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Wolverines and wilderness: a review of wolverine response to human disturbance

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Abstract

Wolverines (*Gulo gulo*) are associated with wilderness areas with minimal human-caused habitat degradation and mortality. However, their future is uncertain, as an increasing portion of their range that was de facto wilderness now overlaps with industrial development, recreation, and fur harvest. We reviewed the North American wolverine literature, with insights from Fennoscandia, to determine the relative effects of nonlethal and lethal human disturbances on wolverines and whether populations in nonwilderness habitats can be viable. Wolverines occupy home ranges that partly or completely overlap areas with industrial development and recreation. There are positive nonlethal effects, including wolverine use of industrial infrastructure for cover, movement, reproductive den sites, or forage. Nonetheless, much of the evidence suggests that wolverines do not use areas with nonlethal human disturbance, with occlusion stronger as the magnitude of human activity increases. Nonlethal disturbances also might have negative effects on reproduction and increase competition. There appears to be an association between population decline and nonlethal human disturbance, although it can be difficult to disentangle from lethal human disturbances that often occur coincidentally. In landscapes with human disturbances, most deaths are associated with fur harvest facilitated by road access, while vehicle collision, nuisance control, and predation occur to a lesser extent. We found a relatively clear link between population decline and lethal human disturbances at local and intermediate scales, particularly in fragmented habitats in the southern mountains, although we are uncertain how this relationship translates to broader scales. We suggest the viability of wolverines in nonwilderness habitats will vary based on the type and magnitude of human disturbance, with populations potentially capable of overlapping with low-intensity nonlethal human disturbances if mortality is controlled. Wolverine conservation should focus on the creation of refugia, but we propose numerous methods to achieve this outside of creating protected areas that include land-use planning, caribou habitat management, reduced incidental harvest, and management of industrial attractants. Lastly, our review highlights the need for monitoring and enhanced research aligned with the knowledge gaps in wolverine ecology that we identified.

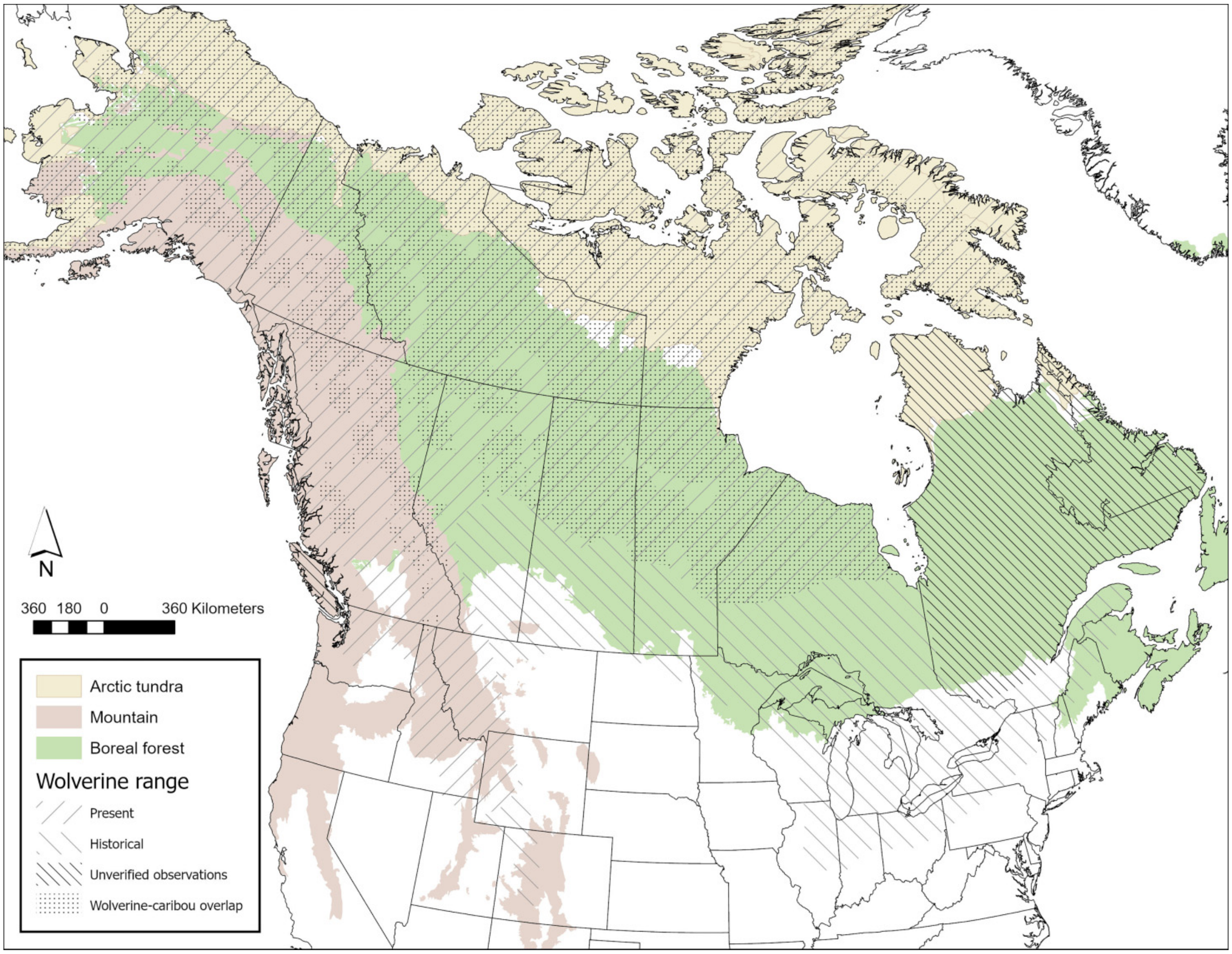
Key words: Conservation, fur harvest, *Gulo gulo*, industrial disturbance, recreation, wolverine

1. Introduction

Biodiversity loss has occurred across the world commensurate with human population growth (Koh et al. 2004; Pereira et al. 2010). Large carnivore decline has been linked to their expansive space needs that put them in conflict with humans (Estes et al. 2011; Chapron et al. 2014; Ripple et al. 2014). These declines are likely to continue as human footprint expands and there is increased overlap with wildlife (Watson et al. 2016; Hirsh-Pearson et al. 2022; Ma et al. 2024). Biodiversity conservation can include maintaining and creating parks and protected areas, but these are often too small to fully meet the needs of wide-ranging species (Woodroffe and Ginsberg 1998; Watson et al. 2014). Another strategy is mitigating the effects of human disturbance to promote coexistence (Oriol-Cotterill et al. 2015).

