lynx*. This plan provides updated guidance and identifies management priorities for the conservation of this suite of species over the next 6 years in Idaho.

The Utah Wildlife Migration Initiative, founded in 2017, identifies and protects connective corridors that allow fish and wildlife to migrate to necessary habitat areas around the State. The mission is to document, preserve and enhance wildlife movement for species throughout Utah using state-of-the-art tracking and data management technologies, strong collaborative partnerships, and compelling outreach. The Migration Initiative and its partners are mapping the movements of wildlife, including wolverine, so crossing structures can be placed in areas that coincide with movement corridors. Similar work is being conducted in other states and is coordinated between states.

Colorado Parks and Wildlife had previously considered reintroducing wolverines to Colorado as a nonessential experimental population to further their conservation (see 78 FR 7890). However, that proposal was withdrawn in 2014, when we withdrew our proposed listing rule. There is currently no formal proposal to reintroduce wolverines to Colorado.

Since 2019, Woodland Park Zoo has been coordinating the Washington Wolverine Research and Monitoring Group, a coalition of researchers and conservationists who lead wolverine projects in Washington (Woodland Park Zoo 2022, *in litt.*, p. 1). The goal of this group is to help advance wolverine research and monitoring in Washington by strengthening communication and collaboration among wolverine projects statewide. This group meets several times a year to discuss research efforts, share results and insights, and strategize around wolverine research and conservation in Washington.

Key Areas of Uncertainty for Stressors

Habitat connectivity is central to the conservation of wolverines at the southern terminus of their distribution in North America. However, we currently lack information on the effect of a recent wolverine trapping closure in parts of southern British Columbia on wolverine population growth and dispersal from Canada to the U.S. We also lack long-term data on the impacts of roads on gene flow in the contiguous U.S. and the efficacy of crossing structures in improving wolverine gene flow across road barriers.

Regulated wolverine trapping is closed in the contiguous U.S. and southern British Columbia, but incidental trapping still occurs. Although the known number of incidental trapping occurrences is relatively small, there is presumably some unknown level of incidental trapping that goes unreported. Furthermore, there have also been substantial recent changes in wolf harvest regulations in the contiguous U.S. in Idaho and Montana, and the impact of these changes on incidental wolverine trapping rates is not yet known.

New research has begun to reveal the impact of human recreation and disturbance on wolverine space use, and it appears that certain anthropogenic disturbances can have significant impacts on wolverine occupancy, density, and connectivity. However, the extent of these impacts and their causal mechanisms are still being studied. One mechanism recently uncovered in Canada includes the apparent cascading effects of anthropogenic disturbance on apex carnivore and mesocarnivore community dynamics (Chow-Fraser et al. 2022, entire). These cascading effects have not yet been studied in wolverines in the contiguous U.S.

4.0 Future Condition

4.1 Climate Change Effects

In our 2018 SSA we identified the effects of climate change, such as warming temperatures and loss of snowpack, as the most significant stressors to the wolverine. While we evaluated the impacts of the potential for loss of snow to denning habitat, we did not present a similar analysis of potential impacts to wolverines relative to demographic parameters, or population connectivity. Below, we update our assessment of climate change effects on wolverines in the contiguous U.S. based on new projections of future snow loss. Below, we provide a more granular assessment of projected regional changes in snow loss in some wolverine habitats in the contiguous U.S. (see Snowpack/Snow Cover Projections). Our methods, including the downscaling and delta-change approaches, are best suited for capturing longer-term (e.g., 20-year) median climate change signals, and are not ideal for assessing interannual variability in snowpack.

Losses in future persistent spring snowpack are predicted under climate change in some snow-dominated areas of the western U.S. (McKelvey et al. 2011, entire; Schwartz et al. 2016, p. 317; Livneh and Badger 2020, pp. 453–454). For example, McKelvey et al. (2011, pp. 2886–2892) estimated that the area of persistent spring snow cover (average snow depth of at least 13cm (5.12 in.) on May 1) in the western U.S. and southeastern British Columbia could shrink by up to 63% by 2070–2099. A more recent study in a portion of the southern Canadian Rocky Mountains in British Columbia estimated a loss of 44% of persistent spring snow cover between 2020 and 2080 under a high emissions scenario (Schepens et al. 2023, pp. 10–11). While there is regional variability in anticipated losses of spring snow, for all regions, projected losses are greatest at the locations where historical temperatures are nearest 0 °C (32 °F), and projected increases to temperature increase the frequency of winter and early-spring periods that exceed 0°C. (Livneh and Badger 2020, pp. 453–454). Additionally, spring snow droughts (abnormally low snowpack) have become more prevalent, intensified, and lengthened across the western U.S. from 1980 to 2018 (Huning and AghaKouchak 2020, pp. 19754–19755). Interannual variability in snowpack is expected to continue to change in the future, with an increase in the frequency of spring snow droughts in the western U.S. (Marshall et al. 2019, p. 8885). The increase in the number of consecutive years of snow droughts will likely be greatest in the maritime regions of the Cascades and Sierra Nevada, as well as the lower elevations of the Northern Rocky Mountains (Marshall et al. 2019, p. 8885).

Climate change resulting from increases in carbon dioxide emissions is largely irreversible for hundreds of years after emissions cease (Solomon et al. 2009, p. 1705). Therefore, even if greenhouse gases stopped immediately, the lag effect due to long timescales of atmospheric attenuation and the accumulated reservoir of heat in the world's oceans means that climate change will continue to negatively affect persistent spring snowpack in the western U.S., further restricting and fragmenting wolverine habitat. Although different models use various parameters, model structure, inputs, and emissions scenarios to estimate future changes to climate, most are consistent in the general trend of spring snow loss in the western U.S., especially at lower elevations (see Snowpack/Snow Cover Projections, below). Despite this predicted loss, there will likely continue to be some areas large enough to support small breeding populations of wolverines in the contiguous U.S. (defined as areas greater than 1,000 km^2 (621 mi.), see McKelvey et al. 2011, p. 2894).

The precise effect of future changes to snowpack on wolverines is difficult to predict because factors other than the amount of snow may have mechanistic influences on wolverine movement and demography. For example, non-denning wolverines in the arctic appear to be sensitive to the snow's melt status and density (Glass et al. 2021a, p. 894). In the North Cascades of Washington and British Columbia, high variation in the number of frost-free days associated with maritime influences on the western side of the Cascades appears to have precluded wolverine use in some areas despite the presence of deep spring snowpack (Aubry et al. 2023, p. 13). Therefore, while estimates of the loss of snow provide a coarse-filter assessment of potential changes to the wolverine's range, they represent only one component of wolverine habitat selection. More complex changes to second- and third-order habitat selection (home range and within home range selection, respectively) due to climate change may occur in the future, and mechanisms that influence wolverine demography at these scales are not yet well understood (Aubry et al. 2023, p. 16).

Snowpack/Snow Cover Projections

Snow projections were performed over five modeling domains in the U.S. Rocky Mountain and Cascades ranges by researchers at the University of Colorado, University of Maryland, and NASA Goddard Space Flight Center (collectively) at the request of the USFWS. These modeling domains were selected to overlap with occupied and potential wolverine habitat in the contiguous U.S. across latitudinal, longitudinal, and elevation gradients. Modeling domains did not overlap with all known denning locations due to computational and time limitations.

The domains were selected to cover the range of denning latitudes, spanning multiple snow climate regimes along a southeast to northwest gradient between the interior Colorado Rocky Mountains and Pacific Northwest Washington Cascades. This spatial expansion is a major improvement from the snow projections used in our 2018 assessment, which focused only on Rocky Mountain National Park (Colorado) and Glacier National Park (Montana). The five modeling domains are named: (1) Cascades (Washington); (2) Northern Rocky West (Washington, Idaho, and Montana); (3) Northern Rocky (Idaho and Montana); (4) Mid-Rocky (Idaho, Montana, and Wyoming); and (5) Southern Rocky (Colorado and New Mexico).

Two scenarios were chosen from the Intergovernmental Panel on Climate Change (IPCC) Sixth Assessment Report to bracket the uncertainty regarding future greenhouse gas emission scenarios (Figure 6) (Tebaldi et al. 2021, p. 258). The two scenarios we chose are referred to as SSP2-4.5 and SSP5-8.5, where SSP means Shared Socioeconomic Pathways (SSPs), the term which replaced Representative Concentration Pathways (RCPs) from prior IPCC reports. The numerical suffixes (e.g., 2-4.5 and 5-8.5) represent the approximate level of radiative forcing (the change in energy flux in the atmosphere caused by natural or anthropogenic factors of climate change) in 2100 (compared to preindustrial levels) in units of watts per meter squared (W/m^2). The SSP2-4.5 pathway (modest mitigation) used in this analysis is similar to the RCP 4.5 scenario used in past reports, whereas the SSP5-8.5 pathway represents one of the most pessimistic estimates of greenhouse gas emissions, a future with no mitigation policy. The SSP5-8.5 pathway was included in this analysis to provide a lower-boundary estimate of future snow cover available for wolverines within the selected domains (OSTP 2023, p. 11).

Model methods

The high spatial resolution (0.01° or approx. 1 km x 1 km (0.62 mi. x0.62 mi.) snow depth projections performed for this SSA Addendum were made using a two-step modeling approach, which (1) developed a baseline simulation representative of average snow evolution in historical periods tailored to mountainous terrain, and (2) perturbed the baseline simulation with future climate-change signals. This change-factor approach (also termed the “delta method”) is a reliable approach for determining hydrological and ecological climate sensitivities when considering the evolved snowpack in springtime (Sofaer et al. 2017, p. 2549; Barsugli et al. 2020, p. 4). The model focused on developing snow simulations that represent changes in expected snow conditions between historical and future periods. We summarize our snow modeling methods below.