The wolverine (*Gulo gulo*) is a carnivore that exists throughout circumboreal regions. Their low reproductive rates and densities leave them vulnerable to habitat loss and mortality associated with human disturbance (Mowat et al. 2020). Wolverine distribution in North America declined in the 19th and 20th centuries coincident with landscape disturbance and habitat conversion associated with settlement and unregulated fur harvest and poisoning (Fig. 1; Laliberte and Ripple 2004; Aubry et al. 2007; Slough 2007; Mckelvey et al. 2014). Wolverines rebounded during the latter half of the 20th century and beginning of the 21st century with new regulations to limit fur harvest and the use of poison for predator control (Newby and McDougal 1964; Johnson 1990; Ray et al. 2018; Lukacs et al. 2020). Today, wolverines occur in approximately 63% of their former North American range (Laliberte and Ripple 2004) and are considered a species of special concern in

Fig. 1. North American wolverine range (current and historical) and associated regions (Arctic tundra, mountain, and boreal forest). The "Arctic tundra" region includes the Tundra and Arctic Cordillera level 1 ecoregions, the "Mountain" region includes the Northwest Forested Mountains and Marine West Coast Forest level 1 ecoregions, and the "Boreal forest" region includes Northern Forests, Taiga, and Hudson Plains level 1 ecoregions (epa.gov). Wolverine range in North America includes 8027 586 km^2 and caribou range includes 7572 417 km^2. The overlap of these ranges includes 5547 573 km^2. Therefore, 69% of current wolverine range is also caribou range in North America.



Canada under the Species at Risk Act (Environment and Climate Change Canada (ECCC) 2024) and threatened under the Endangered Species Act in the contiguous United States (U.S. Fish and Wildlife Service (USFWS) 2024).

Researchers often associate wolverines with wilderness or use the term to describe their habitat requirements (Banci 1994; Petersen 1997; May et al. 2006; Chapron et al. 2014; Fisher et al. 2022; Kukka et al. 2022; Moqanaki et al. 2025). Wilderness has political and ideological definitions (Nash 1967) that broadly share the criteria of a landscape with limited human infrastructure or use (Watson 2021; Merriam-Webster 2022). The United States National Wilderness Act (1964) defines wilderness as "an area where the earth and its community of life are untrammeled by man, where man himself is a visitor who does not remain" (United States Congress 1964). In using the term wilderness to describe wolverines and their habitats, researchers are suggesting that the species requires habitats with limited human disturbance and mortality (Krebs et al. 2004; Golden et al. 2007; Fisher et al. 2022; Kukka et al. 2022). For example, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) stated, "The wolverine needs vast undisturbed areas to maintain viable populations…" (COSEWIC 2014).

Wolverines nonetheless exist and are expanding into former ranges in North America that do not resemble wilderness (Ray et al. 2018; Lukacs et al. 2020); an analogous situation is occurring in Fennoscandia (Moqanaki et al. 2025). These areas have human disturbances that are more widespread but often less intense than those associated with settlement. Recreation is common in mountainous areas of southern Canada and the United States (Leung and Marion 2000; Balmford et al. 2015; Larson et al. 2016; Loosen et al. 2023). For example, winter recreation in the Rocky Mountains of Idaho covered over 40% of some wolverine home ranges, with motorized recreation occurring on average in 22% of female home ranges and 14% of male home ranges (Heinemeyer et al. 2019). Industry is prevalent in southern latitudes (<56°N latitude) of the boreal forest and the foothills of the western Rocky

Mountains (Brandt et al. 2013; Pasher et al. 2013; Pickell et al. 2015; Pattison et al. 2016; Vernier et al. 2022). Wolverine home ranges in montane western North America included roads and recent logging (Hornocker and Hash 1981; Krebs et al. 2007; Inman et al. 2012; Kortello et al. 2019). In boreal Alberta and Ontario, wolverines' home ranges included extensive oil, gas, mining, and forestry disturbance (Scrafford et al. 2018, 2024). The mountain, boreal forest, and Arctic tundra regions of Alaska, Yukon, and Northwest Territories are characterized as intact (Lee and Cheng 2014; Hirsh-Pearson et al. 2022) but disturbance is projected to increase in the future (Cooke 2017; Glass et al. 2022). Industrial development in the Arctic tundra primarily includes oil and gas production in Alaska's North Slope and scattered gold and diamond mines throughout the larger region (Haley et al. 2011).

There is a conservation need to enhance understanding of the viability of wolverine populations coexisting with human disturbance. A useful framework for understanding the wolverine's association with human disturbance is to consider the distinction between lethal and nonlethal effects. Nonlethal effects include changes to wolverine behavior, movement, or foraging but are not directly responsible for mortality. Nonlethal effects could have a positive effect on populations, such as providing foraging opportunities (Scrafford et al. 2020) or shelter (Scrafford and Ray 2022), or negative by reducing habitat availability, quality (Heinemeyer et al. 2019), or movement (Sawaya et al. 2019). There is evidence that nonlethal effects can have fitness consequences on wildlife by provoking anti-predator behaviour (Frid and Lawrence 2002; Creel et al. 2007). Lethal effects of human disturbance are those that directly lead to mortality. These can include licensed, subsistence, and incidental wolverine harvest, as well as vehicle- and nuisance-related mortalities (Krebs et al. 2004; Golden et al. 2007; Kukka et al. 2022). Many wolverine populations must contend with both nonlethal and lethal effects of human disturbances, with the magnitude of cumulative effects varying for each region (Heim et al. 2017; Ray et al. 2018).

We reviewed the North American and Fennoscandian wolverine literature to synthesize the relative effects of nonlethal and lethal human disturbances on the species. Our aim was to understand better the relationship of wolverines with wilderness and whether the species is viable in nonwilderness habitats. We used these insights to develop recommendations for the conservation and management of wolverines in North America.

2. Approach

We reviewed peer-reviewed wolverine literature from 2000–2025 from North America and Fennoscandia using Google Scholar and BioOne search engines and the search terms "*Gulo gulo*" and "wolverine". We cross-referenced our search results with reviews in COSEWIC (2014), Fisher et al. (2022), and Glass et al. (2022). We categorized each article to identify its research topic (e.g., local distribution, mortality, health), its region (mountain, boreal forest, Arctic tundra), whether it used quantitative analyses to investigate the effects of human disturbance, or whether it was a review of the effects of human disturbance. A single article could be grouped into more than one research topic or region. We defined human disturbance as either human developments (e.g., roads, forestry cutblocks) or human activity (e.g., vehicle traffic, recreation, fur harvest/hunting). We cite relevant literature in our review even if published before 2000 or if not peer-reviewed but from a credible source (e.g., status reports).

Table 1. The frequency of wolverine research topics in the North American ($n = 185$) and Fennoscandian ($n = 89$) peer-reviewed literature from 2000 to 2025.