Interannual climate variability can often exceed the underlying climate change trends at shorter periods of time and can complicate the determination of representative change factors from the climate models. Twenty-year timeframes minimized the impact of annual climate variability on median air temperature and precipitation. Therefore, we partitioned the historical and future model output into discrete periods that were long enough to encompass climate variability, while short enough to compare climate impacts on snow volume across multiple periods between present-day and 2100. Hourly snow depth was modeled using 20-year historical and calibrated forcing (a measure of the imbalance in the Earth's energy budget), perturbed using change factors calculated for four 20-year future periods (2016–2035, 2036–2055, 2056–2075, and 2076–2095). Change factors were calculated between the future and historical timeframes for an ensemble of 23 Global Climate Models (GCM), and 2 emissions scenarios (SSP 2-4.5 and SSP 5-8.5), to generate an ensemble of 20-year median snow simulations across each of the four future 20-year periods.

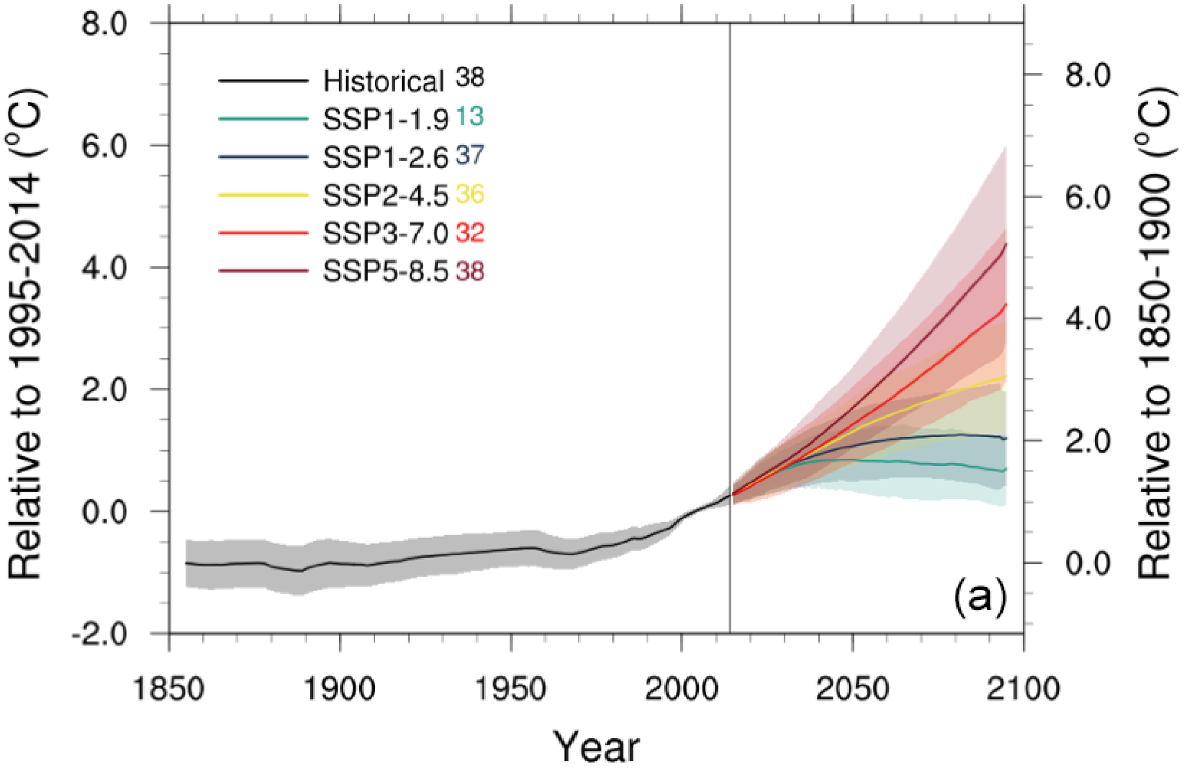

Figure 6. Global average temperature time series (11-year running averages) of changes from current baseline (1995–2014, left axis) and pre-industrial baseline (1850–1900, right axis, obtained by adding a 0.84 ◦C offset) for SSP1-1.9, SSP1-2.6, SSP2-4.5, SSP3-7.0 and SSP5-8.5 (Tebaldi et al. 2021).

Ensemble climate models are useful for exploring uncertainty and capturing variability in future projections due to different parameterizations and physics within individual GCMs. For our ensemble snow simulations, we calculated the lower-quartile (25th percentile), median (50th percentile), and upper-quartile (75th percentile) at each individual grid cell and timestep.

We chose a snow depth threshold of ≥1m (40 in.) to represent significant snow cover on May 1 based on published literature, our prior analyses in the 2018 SSA, and studies indicating that den site abandonment generally occurs before May 1 (see *Use of Dens and Denning Behavior discussion in Reproduction and Growth* section of the 2018 SSA). The snow depth threshold representing significant snow cover used in this analysis (≥1m on May 1) provides a more conservative estimate than was used in the 2018 SSA (≥0.5m [20 in] on May 1). Figures 7 and 8 show the historical (1995–2014) and potential future (2036–2055, 2056–2075, and 2076–2095) spatial distribution of snow ≥1 m on May 1 across five domains for SSP 2-4.5 and SSP 5-8.5, respectively. These results for the historical (median) and the 23 GCMs (lower quartile) included in the model are the most conservative future snow projections available. For example, the lower quartile ensemble of GCMs using SSP5-8.5 depicted in Figure 8 represents the estimate of future snow based on a family of high-end emission pathways.

Tables 11 and 12 show the area (km^2) where modeled snow depth exceeds the threshold (≥1m (3.28 ft.)) on May 1 for the SSP2-4.5 and SSP5-8.5 projections, respectively. We report modeled results for all domains and 20-year future projections and display the percentage increase or decrease in area exceeding the snow threshold, relative to median snowpack in the historical timeframe (1995–2014). To capture the variability of the GCMs used in snow projections we report these modeled estimates for the lower quartile of GCMs (depicted in Figures 7 and 8) as well as the upper quartile GCMs and the median (not depicted in Figures 7 and 8).

For SSP2-4.5 (Table 11) and the domains in total, the modeled range of potential change in snow depth threshold (≥1m (3.28 ft.)) on May 1 in the 2036–2055 timeframe is +15% to -17%, relative to historical snow levels. By 2056–2075, this range spans +3% to -26% and for 2076–2095, the range of change is estimated to be +2 to -33%. For SSP5-8.5 (Table 12), the most pessimistic emission pathway, the modeled range of potential change in snow depth threshold (≥1m (3.28 ft.)) on May 1 across all domains modeled is +6% to -22% for 2036–2055, -6% to -37% for year 2057–2075 and -13% to -45% for year 2076–2095. It is important to note that the modeled totals across all domains are skewed by the Mid-Rocky domain that is the largest domain in terms of historical snow ≥1m on May 1, and the domain with the least amount of snow loss in future time steps. The most extreme modeled decreases in projected snow depth threshold in 2076–2095 for SSP2-4.5 occur in the Southern Rocky domain (-49% for lower quartile GCMs) and for SSP5-8.5 a -69% decrease (lower quartile GCMs) in the Northern Rocky West domain.

Figures 9–13 show percent-change in the future area with snow exceeding the snow depth threshold (≥1 m (3.28 ft.)) on May 1, relative to the historical period across 100m elevation bands for each of the five modeling domains. These figures also show the percent of the domain that falls within each elevation band, and the elevation of documented historical den sites within the modeling domains. Finally, they depict the modeled range of percent change surrounding the median (lower and upper quartiles) for each future time period across the elevation gradient.

Interpretation of future snow projections and percent change

Results from this modeling effort are consistent with earlier studies predicting greater snow loss at lower elevations across all domains. Barsugli et al. (2020, pp. 8–10) reported similar elevational patterns for Rocky Mountain and Glacier National Parks with greater reductions in future snow cover at lower elevations. This is partially explained by a greater percentage of future precipitation falling as rain due to higher temperatures, and earlier snowmelt onset for thinner snow and warmer conditions. Snowpack in the high country is not as affected by projected temperature increases but is likely more strongly controlled by projected precipitation changes (Barsugli et al. 2020, pp. 6–11; Scalzitti et al. 2016, p. 5367; Sospedra-Alfonso et al. 2015, p. 4429).

The elevational distribution of historical den sites varies by latitude, with a general trend of dens being found at higher elevations the further south they are found. For example, dens in the Northern Rocky domain are found at elevations ranging from ~1,500–2,400m (Figure 12), whereas dens in the Mid-Rocky domain are found from ~2,400–3,000m (Figure 13). Additional den sites outside of the modeling domains could expand these elevation bands. The majority of historical dens across the domains are located in elevational bands that are predicted to experience relatively small decreases in future snow cover at the higher denning elevations and moderate decreases for lower denning elevations. The percentage change in future snow depth threshold (≥1m) on May 1 (median) for SSP2-4.5 (2076–2095) for the upper denning elevations in Northern Rocky West, Northern Rocky, and Mid-Rocky domains is <10% decrease, whereas the percentage change for the Cascades domain is <25% decrease. The percentage change in future snow depth threshold (≥1m) on May 1 (median) for SSP2-4.5 (2076–2095) for the lower denning elevations in Northern Rocky is a 10–50% decrease, and for Mid-Rocky is a 10–25% decrease, whereas the percentage change for the Cascades domain is a <25% decrease.

Elevations above historical den elevations are predicted to have small decreases (<10%) in the future area with snow depth exceeding the threshold (≥1m) on May 1 (median) for SSP2-4.5 (2076–2095) across the domains and in some cases (e.g., Northern Rocky and Mid-Rocky domains), increases in predicted future area with snow exceeding the ≥1m (3.28 ft.) May 1 threshold. This is driven by the increases in future precipitation expected in all five domains, and elevations with temperatures sufficiently cold enough to sustain snowfall, even with future warming. The lowest elevation areas within all domains (the lowest ~500m (1640 ft.) of domains modeled) are predicted to have the greatest decreases in the future snow depth threshold (≥1m (3.28 ft.)) on May 1. For example, the Northern Rocky domain is predicted to experience decreases from -50 to -100% at 1,000–1,500m of elevation (Figure 13). Similar patterns are seen in the other four domains.

The modeling methods (ensemble) used here differ from the methods of Barsugli et al., (2020, pp. 4–6) in that they do not capture the interannual (year-to-year) variability in snowpack. Snowpack in wet and dry years and/or hot and cool years may be impacted differently by climate change. Ensemble models result in average snow conditions for several GCMs for multiple years (e.g., 2076–2095). Table 13 shows a comparison of methodologies used by: This SSA Addendum, Barsugli et al. (2020, pp. 4–6), Copeland et al. (2010, pp. 234–238) and McKelvey et al. (2011, pp. 2884–2886). The predicted changes (mostly negative) in the future snow depth threshold (≥1m (3.28 ft.)) on May 1 with respect to wolverine persistence is difficult to quantify as no thresholds are currently known and many questions remain unanswered. While decreases are projected across the domains, the specific thresholds that could impact wolverine persistence at the population level are not known or are uncertain.

There are many other aspects of snow that are predicted to change as the climate warms, which could influence wolverine behavior, but are beyond the scope of this model update. These include: changes in snow dynamics that modify microclimates and refugia potential (Marshall et al. 2019, p. 8883; Morelli et al. 2020, p. 232), frequency of rain on snow events (Musselman et al. 2018, p. 808), frequency of extreme winter storm events (Prein et al. 2017, p. 48) and how these events could buffer increased snowmelt from warming (Marshall et al. 2020, p. 1). Temporal and spatial-scale issues affecting snowpack include cold air pooling and the potential for this pooling to create late-season snow refugia (Pastore et al. 2022, p. 10), small-scale microclimates influenced by forest features, local water balance, topography, and landscape composition (De Frenne et al. 2021, p. 2279), and the interplay of changing future snow dynamics on microclimate conditions. The interaction of these factors could influence future climate microrefugia and species distribution (Lenoir et al. 2017, p. 262) across the wolverine range, den site selection, and many other aspects of wolverine behavior.

Table 11. Area (km^2) of snow depth threshold ($\geq$ 1m) on May 1 relative to the historical period for five modeling domains in the western U.S. using SSP2-4.5 projection. Percent change from the historical period shown in parentheses.

Domain	Historical	2036–2055	2056–2075	2076–2095
Cascades				
Upper quartile		5,062 (+6%)	4,455 (-6%)	4,487 (-6%)
Median	4,763	4,584 (-4%)	3,873 (-19%)	3,944 (-17%)
Lower quartile		3,935 (-17%)	3,377 (-29%)	3,439 (-28%)
Northern Rocky West				
Upper quartile		3,284 (-6%)	2,944 (-16%)	2,768 (-21%)
Median	3,508	2,882 (-18%)	2,527 (-28%)	2,293 (-35%)
Lower quartile		2,481 (-29%)	2,106 (-40%)	1,949 (-44%)
Northern Rocky				
Upper quartile		7,315 (+13%)	6,573 (+2%)	6,398 (-1%)
Median	6,449	6,428 (0%)	5,650 (-12%)	5,389 (-16%)
Lower quartile		5,583 (-13%)	4,747 (-26%)	4,569 (-29%)
Mid-Rocky				
Upper quartile		24,226 (+18%)	22,824 (+11%)	23,387 (+14%)
Median	20,493	21,116 (+3%)	19,988 (-2%)	19,486 (-5%)
Lower quartile		18,867 (-8%)	17,046 (-17%)	15,673 (-24%)
Southern Rocky				
Upper quartile		14,510 (18%)	12,192 (0%)	11,192 (-9%)
Median	12,245	11,970 (-2%)	9,972 (-19%)	9,127 (-25%)
Lower quartile		8,733 (-29%)	7,942 (-35%)	6,271 (-49%)
Total of All Domains				
Upper quartile		54,396 (+15%)	48,988 (+3%)	48,231 (2%)
Median	47,458	46,980 (-1%)	42,010 (-11%)	40,239 (-15%)
Lower quartile		39,598 (-17%)	35,218 (-26%)	31,900 (-33%)

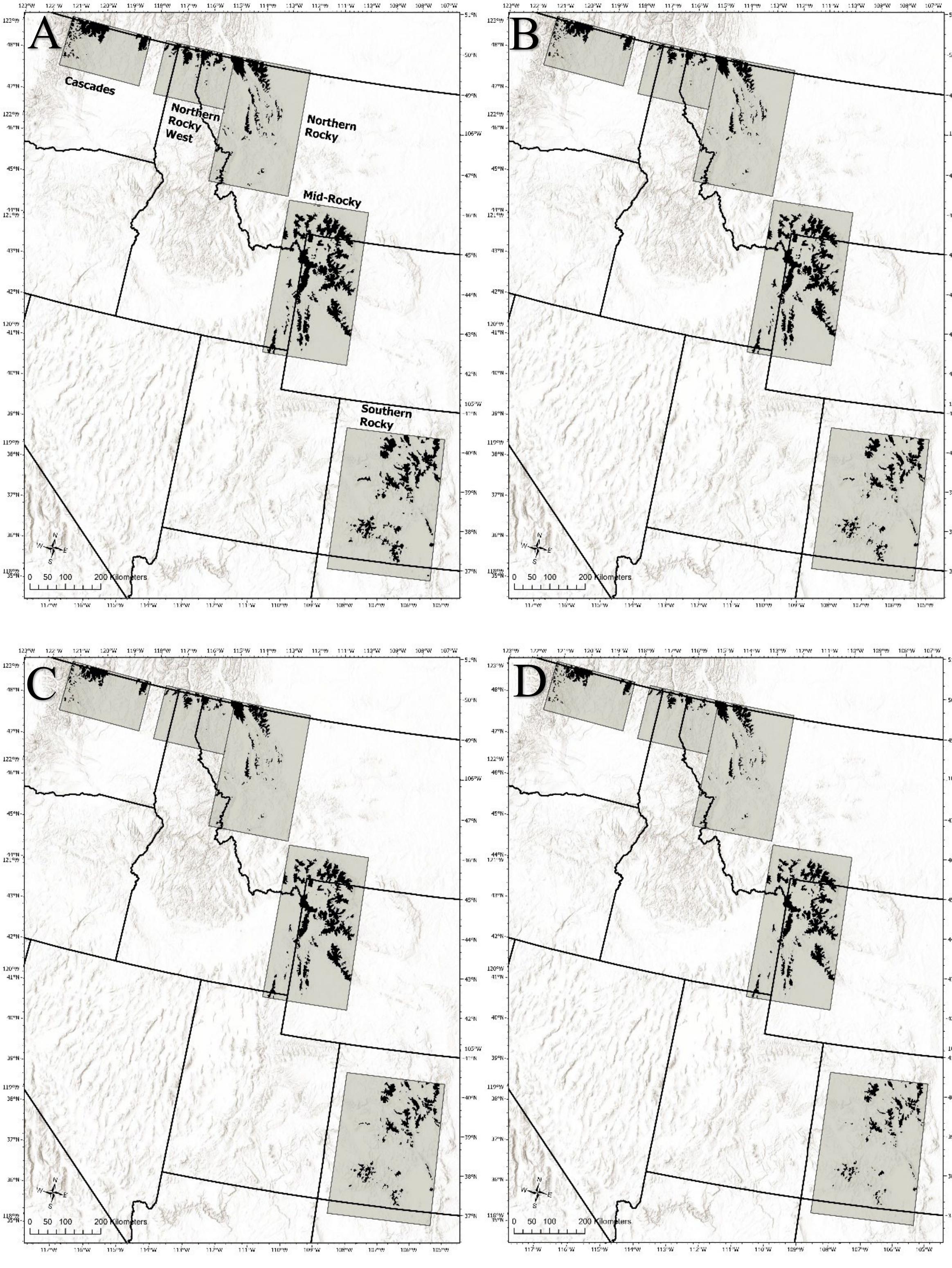

Figure 7. Snow model projections ≥ 1m on May 1 (lower quartile for future projections) using SSP 2-4.5 projection. A. Historical (1995–2014); B. (2036–2055); C. (2056–2075); and D. (2076–2095). Model domains shown in gray, and snow depth threshold (≥1m) on May 1 is black.