Category	Frequency*	
	North America	Fennoscandia
Local distribution	39	17
Foraging	20	13
Broad-scale distribution	19	11
Broad-scale genetics	19	20
Health	18	4
Methods	17	17
Behaviour	15	17
Abundance	14	15
Conservation/review	13	18
Climate change	13	1
Harvest/hunting/culling	9	13
Reproduction	8	15
Natural history	8	9
Dispersal	7	4
Physiology	5	2
Anatomy	5	0
Historical distribution	5	4
Social	5	11
Predation	5	15
Economics	1	12

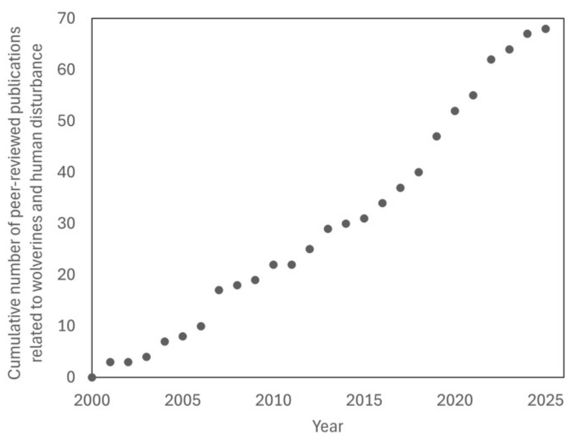
*A single research study can appear in multiple research topics.

3. Findings

We found 185 North American peer-reviewed publications related to wolverines from 2000 to 2025 (Table 1, Appendix S1). The most common research topics included local distribution ($n = 39$), broad-scale distribution ($n = 19$), foraging ($n = 20$), and broad-scale genetics ($n = 19$) (Table 1). North American wolverine research on the effects of human disturbance has been increasing since 2000 (Fig. 2). We found 51 publications related to the effects of human disturbance on wolverines, with 47 including a quantitative analysis and four reviewing effects (Table 2). The most common research topics were local distribution in the mountain region ($n = 15$) and boreal forest ($n = 7$) (Table 2).

We found 89 Fennoscandia publications related to wolverines from 2000 to 2025 (Table 1, Appendix S1), with the most common research topics including broad-scale genetics ($n = 20$) and general conservation ($n = 18$), with 17 publications related to each of local distribution, methods, and behaviour (Table 1). We identified 17 publications related to

Fig. 2. The cumulative number of peer-reviewed publications detailing the response of wolverines to human disturbance in North America and Fennoscandia from 2000 to 2025.



the effects of human disturbances on wolverines, with 16 including a quantitative analysis and 1 review (Table 2). Most Fennoscandia publications analyzed human-caused mortality from hunting, poaching, or culling ($n = 10$) or broad-scale distribution ($n = 6$) (Table 2).

4. Discussion

4.1. Nonlethal effects of human disturbance

Human disturbance might have positive effects on wolverine movement and shelter. Individuals in the Arctic tundra used building skirting as cover (NT Species at Risk Committee 2014). A single Geographic Positioning System (GPS)-collared female was observed entering a snow cave dug into the berm of a borrow pit (hole dug to extract dirt for road construction) along an industrial road (Scrafford et al. 2020). GPS-collared males in montane Idaho selected for habitats near forestry roads (Heinemeyer et al. 2019). Wolverines, or their tracks, have been observed on recreational or industrial roads (Johnson et al. 2005; Copeland et al. 2007; DeBeers Canada Inc. 2021). Wolverine tracks followed for nearly 40 km in boreal Alberta revealed that individuals travelled on 17 different linear corridors (including winter roads, seismic lines, snowmobile trails, and all-terrain vehicle tire tracks) for a distance ranging from 3 to 3000 m (Wright and Ernst 2004). Animals travelled on compacted linear corridors 100% of the time when they were available and never chose to travel on noncompacted linear corridors. The authors suggested individuals used compacted linear corridors for more efficient travel (Wright and Ernst 2004).

Industrial disturbances also might provide wolverines with foraging opportunities. Wolverines have foraged at camp kitchens, sludge dumps, and landfills in the Arctic tundra (Rescan Environmental Services Ltd. 2012; Gebauer et al. 2014; Coulton et al. 2017; De Beers Canada Inc. 2018). Diavik Diamond Mine in the Northwest Territories deterred wolverines frequenting the area near its mine 47 times between 2000 and 2011 (NT Species at Risk Committee 2014). Wolverine GPS relocations in boreal Alberta were significantly closer to seismic lines and the edges of intermediate-aged forestry cutblocks (11–25 years old) than was expected given their availability on the landscape; the authors hypothesized these areas had early-seral vegetation that supported important prey species including moose (*Alces alces*), grouse (e.g., *Bonasa umbellus*), and snowshoe hare (*Lepus americanus*) (Scrafford et al. 2017). Likewise, male wolverines in montane British Columbia selected for recently logged areas with early-seral vegetation (Krebs et al. 2007). GPS-collared individuals in boreal Alberta selected distances closer to borrow pits along industrial roads (Scrafford et al. 2017) presumably to prey on beavers (*Castor canadensis*) that had colonized pits (Scrafford et al. 2020).

Most evidence relays negative effects of nonlethal human disturbance on wolverines. Individuals moved slowly through forested montane habitats in Montana but quickly through open cutblocks presumably perceived as risky (Hornocker and Hash 1981). Females in montane British Columbia avoided logged areas in the summer as well as areas with helicopter and backcountry skiing in the winter (Krebs et al. 2007). Females, but not males, selected for core areas without roads (Krebs et al. 2007). Females in boreal Alberta selected against habitats near winter roads used to access oil and gas infrastructure and avoided the interior of cutblocks (Scrafford et al. 2017). Wolverines in Arctic Alaska ($n = 6$) positioned their home range boundaries along industrial roads, potentially because the roads acted as a barrier to movement (Glass et al. 2022). Wolverines avoided habitats within 0−5 km of roads in montane Norway (May et al. 2012). Wolverine tracks were less likely to occur near human settlements in Finland (Koskela et al. 2013). Trappers reported wolverines were a regular occurrence on 41% of trap lines in northern Alberta (~55°N latitude), 0% of traplines in the southern boreal forest (~52–55°N latitude), and 14% of traplines in the Rocky Mountain foothills, with habitat fragmentation and human disturbance, particularly in southern latitudes, negatively associated with the chance a trapper reported observing recent wolverine sign (Webb et al. 2019). Road density where trappers observed wolverine sign versus did not observe sign was 0.13 and 0.23 km/km^2, respectively (Webb et al. 2019). Wolverine probability of occupancy in 100 km^2 hexagons in Ontario was nearly 100% above 52°N latitude but quickly declined to 0% below ~51°N latitude, with the authors associating this decline with road density and other variables (e.g., climate) at low latitudes (Ray et al. 2018). Higher wolverine occupancy probability (100 km^2 sampling units) within protected areas in montane British Columbia (~60%) versus outside (~30%) was associated with less human disturbance in protected areas during winter (Kortello et al. 2019). Here, the probability of wolverine occupancy decreased by ~20% for every 0.20 km/km^2 increase in road density, with the authors suggesting historical and present day nonlethal human activity, such as backcountry recreation, was the primary driver (Kortello et al. 2019). Wolverine occurrence probability in 144 km^2 sampling units was 88% in the National Parks of Alberta but 36% in the Kananaskis Region, with the authors relating reduced occupancy in the

Table 2. The frequency of topics of peer-reviewed studies detailing the effects of human disturbance on wolverines in North America and Fennoscandia from 2000 to 2025.