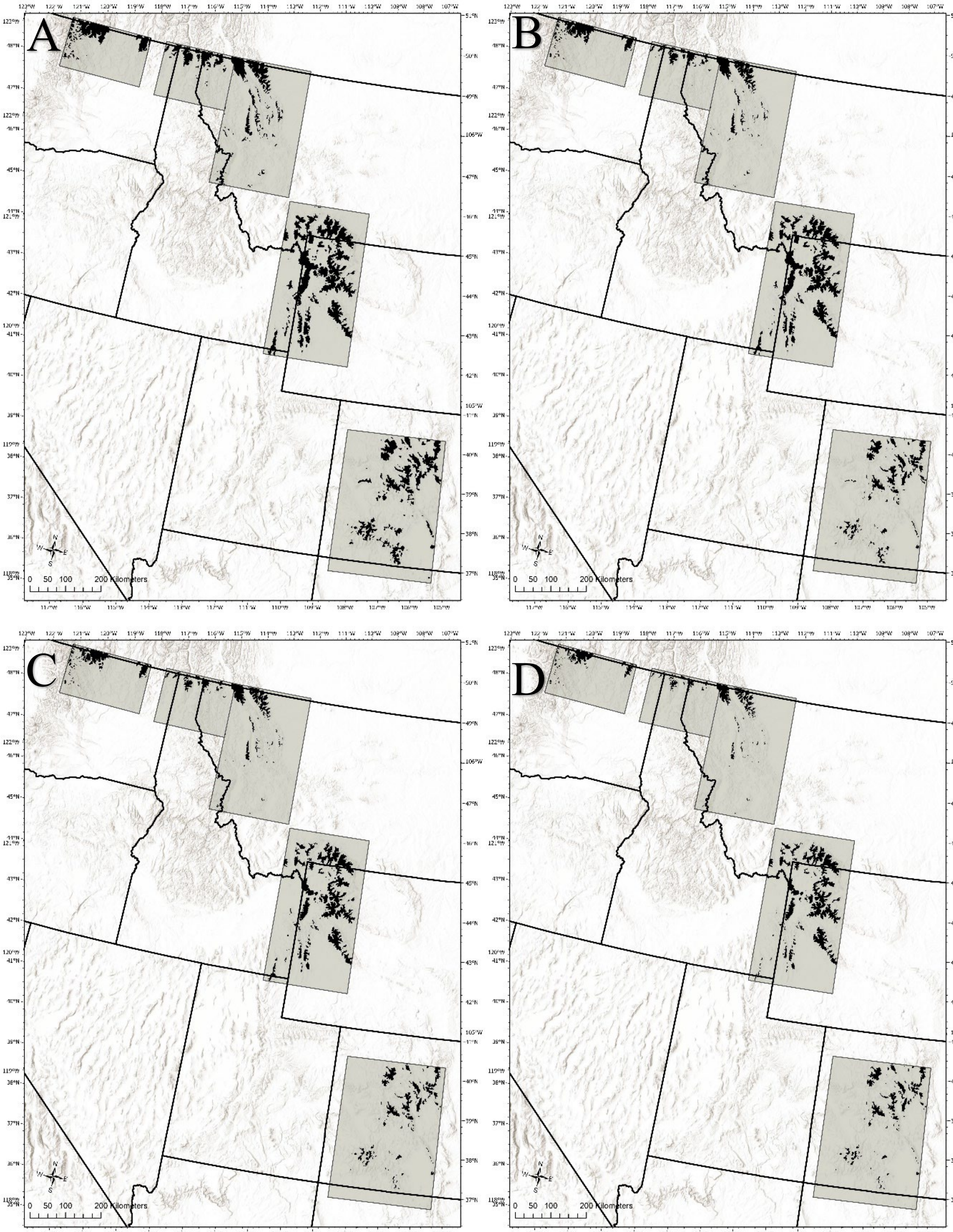

Figure 8. Snow model projections ≥1m on May 1 (lower quartile for future projections) using SSP 5-8.5 projection. A. Historical (1995–2014); B. (2036–2055); C. (2056–2075); and D. (2076–2095).

Table 12. Area (km^2) of snow depth threshold (≥1m) on May 1 relative to the historical period for five modeling domains in the western U.S. using SSP5-8.5 projection. Percent change from the historical period shown in parentheses.

Domain	Historical	2036–2055	2056–2075	2076–2095
Cascades				
Upper quartile		4,547 (-5%)	4,076 (-14%)	3,786 (-21%)
Median	4,763	4,029 (-15%)	3,458 (-27%)	2,925 (-39%)
Lower quartile		3,600 (-24%)	3,022 (-37%)	2,239 (-53%)
Northern Rocky West				
Upper quartile		2,894 (-17%)	2,473 (-30%)	1,959 (-44%)
Median	3,508	2,493 (-29%)	2,007 (-43%)	1,575 (-55%)
Lower quartile		2,161 (-38%)	1,676 (-52%)	1,104 (-69%)
Northern Rocky				
Upper quartile		6,510 (+1%)	5,890 (-9%)	5,087 (-21%)
Median	6,449	5,383 (-17%	4,574 (-29%)	4,008 (-38%)
Lower quartile		4,633 (-28%)	3,791 (-41%)	2,902 (-55%)
Mid-Rocky				
Upper quartile		23,839 (+16%)	22,375 (+9%)	19,982 (-2%)
Median	20,493	20,913 (+2%)	18,385 (-10%)	16,730 (-18%)
Lower quartile		19,563 (-5%)	15,640 (-24%)	14,353 (-30%)
Southern Rocky				
Upper quartile		12,722 (+4%)	9,951 (-19%)	10,484 (-14%)
Median	12,245	10,053 (-18%)	7,611 (-38%)	8,473 (-31%)
Lower quartile		7,294 (-40%)	5,705 (-53%)	5,626 (-54%)
Total of All Domains				
Upper quartile		50,513 (+6%)	44,764 (-6%)	41,297 (-13%)
Median	47,458	42,871 (-10%)	36,035 (-24%)	33,711 (-29%)
Lower quartile		37,250 (-22%)	29,833 (-37%)	26,224 (-45%)

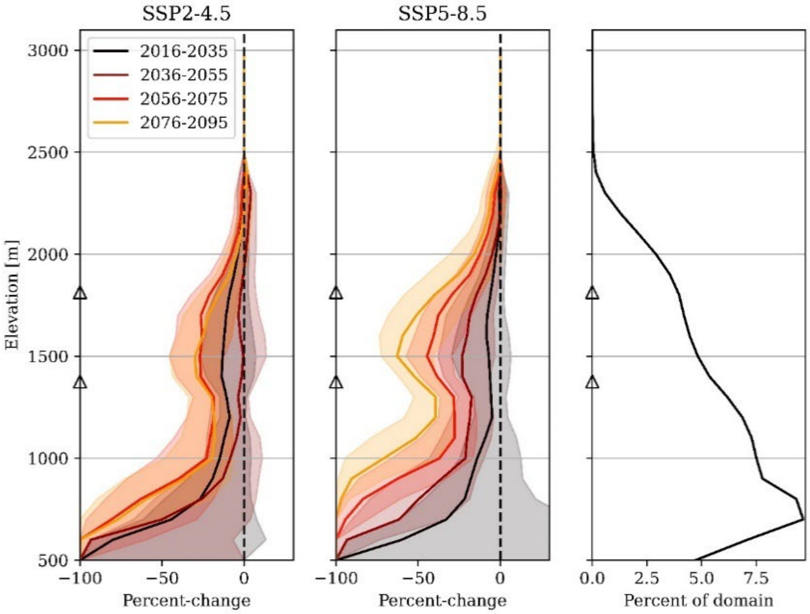

Figure 9. Percentage change in snow depth threshold (≥1m) on May 1 for the Cascades domain. Triangles on y-axis represent the elevations of documented historical wolverine dens within this domain.

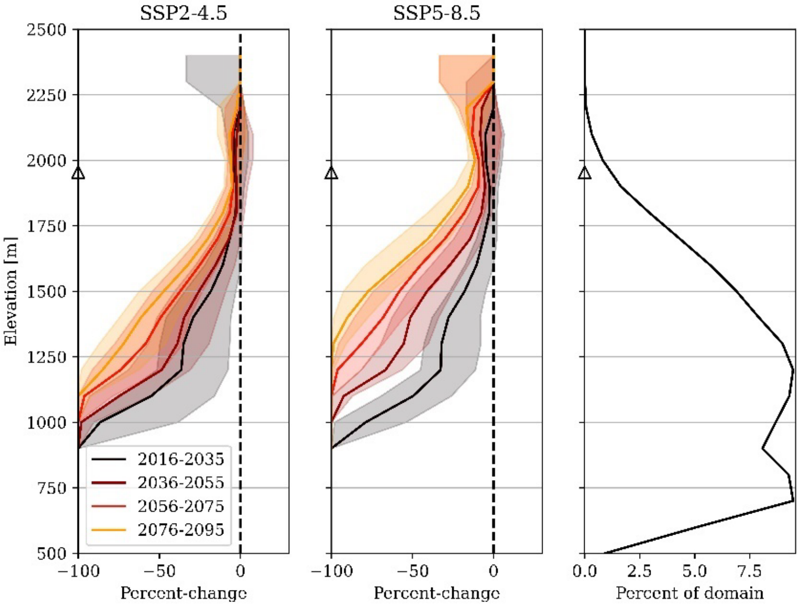

Figure 10. Percentage change in snow depth threshold (≥1m) on May 1 for the Northern Rocky West domain. Triangles on y-axis represent the elevations of documented historical wolverine dens within this domain.

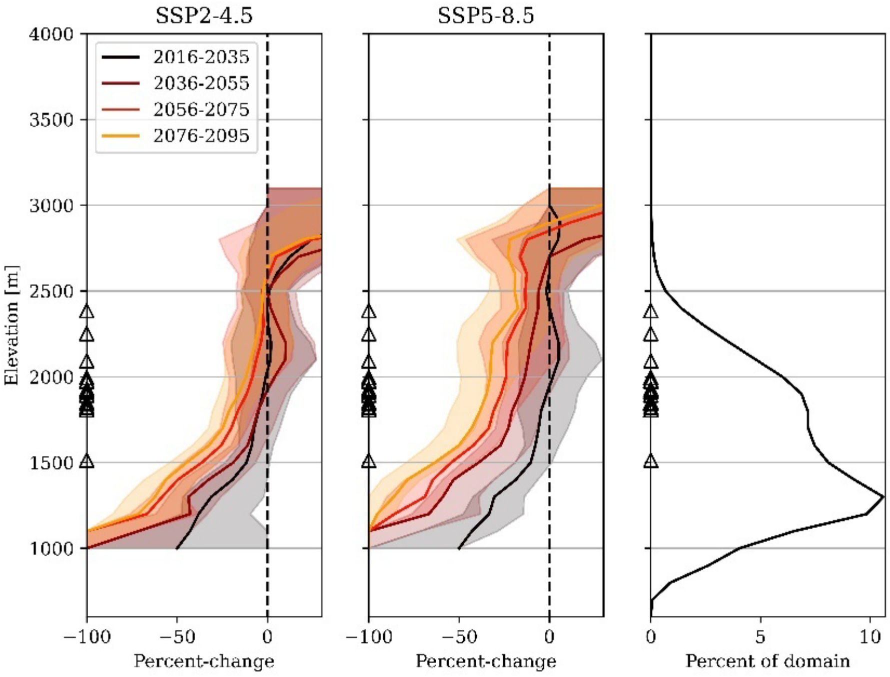

Figure 11. Percentage change in snow depth threshold (≥1m) on May 1 for the Northern Rocky domain. Triangles on y-axis represent the elevations of documented historical wolverine dens within this domain.

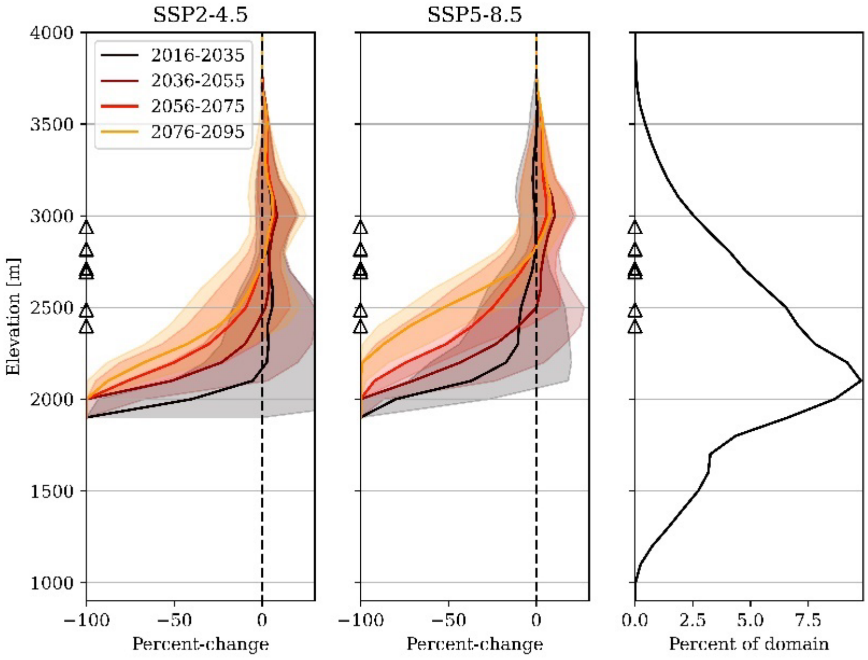

Figure 12. Percentage change in snow depth threshold (≥1m) on May 1 for the Mid-Rocky domain. Triangles on y-axis represent the elevations of documented historical wolverine dens within this domain.

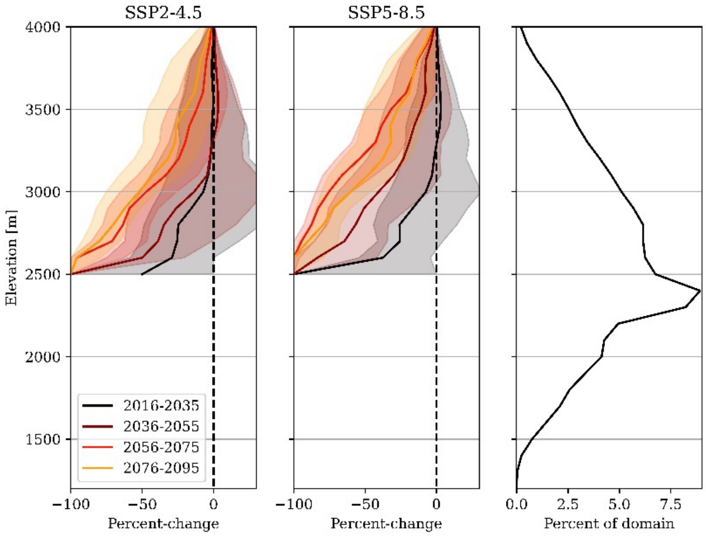

Figure 13. Percentage change in snow depth threshold (≥1m) on May 1 for the Southern Rocky domain. Triangles on y-axis represent the elevations of documented historical wolverine dens within this domain (none in this domain).

Key Areas of Uncertainty for Future Conditions and Climate Change Effects

Central to our assessment of future conditions is the degree to which changes in persistent spring snow, other snow dynamics (e.g., volume, duration, condition, spatial and temporal variability, etc.) and other climate-related factors will impact wolverines at the population level in the contiguous U.S. Key uncertainties that remain regarding these relationships include: (1) the extent to which wolverine population connectivity and gene flow will be affected by these changes; (2) impacts of climate change on ecosystem drivers of wolverine persistence (i.e., changes in community dynamics, including prey availability and competition with other predators that might impact wolverine demographic rates); (3) the volume and duration of snow required for wolverines to successfully acquire and cache food for future use; (4) the impacts of climate change on the ability of wolverines to thermoregulate under changes in climate, and whether they might experience any sublethal effects from changes in temperature (e.g., impacts to reproduction) (see Thiel et al. 2019, entire); (5) whether the observed associations of the wolverine's distribution with snowy and cold environments are driven by reproductive denning needs, other ecological requirements, or physiological constraints (Aubry et al. 2023, p. 16); (6) the adaptive capacity of wolverines to move to higher elevations for denning given predicted snow loss at lower elevations within their historical denning range (assuming snow is always required for denning); and (7) the importance of snow and the impact of decreases in future snow within historical denning elevations on reproductive success. In summary, specific thresholds regarding snow dynamics and how changes in these factors will impact wolverines in the future at the population level remain uncertain.

Table 13. Comparison of snow analysis methodologies employed in SSA Addendum, Barsugli et al. (2020), Copeland et al. (2010) and McKelvey et al. (2011).

Feature	SSA Addendum	Barsugli et al. (2020)	Copeland et al. (2010) and McKelvey et al. (2011)
Spatial resolution	0.01 degrees (~1 km x 1 km)	250 m x 250 m = 62,500 m^2 or 0.0625 km^2 (0.24 mi^2)	0.125 degrees (~5 km x 7 km; 37 km^2 (14.29 mi^2))
Geographic area	Western US Rocky Mountains and North Cascades (in WA, ID, MT, WY, CO, and NM)	Glacier and Rocky Mountain National Parks, 300 m below treeline and above	Western United States, except California and Great Basin
Topography	Slope, aspect, and shading were used	Slope, aspect, and shading were used	Slope and aspect were not used
Validation	Western US snow reanalysis	SNOTEL (in-situ observations) and MODIS (satellite remote sensing)	None specific to the snow dataset used
Future scenario method	Delta Method, used to project 1995 – 2014 conditions out to: 1) 2016 – 2035, 2) 2036 – 2055, 3) 2056 – 2075, and 4) 2076 – 2095	Delta Method, used to project 2000–2013 conditions out to Year 2055 (average of 2041–2070)	Delta Method (Years: 2045 (2030–2059), 2085 (2070–2099)
Future scenarios (GCMs)	CMIP6 SSP2-4.5 and SSP 5-8.5. GCMs: *ACCESS-CM2, ACCESS-ESM1-5, CESM2, CESM2-WACCM, CMCC-ESM2, CNRM-CM6-1, CNRM-ESM2-1, EC-Earth3, FGOALS-gr3, GFDL-CM4, GFDL-CM4-gr2, GFDL-ESM4, GISS-E2-1-G, IITM-ESM, INM-CM4-8, INM-CM5-0, KACE-1-0-G, MIROC-ES2L, MPI-ESM1-2-HR, MPI-ESM1-2-LR, MRI-ESM2-0, NorESM2-LM, NorESM2-MM*	*miroc*, *giss*, *fio, cnrm* (both study areas); *canesm* (Glacier National Park only) *hadgem2* (Rocky Mountain National Park only)	CMIP3: Ensemble mean of 10 GCMs, *pcm1*, and *miroc 3.2*
Time-related results	Long-term medians	Long-term means and year-to-year variability (i.e., wet, near normal, and dry years)	Changes in long-term mean snowpack only
Snow detection and measurements	"Significant snow": snow depth (1.0 meter (3.28 feet)) threshold on May 1.	Snow presence: 1.25 cm (0.5 in) snow depth threshold on May 15. "Significant snow": snow depth (0.5 meter (20 in) threshold. Snow depth determined by conversion from Snow Water Equivalent using bulk snow density.	Snow presence (13 cm (5.12 in) snow depth threshold on May 1). Snow depth determined by VIC model.
Number of years of MODIS data	17 (2000–2016)	17 (2000–2016)	7 (2000–2006)
Snow model	Noah-MP (Niu et al. 2011)	DHSVM (University of Washington)	VIC (University of Washington)
Snow cover dates analyzed	May 1	April 15, May 1, and May 15	May 15 (derived from May 1), May 29 (derived from May 1)