	Human-caused mortality*	Local distribution	Broad-scale distribution	Abundance
North America				
Mountain	3†	15	2	4
Boreal forest	1	7	2	1
Arctic tundra	0	1	0	0
Varied	5	1	3	2
Total	9	24	7	7
Fennoscandia				
Mountain	0	0	0	0
Boreal forest	0	0	0	1
Arctic tundra	0	0	0	0
Varied	10	2	5	4
Total	10	2	6	5

*Human-caused mortality includes hunting, fur harvest, and culling. †Studies could be classified into multiple categories.

Kananaskis Region to linear features and recreational noise (among other variables) (Heim et al. 2017). Wolverine abundance was 6.8 wolverines/1000 km^2 in the Willmore Wilderness Park of Alberta (later revised to 5.43 (Fisher et al. 2025)) but 1.8 wolverines/1000 km^2 in the adjacent foothills, with the authors associating this disparity with anthropogenic disturbance such as higher seismic line density in the foothills (Fisher et al. 2013).

Wolverine avoidance behaviours might be driven by conflict with people or predators (May et al. 2006; Mowat et al. 2020). Wolverines in montane Sweden selected steep and rugged habitats that humans, who often poach wolverines, could not easily reach; selection for these habitats was strongest in winter when humans have increased access to wolverine habitats with snow machines (Rauset et al. 2015). Even rare human activity on recreational trails (0–10 recreational groups travelling through over a two-week period) in montane Alberta and British Columbia was associated with a 1% decline in wolverine detection at camera stations (Barrueto et al. 2022). GPS-collared wolverines in boreal Alberta avoided industrial roads that were driven infrequently during the day or night (0–5 vehicles/12 h) (Scrafford et al. 2018). The authors hypothesized that wolverines view all roads as risky habitats because of nonlethal human disturbance and because wolves (*Canis lupus*) travel roads and will sometimes kill wolverines they interact with in industrial landscapes (Scrafford et al. 2018, 2024).

The magnitude of human activity can shape additional nonlethal effects. Researchers in montane Idaho used GPS transmitters to track backcountry skiers and snowmobilers and counted human activity on trails in wolverine range (Heinemeyer et al. 2019). The average intensity of motorized recreation within wolverine home ranges varied from 0.00 to 42.20 m of tracks/100 m^2 and nonmotorized recreational intensity was 0.10–9.30 m of tracks/100 m^2. Male and female wolverines avoided areas in their home range with higher relative recreational intensity, avoided habitats near roads and groomed routes, and avoided off-trail motorized and nonmotorized recreation, with the strength of avoidance stronger for females than males. Wolverine avoidance of recreation resulted in the degradation of 14.1% of female habitat and 10.9% of male habitat (Heinemeyer et al. 2019). In montane British Columbia, wolverine occupancy was lower at detection stations near roads with regular use by motorized vehicles than at roads that were used less frequently (Kortello et al. 2019). In the same area, wolverines exhibited increased latency to climb run poles at baited detection sites as human influence increased within the surrounding 10 km^2 area (Kortello et al. 2024). Wolverine abundance and occupancy declined by 39% in montane Alberta and British Columbia from 2011 to 2020, with wolverine density 2–3× higher inside Banff and Kootenay National Parks relative to areas that were not protected (Barrueto et al. 2022). Here, wolverines had lower occupancy and abundance in habitats with high levels of recreation (50–100 trail user groups per two weeks) and light intensity (proxy for denser human developments) (Barrueto et al. 2022). GPS-collared male and female wolverines in boreal Alberta increased their 2 h movement rates when near industrial roads by 300 and 400 m, respectively, with movement rates increasing more when near high-traffic roads (20–25 vehicles/12 h) versus low-traffic roads (0–5 vehicles/12 h), likely because of displacement from more frequent vehicle traffic (Scrafford et al. 2018).

There is evidence of tolerance to human disturbance close to reproductive den sites; a female used an airplane hangar as a den across multiple reproductive periods (Starova et al. 2014), and researchers found seven den sites in forestry slash piles (generally branches and smaller diameter logs) and log decks (logs that are piled for transport) in regenerating forests in boreal Alberta and Ontario (Jokinen et al. 2019; Scrafford and Ray 2022). Den sites are not always situated in habitats far from active roads or other human developments. Den sites in boreal Alberta and Ontario ($n = 17$) were on average 2.5–4.8 km from primary industrial roads and 0.9–1.0 km from operational roads (Scrafford and Ray 2022). Den sites ($n = 6$) in north-central Alberta were 0.4–12 km from petroleum wells and roads (Jokinen et al. 2019). Hausleitner et al. (2024) reported that 21 of 24 den sites were within 5 km of a forest road. Future analyses with the above data sets should try to understand den site selection relative to available habitats. For example, researchers in montane Norway found that den sites ($n = 50$) were established 7.5 km from low-elevation (public) roads and 1.4 km from high-elevation (private) roads, which was significantly farther than expected given available habitat (May et al. 2012).

There is a poor understanding of how nonlethal human disturbances affect reproductive success. Wolverine reproductive output is tied to food availability (Persson 2005) and reductions in habitat quality or availability with human disturbance could conceivably impact population trends. This is a conservation concern considering evidence that female habitat might be more easily degraded by human disturbances than males (Krebs et al. 2007; Scrafford et al. 2018; Heinemeyer et al. 2019). Moreover, stress associated with increased predation risk or human disturbance could negatively affect wolverine survival and reproduction, as has been shown in a variety of wildlife species (Boonstra et al. 1998; Creel et al. 2011; Sievert et al. 2019; Allen et al. 2022). A decline in wolverine recruitment in recreational areas in montane Alberta and British Columbia over 10 years (2011–2020) was evidenced by a declining trend in the number of young at camera stations (Barrueto et al. 2022). In human-disturbed landscapes in boreal Alberta and Ontario, sub-adult wolverines made up half of wolverine abundance (Scrafford et al. 2024), and females known to be denning in areas with human disturbance had kits surviving into the following year (M. Scrafford, unpublished data). However, the survival of juveniles and sub-adults was relatively low in these habitats (discussed below) (Scrafford et al. 2024).