5.0 Risk Assessment

In this section, we assess risk to the wolverine's viability in the contiguous U.S. Viability is the ability of a species to maintain populations in the wild over time. To assess viability, we use the conservation biology principles of resiliency, redundancy, and representation (Shaffer and Stein 2000, pp. 307–310). These principles are rooted in ecological theory and empirical studies showing that, all else being equal, larger range, more populations, larger populations, larger habitat areas, sufficient gene flow, and distribution across a variety of ecosystems all lower extinction risk (Wolf et al. 2015, p. 204). We use definitions of resiliency, redundancy, and representation based on Smith et al. (2018, pp. 306–307), which were derived specifically for species status assessments. Our definitions are somewhat different than those presented in Shaffer and Stein (2000, pp. 307–310) because our focus is on assessing the viability of a particular species rather than their broader focus on ecosystem function and biodiversity. A species with a high degree of resiliency, representation, and redundancy is better able to rebound from environmental stochasticity (resiliency), withstand catastrophes (redundancy) and adapt to changes in its biological and physical environment (representation). In general, species viability increases with increases in resiliency, redundancy, and representation (Smith et al. 2018, p. 306).

Resiliency is the ability of a species to withstand environmental stochasticity (normal, year-to-year variations in environmental conditions such as temperature and rainfall), periodic disturbances within the normal range of variation (fire, floods, and storms), and demographic stochasticity (normal variation in demographic rates such as mortality and fecundity) (Redford et al. 2011, p. 40). Simply stated, resiliency is the ability to sustain populations through the natural range of favorable and unfavorable conditions.

We can best gauge resiliency by evaluating the following population-level characteristics: demography (abundance and the components of population growth rate including survival, reproduction, and migration); genetic health (effective population size and heterozygosity); connectivity (gene flow and population rescue); and habitat quantity, quality, configuration, and heterogeneity. For species prone to spatial synchrony (regionally correlated fluctuations among populations), distance between populations and degree of spatial heterogeneity (diversity of habitat types or microclimates) are also important considerations.

Redundancy spreads risk among multiple populations or areas to increase the ability of a species to withstand catastrophes. Catastrophes are stochastic events that cause substantial decreases in population size and can increase extinction risk, even in large populations (Mangel and Tier 1993, p. 1083).

We can best gauge redundancy by analyzing the number and distribution of populations relative to the scale of anticipated species-relevant catastrophic events. The analysis entails assessing the cumulative risk of catastrophes occurring over time. Redundancy can be analyzed at a population or regional scale, or, for narrow-ranged species, at the species level.

Representation was originally conceived as the conservation of species within an array of different environments or ecological settings as part of conserving functioning ecosystems (Shaffer and Stein 2000, pp. 307–308). However, in the context of assessing species viability, representation in different ecological settings is a proxy for adaptive capacity (Smith et al. 2018, p. 306), which is the ability of a species to adapt to both near-term and long-term changes in its physical (climate conditions, habitat conditions, habitat structure, etc.) and biological (pathogens, competitors, predators, etc.) environments. Therefore, we define representation as the ability to adapt to new environments.

Although representation across the range of ecosystems in which a species occurs is one measure of how a species may be able to withstand or adapt to environmental change, we also use more direct measures of adaptive capacity to assess representation. Species can adapt to novel changes in their environment by either (1) moving to new, suitable environments, or (2) altering their physical or behavioral traits (phenotypes) to match the new environmental conditions through either plasticity or genetic change (Nicotra et al. 2015, p. 1270; Beever et al. 2016, p. 132). The latter (evolution) occurs via the evolutionary processes of natural selection, gene flow, mutations, and genetic drift (Crandall et al. 2000, pp. 290–291; Sgrò et al. 2011, p. 327).

We can best gauge representation by examining the breadth of genetic, phenotypic, and ecological diversity found within a species and its ability to disperse and colonize new areas. In assessing the breadth of variation, it is important to consider both larger-scale variation and smaller scale variation. Larger-scale variation includes both (1) morphological, behavioral, or life history differences, which might exist across the range, and (2) environmental or ecological variation across the range. Smaller-scale variation includes measures of interpopulation genetic diversity. In assessing the dispersal ability, it is important to evaluate the ability and likelihood of the species to track suitable habitat and climate over time. Lastly, to evaluate the evolutionary potential that contributes to maintaining adaptive capacity (Forester et al. 2022, entire), it is important to assess: (1) natural levels and patterns of gene flow, (2) degree of ecological diversity occupied, and (3) effective population size.

5.1 Resiliency and Redundancy

Current Condition

Currently, wolverines are distributed in five primary core regions in the contiguous U.S., including the Northern Cascades in Washington, the Salmon-Selway in central Idaho, the northern Continental Divide in northwest Montana, the Central Linkage region of Idaho and Montana, and the Greater Yellowstone Ecosystem (Figure 14). Although long-distance dispersers (primarily males) occasionally reach potentially suitable habitat in other regions, known breeding populations are currently limited to these core regions.

The precise size of the wolverine populations in the contiguous U.S. are currently unknown, but may be small due in part to their large territories and the limited amount of available habitat in the contiguous U.S. Estimates based on extrapolations of densities and suitable habitat suggest there could have been approximately 318 wolverines (95% CI = 249–926) in the contiguous U.S. more than a decade ago (Inman et al. 2013, p. 282). The best available estimates of effective population size of wolverines in the contiguous U.S. portions of the Northern Rocky Mountains and North Cascades are likely <50 (Schwartz et al. 2009, p. 3226). The wolverine's population trend in the contiguous U.S. is unknown; however, results from a multi-state occupancy survey found some changes to wolverine occupancy between the 2016–2017 and 2021–2022 sampling periods within their known breeding range. In a portion of southwestern Canada encompassing a Rocky Mountain National Park complex and surrounding unprotected lands, the wolverine population declined approximately 40% from 2011–2020 likely due largely to overharvest through trapping (Barrueto et al. 2022, p. 4), which is no longer permitted in this area.