Foraging competition is increasingly recognized as a nonlethal effect of human disturbance. Wolverine occurrence in 144 km^2 hexagons in montane Alberta was 20% in areas without linear features, and coyotes (*Canis latrans*) were nearly absent from these habitats (Chow-Fraser et al. 2022). Wolverine occurrence was nearly 0% in hexagons that coyotes had visited within the week and that had linear features, with the authors associating the lack of wolverine occurrence with resource competition (Chow-Fraser et al. 2022). Likewise, researchers have suggested that reduced wolverine occurrence in human-disturbed areas is related to increased coyote densities associated with apex predator culling (mesopredator release) (Heim et al. 2019). Wolverine occurrence probability in 100 km^2 hexagons in boreal Ontario (<52°N latitude) was negatively associated with deciduous forests, which was 3.9 times more important in determining occurrence than roads, cutblocks, or other spatial variables (Bowman et al. 2010). The authors suggested deciduous forests promoted higher carnivore densities that might have caused wolverine occurrence to decline through competition (Bowman et al. 2010).

Although wolverines are capable of long-distance dispersals (Vangen et al. 2001; Gardner and Lawler 2007; Packila et al. 2017), there is concern about how human disturbances affect population connectivity (Ruggiero et al. 2007; Day et al. 2024). This is a major threat to wolverines in the southern mountains of Canada and the contiguous United States, where broad-scale population sustainability requires dispersals between small metapopulations that are an artifact of the fragmented nature of suitable habitats (Ruggiero et al. 2007; Inman et al. 2013). Here, valley-bottom human disturbance and climate change are degrading wolverine movement potential through important dispersal corridors (Schwartz et al. 2009; Inman et al. 2013; Mckelvey et al. 2014; Balkenhol et al. 2020). For example, female wolverines in Banff National Park had distinct population clusters separated by the Trans-Canada highway, which likely served as a barrier to movement (Sawaya et al. 2019; Day et al. 2024). Although poorly studied, genetic connectivity appears greater in northern wolverine habitats relative to the periphery (e.g., southern mountains) (Kyle and Strobeck 2002), probably because northern habitats are more homogenous and have less human disturbance (Copeland et al. 2010; Haley et al. 2011; Lee and Cheng 2014; Hirsh-Pearson et al. 2022).

4.2. Lethal effects of human disturbance

The wolverine's low reproductive rate and density make the lethal effects of human disturbance particularly harmful to population persistence (Persson et al. 2006; Rauset et al. 2015; Mowat et al. 2020). Roads and other industrial developments contribute to wolverine mortality because they serve as an interface, and sometimes as an attractant, for interactions with humans and predators (Scrafford et al. 2024). In the Northwest Territories, De Beers mining company killed 11 wolverines at its camps from 1996 to 2014; 27 wolverines were reported as either being killed or relocated from other mines in the Lac de Gras region (Northwest Territories) between 1998 and 2011, and there were 30 deterrence events and two wolverine mortalities at the Meadowbank gold mine in Nunavut between 2011 and 2012 (NT Species at Risk Committee 2014). Nine wolverines were killed by vehicles in an industrial area in northern Alberta between September 2013 and April 2015 (data provided by Alberta Transportation), and trains or vehicles killed 17 wolverines in northern Ontario between 2008 and 2020 (data provided by the Government of Ontario, Thunder Bay).

Wolves are a source of wolverine mortality (Krebs et al. 2004; Young et al. 2023), and kills might be a form of interference competition (Ballard et al. 2003). Wolves dug up a wolverine reproductive den site to kill kits and might have killed a female to protect a wolf den site (White et al. 2002). Wolves travel on roads (Dickie et al. 2017) and are known to kill wolverines they encounter; wolves killed three GPS-collared wolverines either on or very close to industrial roads in boreal Alberta and Ontario (Scrafford et al. 2024). Wolf abundance increases in landscapes with human disturbance, particularly forestry, because of larger ungulate populations sustained by younger forests (Latham et al. 2011). Although there is the potential that more wolves and ungulates could benefit wolverines by increasing foraging opportunities, there also is the potential it could increase wolverine mortality.

Roads improve access to wolverine habitats and therefore increase fur harvest pressure on wolverines (Banci 1994). In boreal Alberta, the average annual harvest of wolverines increased from five between 1985 and 1989 to 15 between 2005 and 2011, coincident with oil sands infrastructure development (Webb et al. 2013). Over 27 years in the Yukon, registered traplines with wolverine harvest in ≥15 harvest seasons were often located near population centers and all-season roads, whereas remote traplines without all-season road access had wolverine fur harvest in ≤8 seasons (Kukka 2017). Harvest density was relatively low (0.0–0.29 wolverines harvested/1000 km^2) in remote areas of the Yukon and higher (>1 wolverine/1000 km^2) near human settlements (Kukka et al. 2022). Areas of Alaska with better road access did not have higher harvest densities (Kenai Peninsula = 0.3–1.2 wolverines/1000 km^2) compared to areas with only snow machine or aircraft access (West Cook Inlet = 0.1–1.8 wolverines/1000 km^2), suggesting snow machine access might also be an important predictor of harvest (Golden et al. 2007).

Fur harvest is often the largest single source of human-caused mortality for wolverines. Based on a meta-analysis of radiotelemetry studies from North America, mortalities in landscapes permitting fur harvest were predominantly from fur harvest ($n = 22$) but also included vehicle collisions ($n = 3$), starvation ($n = 16$), and predation ($n = 9$) (Krebs et al. 2004). Among 52 individuals monitored with GPS-collars in Ontario, where the species is protected from licensed harvest, six were killed by trappers (incidental harvest), two by vehicles, and two by predators (Scrafford et al. 2024). Among 43 wolverines monitored in boreal Alberta with GPS-collars, where there is licensed harvest, eight were killed by trappers, one by a vehicle, and two by predators (Scrafford et al. 2024). In northwest Montana, 9 of 14 mortalities reported during a telemetry study were from fur harvest (Squires et al. 2007). Between 1995 and 2011 in Alberta, harvest accounted for an average annual harvest of 30.82 wolverines while other human sources (vehicles, incidental harvest) killed 1.18 wolverines annually (Webb et al. 2013). In a 14 000 km^2 study area in montane British Columbia and Alberta, 59 wolverines were killed by fur trappers, and one was killed by a vehicle from 2011 to 2020 (Barrueto et al. 2022).