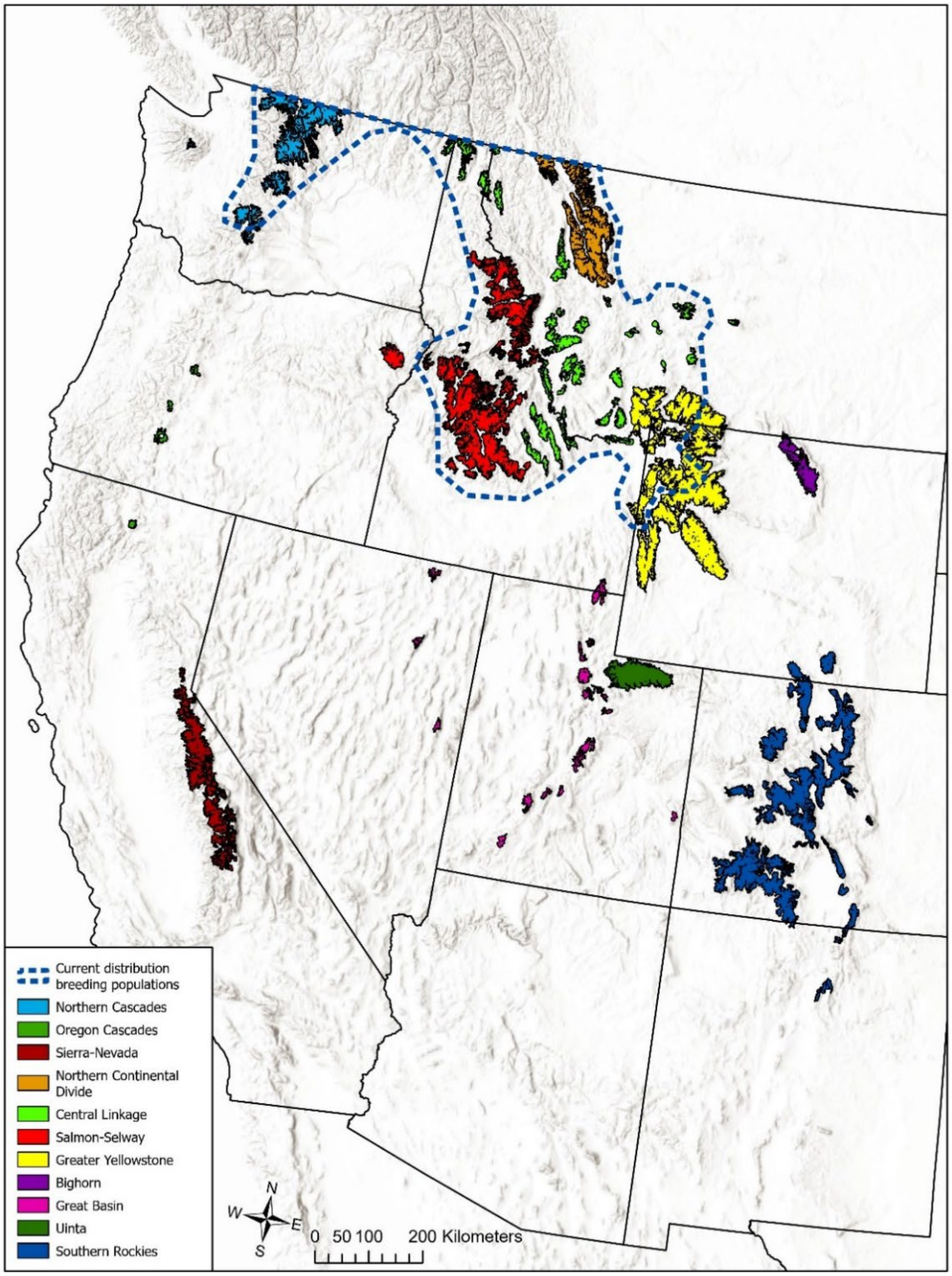

Figure 14. Major blocks (>100 km^2) of primary wolverine habitat (suitable for use by resident adults) in the western U.S. as predicted with a first-order (species distribution) logistic regression and grouped into management regions (from Inman et al. 2013). Current distribution of known breeding populations based on contemporary records are also depicted with the dashed line, updated to show current distribution of breeding populations.

Contiguous U.S. contemporary wolverine populations are most likely the result of wolverine immigration from Canada following a period of persecution in the U.S. (USFWS 2018, p. 49). Wolverine genetic diversity in the contiguous U.S. is relatively low and there are no known unique mitochondrial DNA haplotypes present in contiguous U.S. wolverine populations (Sawaya et al. 2023, pp. 10–11). Due to the limited amount of potential wolverine habitat in the U.S., connectivity and gene flow with Canada is necessary for the long-term genetic health and viability of wolverines in the western U.S. In the North Cascades, new GPS tracking information shows that wolverines in western Washington and southern British Columbia form a small transboundary population (Aubry et al. 2023, p. 4), although they are isolated from other wolverine populations in the U.S. and Canada (Sawaya et al. 2023, pp. 9–13, 16). In the Northern Rocky Mountains, the best available data indicate genetic differences between populations despite some (mostly male-mediated) gene flow (Cegelski et al. 2006, pp. 204–205, 208; Sawaya et al.2023, pp. 12, 17). This result is consistent with previously reported measurable differences in mitochondrial DNA haplotype diversity and nuclear microsatellite DNA allele frequencies between the U.S. Rocky Mountain populations and Canada populations (Cegelski et al. 2006, p. 203). There is currently no evidence of inbreeding depression in wolverine populations in the contiguous U.S.; however, there is potential for inbreeding given the relatively small population sizes of wolverines here, especially in the Cascades (M. Sawaya, pers. comm. 2023).

Future Condition

We expect wolverine resiliency and redundancy in the contiguous U.S. to decline to some extent. Wolverine habitat in the contiguous U.S. is projected to decrease in areas that were modeled and become more fragmented because of climate changes that result in increasing temperatures, earlier spring snowmelt, and loss of deep, persistent spring snowpack, primarily at lower elevations (see **Climate Change Effects** section above). Winter recreation, which has been shown to negatively influence wolverine behavior, in these diminished habitats may increase as human populations increase (U.S. Forest Service 2016, pp. 12–13, 12–14). In addition, snow-dependent recreation that was formerly distributed over a wider elevation gradient will be constrained to that part of the gradient that contains quality snow into the future. Concurrently, human development may continue to expand in areas between core habitats that are important for maintaining wolverine population connectivity. While wolverines are capable of crossing areas with some human disturbance during dispersal, they also have shown some sensitivity to human development and other human impacts in rugged areas located between typical core wolverine habitats (Balkenhol et al. 2020, p. 799; Barrueto et al. 2022, p. 4). Increased human development, infrastructure and associated anthropogenic disturbance are expected to have direct and indirect effects to wolverine populations in the contiguous U.S. including reducing the number of wolverines that can be supported by available habitat and reducing the ability of wolverines to travel between patches of suitable habitat. A reduction in population size and connectivity may affect metapopulation dynamics, making it more difficult for subpopulations to recolonize currently extirpated areas and augment the genetics or demographics of adjacent subpopulations.

We have identified significant uncertainties that hamper our ability to predict the scope, scale, and timing of future demographic outcomes for wolverines in the contiguous U.S. These include uncertainties in mechanistic habitat relationships, census and effective population sizes, and the cumulative impact of multiple stressors on population connectivity, survival, and reproduction. Nevertheless, habitat loss through climate change, combined with other stressors, is likely to negatively impact wolverines in the contiguous U.S. over the next century. Moreover, there are few actions that are reasonably certain to occur in the future that would compensate for these negative impacts.

5.2 Representation

Current and Future Condition

We evaluated the wolverine's ability to respond to environmental change in two ways. First, we examined core attributes of the wolverine's adaptive capacity in relation to standardized attributes to characterize the likelihood that wolverines in the western U.S. will be able to adapt to changed conditions (Thurman et al. 2020, entire; Figure 15). Second, we evaluated the current and potential distribution of wolverines across ecological regions of the western U.S. given that ecological changes may vary across space, and that wolverines in different ecological contexts may have dissimilar responses to these changes.

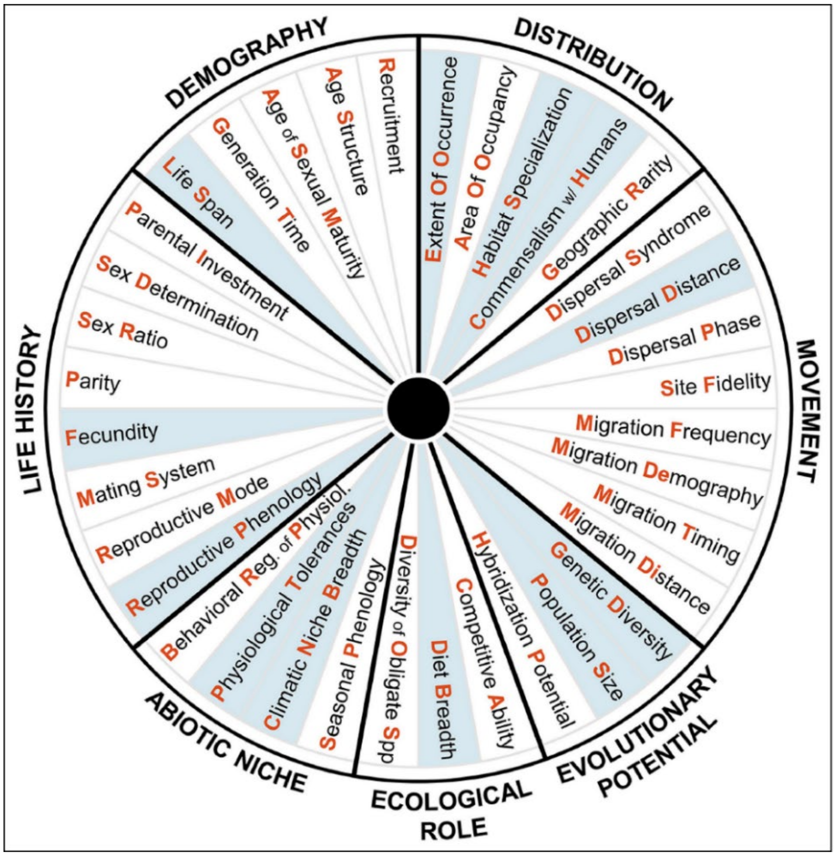

Figure 15. Standardized attributes related to adaptive capacity from Thurman et al. (2020). Core standardized attributes from Thurman et al. (2020) are highlighted blue.

Adaptive Capacity

The wolverine's ability to adapt to climate change and other environmental changes, its adaptive capacity (AC), is key to reducing its vulnerability to these changes. We applied Thurman et al.'s (2020, entire) AC analysis to wolverines to help describe their ability to adapt to environmental change, inclusive of climate change. Thurman et al. (2020, entire) organized AC into 36 species' attributes (Figure 15), 12 of which were considered core attributes related to AC for the wolverine (Table 14). Each attribute score ranges from low (worst) to high (best) AC based upon the species' ability to adapt to changing environmental conditions. Our qualitative application of the AC analysis to wolverine was based on life history characteristics and showed that several intrinsic factors make them susceptible to negative outcomes from future environmental change. Their specialized habitat associations, low genetic diversity and population size, narrow ecological niche, low tolerance for human disturbance, and slow reproductive rate, all contribute to the wolverine's relative difficulty in adapting in-place to future environmental change (Table 14). Factors that may partially mitigate the wolverine's low AC are their ability to disperse long-distances, their relatively wide-distribution in the Northern Rocky Mountains and in the North Cascades (albeit in a narrow climactic niche), and their flexible diet (Table 14). Stressors that lessen the ability of wolverines to disperse, or that decrease their distribution, are likely to also degrade their AC, leaving them more vulnerable to environmental change.

Table 14. Core attributes of adaptive capacity relevant to wolverine, an explanation of each attribute, the score we assessed for wolverines in the western U.S. for each attribute, and the justification for wolverines fitting the score categories as defined by Thurman et al. (2020).

Category: ***Attribute***	**Explanation**	**Adaptive Capacity Score**	**Justification**
Distribution: ***Extent of occurrence***	The area that encompasses all known, inferred, or projected sites of present occurrence	High	Area is greater than 20,000 km^2 (12,427 mi^2)
Distribution: ***Habitat specialization***	Habitat specificity, or the degree to which a species can use multiple habitats vs. being confined to specific or narrow subset of habitats	Low	Highly associated with alpine ecosystem in the contiguous U.S.; not specialized in dispersal habitat
Distribution: ***Commensalism with humans***	Degree of tolerance of human interaction and infrastructure	Low	The species occurs in areas with low human occupation, but the precise amount of human disturbance that causes wolverines to avoid or abandon areas is not known.
Movement: ***Dispersal distance***	The distance an individual can move from an existing population's location	High	Excellent dispersal capability (>50 km (31 mi.) on average); can be

Category: ***Attribute***	**Explanation**	**Adaptive Capacity Score**	**Justification**
			restricted by highways and other infrastructure.
Evolutionary Potential: ***Genetic diversity***	The diversity of genotypes within a species	Low	Genetic effective population sizes likely <50; few mitochondrial haplotypes
Evolutionary Potential: ***Population size***	The number of individuals in the population	Low	Genetic effective population sizes likely <50. Census population size is unknown but could be <250 individuals.
Ecological Role: ***Diet breadth***	The ability to use a range of food resources	High	Flexible diet
Abiotic Niche: ***Climate niche breadth***	Niche specialization or the range of abiotic conditions to which a species is adapted	Low	Adapted to snowy, cold environments
Abiotic Niche: ***Physiological tolerances***	The degree to which a species is restricted to a narrow range of abiotic conditions and the degree of tolerance of physiological stressors	Low	Core habitats are restricted to snowy, cold, alpine environments.
Life History: ***Reproductive phenology***	The timing of reproductive events within a species life cycle	Moderate	Reproductive females do not rear a litter every year. Low reproductive rates are presumed to be a function of a female's winter body condition and demands of lactation and winter food availability, rather than directly associated with an environmental cue.
Life History: ***Fecundity***	Number of offspring produced on average	Low	Average is mostly less than three (1.75–3.5); Females may not breed every year depending on food availability.
Demography: ***Life span***	Average period between birth and death of an individual	Moderately High	Average generation time is 7.5 years.

Distribution among Ecoregions

Maintaining a species across their full breadth of ecological variation can reduce extinction risk from known and unknown threats in two ways (Forester et al. 2022, p. 512). First, ecological variation can correlate with species-wide evolutionary potential when a species has evolved local adaptations (Forester et al. 2022, p. 511). Second, ecoregions can be differentially exposed or affected by various stressors such that a species has greater resistance (ability to remain essentially unchanged when subject to disturbance) or resilience (ability to recovery from disturbance) within certain ecoregions.

To assess evolutionary potential, ecological resistance, and resilience, we examined the wolverine's current distribution across different ecoregion provinces. Ecoregion provinces incorporate temperature, precipitation, and vegetation data, and therefore represent landscapes with similar environmental traits (Bailey 2016, entire). Wolverine breeding populations in the western U.S. currently exist in 4 of 10 ecoregions where there is potential wolverine core habitat (Figure 16). Outside of the area with known wolverine breeding, several ecoregions contain only a relatively small area of potential wolverine core habitat. Except for the Sierran Steppe-Forest-Alpine ecoregion, wolverine breeding populations currently inhabit all the ecoregions of the western U.S. with large contiguous blocks of potential wolverine core habitat (Figure 16).

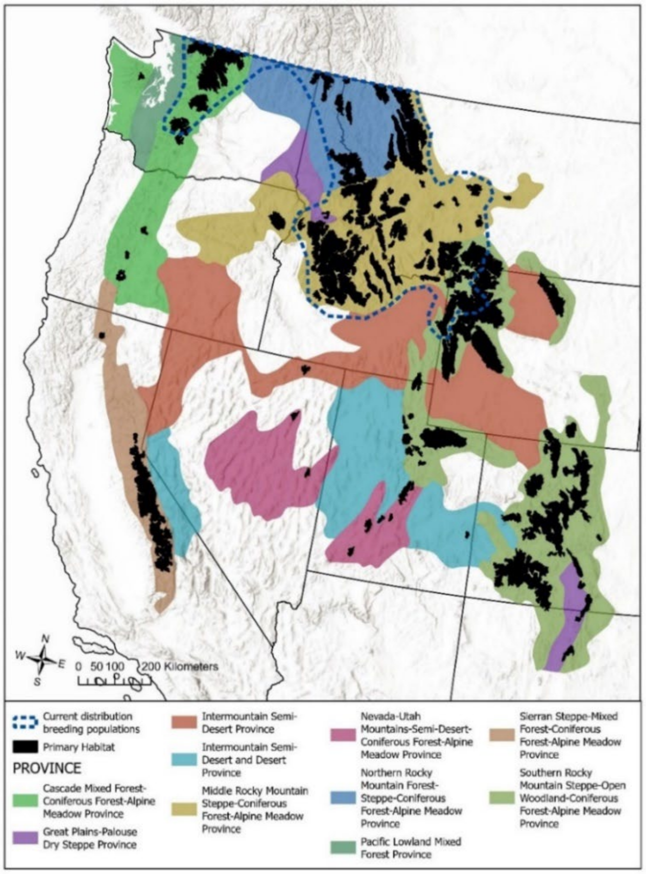

Figure 16. Intersection of wolverine core areas and ecoregions of the western U.S. Primary wolverine habitat polygons from Inman et al. (2013, p. 281).

5.3 Synthesis

In our 2018 SSA, we noted that during the late 1800s and early 1900s, the wolverine population declined or was extirpated in much of the contiguous U.S. (lower 48 States). This decline and range contraction has been attributed to unregulated trapping and habitat degradation (Hash 1987, p. 583). Given the current high-elevation core habitats of wolverines in the contiguous U.S., however, direct mortality through predator poisoning campaigns and unregulated trapping were likely the primary culprits. Similar range reductions and extirpations of some wolverine populations were observed in parts of Canada during this time period (COSEWIC 2014, p. iv; van Zyll de Jong 1975, entire), and are attributed largely to human exploitation and availability of food (e.g., decline in caribou [*Rangifer tarandus*]), not climate or habitat changes (van Zyll de Jong 1975, pp. 434, 436). Wolverine numbers have recovered to some extent from this decline (e.g. Aubry et al. 2007, p. 2151, Aubry et al. 2016, pp. 14–15; Magoun et al. 2013, p. 27 USFWS 2018, p. 1).

Wolverine populations in the contiguous U.S. are small, fragmented, and relatively isolated from larger populations in Canada (Cegelski et al. 2006, pp. 206–207, 210; Sawaya et al. 2023, entire). Although male-mediated dispersal shows some level of wolverine population connectivity between the U.S. and Canada along the Rocky Mountains, female wolverines appear to have virtually no recent population connectivity based on genetic analyses (Sawaya et al. 2023, p. 12–14, 17). Small, isolated populations are more vulnerable to extinction through interactions between environmental, genetic, and demographic factors (Caughley 1994, pp. 221–227). Stochasticity in demographic rates at small population sizes causes outsized impacts to vital rates, even in a constant environment, which can greatly increase extinction risk. Small, isolated populations also lose genetic diversity over time, primarily through inbreeding and genetic drift, which can exacerbate extinction risk if demographic rates are further degraded through inbreeding depression (Benson et al. 2016, p. 8). Low genetic diversity can also reduce adaptive capacity and evolutionary potential.

Although historical wolverine populations were likely naturally small and distributed among patches of high-elevation alpine habitats in the contiguous U.S., core wolverine habitats are projected to become smaller and more fragmented in the future as the result of climate change and human disturbance. These changes may degrade wolverine resiliency and redundancy over time, although there are significant uncertainties in the precise amount of degradation, or how much this degradation will affect wolverine viability in the contiguous U.S., or the time period over which it would happen. Despite their current distribution across several ecological regions of the West, the core attributes related to adaptive capacity exhibited by wolverines may limit the ability of this species to adapt and persist in the face of projected environmental change. Long-distance dispersal and recolonization of some of the larger areas outside of the current breeding range of wolverines (e.g., Sierra Nevada and central Rocky Mountains) could partially mitigate their susceptibility to environmental change. Dispersal between currently occupied core habitats may become more difficult in the future with anticipated increases in human development in the valleys between the alpine core areas and increased backcountry winter recreation in core habitats. However, wolverine dispersal could be maintained or improved by human intervention (e.g., conserving wildlife corridors between alpine habitats, constructing highway crossing structures for wildlife).

Overall, future wolverine populations in the contiguous U.S. may be less secure than we described in our 2018 SSA. Uncertainty over the wolverine's future condition in the contiguous U.S. is relatively high. Key questions remain around gene flow between the U.S. and Canada, core habitats and key dispersal corridors among core areas of the contiguous U.S., and the effective population size in the contiguous U.S. Nevertheless, the best available information suggests that habitat loss as a result of climate change and other stressors are likely to impact the viability of wolverines in the contiguous U.S. through the remainder of this century.