Wolverine harvest in the Arctic tundra is concentrated near communities with associated roads providing trappers and hunters access to wolverine habitats (Awan and Szor 2012; Poley et al. 2018; Glass et al. 2022). Wolverine harvest often occurs opportunistically while hunters are traveling by snow machine across the treeless tundra (Cardinal 2004; Glass et al. 2022). Most trappers in the Yukon do not consider wolverines a target species (Kukka et al. 2022). Annual fur harvest from 1987 to 2018 in Arctic Alaska ranged between 70 and 177, and between 61 and 124 from 2009 to 2012 in Nunavut (Awan and Szor 2012; Glass et al. 2022). The mean annual harvest of wolverines in the Arctic/West region of Alaska increased by 16% from 1984 to 2003 (Golden et al. 2007). The arrival of snow machines in the 1980s might have facilitated increased harvest levels in this region, but it is difficult to understand trends because harvest data are reported across broad geographies and many pelts are used or sold locally and not reported to the government (Magoun 1985; Cardinal 2004; Glass et al. 2022).

Wolverines are susceptible to incidental harvest because they are attracted to the bait used by trappers in sets for other species, including marten (*Martes americana*), lynx (*Lynx canadensis*), and wolves. Among 140 interviews with trappers in Ontario, wolverine harvest events were split evenly between the deliberate setting of traps targeting wolverines, opportunistic encounters, and the result of incidental harvest in traps and snares set for other species (J. Ray, unpublished data). The continued incidental harvest of wolverines in Ontario (Dawson et al. 2010; Scrafford et al. 2024), despite their threatened status and a prohibition on commercial harvest (Committee on the Status of Species at Risk in Ontario (COSSARO) 2012), has the potential to slow or inhibit their recovery and range expansion. Likewise, there is concern that wolverine range recolonization in the contiguous United States, often through dispersing individuals establishing small populations in isolated mountain ranges, will be hindered by incidental harvest (J. Copeland, pers. comm.).

Fur harvest can cause wolverine population decline when added to other natural and human-caused mortality sources. Researchers can model population trajectories using survival and fecundity data derived from monitoring individuals with radiotelemetry. These data and methods are often restricted to smaller study areas (e.g., <20 000 km^2) where radiotelemetry is financially and logistically feasible. In general, untrapped wolverine populations often have annual survival estimates (e.g., >0.84) that translate to stable population trajectories at the local scale (Krebs et al. 2004). Areas with active trappers have high human-caused mortality, primarily from fur harvest, that reduces annual wolverine survival estimates below the 0.75 threshold for a declining population (Krebs et al. 2004; Squires et al. 2007; Dalerum et al. 2008; Scrafford et al. 2024).

In the absence of fine-scale radiotelemetry data, researchers can use government fur harvest and wolverine abundance data to infer whether harvest rates are sustainable. The natural growth rate for a wolverine population is approximately 6.4% (Krebs et al. 2004), although researchers often cite 8%–10% as a sustainable harvest rate because of variation in wolverine density by region (Weaver et al. 1996; Banci and Proulx 1999; Kukka 2017; Mowat et al. 2020). For example, in a study area in montane British Columbia and Alberta, 59 wolverines were harvested across 106 traplines between 2011 and 2020, which, after combining with detailed abundance data in the region, resulted in an unsustainable harvest rate of nearly 14% (Barrueto et al. 2022).

Researchers are often interested in fur harvest sustainability across provinces for government status assessments. However, government fur harvest data can be biased by inconsistent reporting and a lack of information on trapper effort (DeVink et al. 2011; McKelvey et al. 2011; Mowat et al. 2020; Barrueto et al. 2022). Moreover, we often lack accurate data on wolverine abundance at these larger scales. Using extrapolated density and survival estimates from two radiotelemetry studies, as well as government fur harvest data, researchers in British Columbia found that from 1984 to 2004, fur harvest was unsustainable in 21% of population units in the province (Lofroth and Ott 2007). Likewise, 31% of ecoregions in the Yukon had unsustainable harvest rates from 1988 to 2014 based on government harvest data and various qualitative and quantitative density estimates (Kukka et al. 2022).

Wolverine fur harvest can be difficult to account for in occupancy and abundance models. Across an 84 400 km^2 study area in the Arctic tundra of Alaska, the lowest wolverine occupancy (0%–20% occupancy in 100 km^2 hexagons) was near a remote cabin with active hunters who likely directly reduced wolverine presence in these areas (Poley et al. 2018). However, the authors could not include fur harvest in their model because of incomplete harvest data (Poley et al. 2018). Wolverine occupancy was not associated with fur harvest intensity in interior Alaska (Gardner et al. 2010). Nonetheless, the authors suggested that two low-elevation regions in their study area with the lowest occupancy had roads and a history of fur harvest (Gardner et al. 2010). Recent harvest was not associated with reduced occupancy in montane British Columbia or Alberta, with the researchers hypothesizing that harvested areas with high-habitat quality were quickly being recolonized by juveniles (Kortello et al. 2019; Mowat et al. 2020).

Aligned with this idea, areas of low or no wolverine harvest might help maintain populations at larger scales by providing individuals to populate heavily trapped areas (Banci 1994; Krebs et al. 2004; Golden et al. 2007). More than 62% of the Yukon was de facto refugia and did not have wolverine harvest on an annual basis from 1988 to 2014 (Kukka et al. 2022). Eighty-two percent of Alberta traplines did not report wolverine harvest from 1989 to 2011, although there was no evidence to suggest wolverines were present at all the traplines (Webb et al. 2013). On an annual basis, from 1984 to 2003, approximately 73%–95% of the Kenai Peninsula and Nelchina Basin regions of south-central Alaska had no wolverine harvest (Golden et al. 2007). However, aside from simulations of source-sink dynamics based on the species' known dispersal capabilities (Dalerum et al. 2008) and hypotheses of suspected source-sink dynamics (Krebs et al. 2004; Kortello et al. 2019; Mowat et al. 2020), we generally have a poor understanding of the movement of individuals between trapped and untrapped areas and whether untrapped areas are truly source populations or areas with few wolverines.

Wolverines in Fennoscandia declined throughout much of the 20th century from lethal human disturbances primarily associated with killing wolverines to reduce predation on semidomestic reindeer (*Rangifer tarandus*) in husbandry areas (Pulliainen and Nyström 1974; Flagstad et al. 2004; Pohja-Mykrä and Kurki 2013; Moqanaki et al. 2023). In Finland, government bounties, combined with greater hunting efficiency with snow machines, resulted in a population decline such that only two wolverine dens were found during surveys in 1973 (Pulliainen and Nyström 1974). Fennoscandian countries have since protected wolverines, and conservation incentive programs have helped wolverines recover, particularly programs rewarding landowners for the number of reproductive dens on their land (Pohja-Mykrä and Kurki 2013; Gervasi et al. 2015; Persson et al. 2023). Poaching is nonetheless still a conservation concern for Fennoscandian wolverines. For example, Persson et al. (2009) monitored radio-marked wolverines with bi-weekly flights in northern Sweden (1993–2008) and found that 51% of adult wolverine deaths (13 of 25 mortalities) were from poaching, although these deaths still resulted in reasonable adult survival (0.91 annual survival). Wolverine harvest rates in Norway increased by 12% from 2003 to 2012, although this trend is likely related to population management goals in Norway to remove 15%–20% of the wolverine population each year (Gervasi et al. (2015).

4.3. Managing human disturbance in wolverine habitats

The weight of evidence suggests that human disturbances have negative nonlethal effects on wolverine habitat quality and behaviour, with these effects intensifying as human activity increases on the landscape. There appears to be a link between population decline and nonlethal human disturbance such as recreation, although these effects can be difficult to disentangle from lethal human disturbances that often occur in the same area. Lethal human disturbance and its synergism with human developments and snow machine access have a relatively clear link to local wolverine population decline in the North American wolverine literature. However, aside from the fragmented habitats in the southern mountains of western Canada and the contiguous United States, there is uncertainty on how these local effects translate to broader scales because of limited population monitoring and incomplete or imprecise fur harvest data. Below we use these insights to develop conservation strategies for the species that promote both habitat preservation and coexistence with human disturbance.

4.3.1. Refugia

Parks or protected areas have the potential to provide wolverine habitats where human-caused habitat mortality and degradation are low. Glacier National Park (United States), before wolverine harvest was prohibited in Montana in 2014, was considered a refuge and source population for surrounding areas where mortality was higher (Squires et al. 2007; Copeland and Yates 2008). The parks in southern montane Alberta and British Columbia also serve as wolverine refugia because harvest is prohibited (Banci 1994; Fisher et al. 2013; Barrueto et al. 2020; Mowat et al. 2020). There are initiatives to increase protected areas in Canada (ECCC 2021) which could expand this source of wolverine refugia. However, managers should be aware that parks often offer less realized refugia because of the species' wide-ranging movements into adjacent unprotected areas that are trapped (Barrueto et al. 2022). Moreover, parks are experiencing increasing recreational activity and other human demands (Woodroffe and Ginsberg 1998; Watson et al. 2014; Loosen et al. 2023). Human access management, as is proposed to conserve grizzly bear (*Ursus arctos*) populations (Proctor et al. 2019), might help to reduce the lethal and nonlethal effects of human disturbance both inside and outside protected areas.

There are other options besides protected areas to create refugia. Indigenous-led land-use planning (NT Species at Risk Committee 2014) or regional impact assessments (Chetkiewicz and Lintner 2014) are useful tools to manage current or future human disturbance and promote refugia for wolverines. For example, northern Ontario is currently a vast roadless area with low human density that likely serves as refugia and a source population for wolverines expanding south (Ray et al. 2018). However, the Ring of Fire area in

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northern Ontario contains critical minerals that are expected to drive extensive road building and industrial vehicle traffic (Chetkiewicz and Lintner 2014). Regional impact assessments and land-use planning are therefore important to anticipate and manage cumulative impacts, helping to meet the habitat needs of vulnerable species like wolverines.

Fur harvest does not occur ubiquitously across wolverine range and unharvested areas could provide de facto refugia (Banci 1994; Krebs et al. 2004; Golden et al. 2007; Lofroth and Ott 2007). Codified refugia in the Arctic may become increasingly important as technological improvements in snow travel facilitate access to previously un-hunted areas (Glass et al. 2022). Researchers suggest that a 2:1 ratio of untrapped to trapped areas, of equal or greater habitat quality, is needed for population stability at the landscape scale (Krebs et al. 2004; Lofroth and Ott 2007). Managers should monitor the spatial distribution of untrapped areas to ensure they provide refugia for wolverines. Consideration also should be given to short-term refugia that allow formerly trapped areas to recover (Kukka et al. 2022). Moreover, future research should investigate whether untrapped areas are truly refugia or simply lack wolverines, as well as the movement of individuals between trapped and untrapped areas.

Refugia also could be a product of caribou habitat management, which has been shown to benefit other boreal species (Bichet et al. 2016; Drever et al. 2019). Over two-thirds of current wolverine range in North America overlaps with caribou range (Fig. 1). Ontario's forest management planning approach assumes that "The landscape-scale approach to the management of woodland caribou habitat is expected to maintain large blocks of unharvested and roadless habitat suitable for wolverines" (Ontario Ministry of Natural Resources (OMNR) 2010). Critical habitat for boreal caribou in Canada is premised on an empirical relationship between landscape disturbance and population decline (Environment Canada 2012). Management actions entail limiting cumulative disturbance on the landscape, and the extent of early seral habitats that favour other ungulates and lead to increased densities of predators that feed on caribou (Schneider et al. 2010; Boutin et al. 2012; Bentham and Coupal 2015). Effective caribou habitat management in theory should also reduce wolverine habitat loss. Another benefit might come from the maintenance or restoration of refugia through careful reclamation and management of linear features. This would help to reduce human and predator-caused mortality, principally through limiting human access to wolverine habitats, and create or maintain untrapped or minimally trapped areas needed to sustain wolverine populations at coarse scales (Krebs et al. 2004; Golden et al. 2007; Lofroth and Ott 2007; Kukka 2017).

Refugia should be connected for wolverines at regional and sub-regional scales to ensure genetic health and maintain populations through source-sink dynamics. Of particular concern at present is the maintenance, creation, and connectedness of refugia within the southern Rocky Mountains (Inman et al. 2013; Idaho Department of Fish and Game 2014; McClure et al. 2016; Balkenhol et al. 2020). Because these populations are patchy, isolated, and sensitive to adult mortality and stochastic events, they have much greater potential for extirpation from human disturbance relative to larger, more continuous northern wolverine populations. Researchers in the contiguous United States reported near complete extirpation of small wolverine populations (e.g., six animals) from mountain ranges because of fur harvest (Squires et al. 2007). The goals of conservation programs that maintain regional habitat connectivity in the southern mountains (<56°N latitude), such as the Yellowstone to the Yukon Conservation Initiative, align well with wolverine habitat needs in the area (Chester 2014).

4.3.2. Best practices

Wolverine mortality at camps, communities, or exploration sites will likely increase as human disturbance expands. Placing limits on the availability of attractants to wolverines, such as garbage or left-over food scraps, can reduce wolverine mortality (Johnson et al. 2005). Mining companies can cover landfills or erect barriers, such as electric fencing, to reduce wildlife access (De Beers Canada Inc. 2021). Other mitigation strategies might include building skirts to limit wildlife access and developing education programs to inform workers and communities about the implications of leaving attractants out (DeBeers Canada Inc. 2021).

There is a need to develop and test the efficacy of practices that might reduce the incidental harvest of wolverines by trappers, as well as communicate to trappers the need to use these methods. For example, wolverines are killed at bait piles (animal carcasses) that are primarily used to attract and snare wolves. Adjusting fur harvest practices, such as setting snares higher and further away from the bait, and regularly maintaining snare height after new snowfall, might reduce incidental wolverine harvest (Ontario Fur Managers Federation (OFMF) 2010). Anchoring traps also might be effective because they give captured wolverines a chance of pulling free or bending break-aways (OFMF 2010; Hiller and White 2013). These methods also might reduce incidental injury. There were eight wolverines live trapped during telemetry projects in boreal Alberta and Ontario that still had fur traps or snares attached to them or had disfigurement or scarring from traps (Scrafford et al. 2024).

Governments often assess the effects of individual projects, such as recreational tenures, ski areas, roads, transmission lines, mines, or forest management plans, on wolverine habitat quality. Government policies can require project proponents to search for wolverine den sites in their project areas and, if located, mitigate the negative effects of their proposed activities (Ontario Ministry of Natural Resources (OMNR) 2010; Alberta Environment and Sustainable Resource Development (AESRD) 2012; Yukon Government 2014). However, wolverine den sites are extremely difficult to find with most survey methods, which limits the conservation value of this approach (Scrafford and Ray 2022). Nonetheless, when a den site is found, the mitigation steps can include a protective buffer (100–5000 m) around a den site, with the duration of that protection based on reuse intervals by the female (OMNR 2010; AESRD 2012; Yukon Government 2014; Hausleitner et al. 2024). British Columbia creates Habitat Management

Areas within denning areas to manage industrial disturbance, with directives that can include road reclamation and timing restrictions (British Columbia 2002). Researchers suggest that den site protections are an ineffective scale to protect wolverines (Scrafford and Ray 2022) but future research could look at its value when combined with other landscape-level habitat management.

4.3.3. Population monitoring

We have a poor understanding of wolverine population status in vast areas of North American wolverine range (COSEWIC 2014; Fisher et al. 2022; Glass et al. 2022). Fur harvest data remain the only means for governments to monitor wolverine populations in many regions (COSEWIC 2014) but there are issues with the reliability of these data. For example, researchers estimate that as much as 35% of annual wolverine harvest in the Northwest Territories is unreported because the pelts are used for subsistence purposes (NT Species at Risk Committee 2014). Because fur harvest data will likely continue to be used by governments to monitor wolverine populations, we suggest two methods to make these data more informative. First, carcass collection programs, such as those that exist in some regions of Arctic and boreal Canada (Awan and Szor 2012; Kukka et al. 2022), could be expanded to other remote regions where subsistence harvest is common (NT Species at Risk Committee 2014). Second, improved monitoring of trapper effort would aid in detecting population trends using harvest statistics (McKelvey et al. 2011). Alberta has encouraged trapper logbooks to help with monitoring trapper effort (Alberta Trappers Association (ATA) 2021). British Columbia has mandatory reporting requirements for wolverine harvest in regions of conservation concern, but there is no reporting that helps to measure trapper effort (Government of British Columbia 2022). More accurate harvest data might facilitate better modeling of wolverine occupancy and abundance relative to fur harvest, source-sink dynamics of populations, and trends in relative abundance.

Wolverine monitoring should not have to rely on harvest statistics. In Fennoscandia, broad-scale monitoring of active reproductive den sites has provided managers with trends in wolverine abundance through time (Bischof et al. 2020; Moqanaki et al. 2025). There are no similar monitoring programs anywhere in North America. There are, however, short-term survey efforts that have the potential to become long-term monitoring initiatives (Schmelzer 2006; Golden et al. 2007; Awan and Boulanger 2016; Ray et al. 2018; Barrueto et al. 2022). Most of these surveys collect information to estimate wolverine abundance or distribution which would help with more accurate estimates of harvest sustainability (Kukka et al. 2022). Other metrics, including gene flow and genetic diversity, could also be a focus of monitoring efforts.

4.3.4. Future research

Even with an increase in wolverine research efforts in North America since 2000, there remains a paucity of information on the consequence of human disturbance on wolverine vital rates and populations. We suggest that researchers design studies that focus on the collection of demographic data to document the vital rates that influence wolverine population growth rates across a broad range of habitats with varying levels of human disturbance—all of which are essential for documenting how populations respond to human disturbance (Environment Canada 2012; Whittington and Sawaya 2015; Proctor et al. 2019). For example, we have highlighted here the lack of information available on the link between nonlethal human disturbance and reproduction.

Advanced technology and statistical techniques should help to collect demographic data for effective population monitoring. Recently, GPS collars with satellite upload were small enough to use on wolverines (Scrafford 2017) which greatly increased the efficiency of tracking wolverines relative to store-on-board collars (Heinemeyer et al. 2019) or very high frequency (VHF) telemetry (Dawson et al. 2010). Scientists recently sequenced the North American wolverine genome (Lok et al. 2022) and efforts are underway to develop advanced single nucleotide variant (SNV) panels that will allow cost-effective genotyping of noninvasively collected field samples (Ekblom et al. 2021). These panels will provide detailed genomic information that can be used to improve estimates of gene flow, genetic diversity, and effective population size (Allendorf et al. 2010). Advanced statistical techniques increasingly allow for estimating spatially explicit demographic parameters from noninvasive sampling programs, even from unmarked populations (Green et al. 2020). More detailed and accurate genetic data might facilitate conservation-related research questions around source-sink dynamics in areas with wolverine fur harvest.

5. Conclusions

Wilderness is important to wolverines because it offers refugia from human-caused habitat degradation and mortality. As humans continue to expand their activities into wolverine habitats that were once de facto wilderness, and as wolverine recolonization fronts push into former range that is now disturbed by humans (Ray et al. 2018; Lukacs et al. 2020; Moqanaki et al. 2025), we need to evaluate whether wolverine populations are viable in nonwilderness areas. We present evidence that the threat to population persistence varies in nonwilderness habitats based on the type and magnitude of lethal and nonlethal human disturbances. Nonlethal human disturbances appear most detrimental to populations when they occur at high levels, suggesting that coexistence might be possible at lower levels of disturbance if mortality is also controlled. Conservation of the species is partly dependent on understanding the synergistic effects of lethal human disturbances with trail and road access. The effect of fur harvest on population decline is relatively clear at the local or intermediate scale, particularly in fragmented southern mountain habitats, but the broad-scale effects on populations remain an important knowledge gap. Wolverine mortality from vehicles, from interactions with wolves on roads, and at industrial sites appears to contribute less to population decline. Refugia is vital to population persistence at broad scales and can be created not only

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through protected areas but also via access control, land-use planning, caribou habitat strategies, or de facto harvest-free zones. We propose using methods that promote coexistence with human disturbance, such as reducing incidental harvest and industrial attractants. We suggest increased efforts to monitor trends in wolverine distribution and population dynamics in areas with human disturbance, particularly those that do not rely on wolverine harvest. We also suggest additional research based on the knowledge gaps that we identified, including the need for a deeper understanding of the demographic consequences of nonlethal human disturbances.

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Supplementary material

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