Colorado Wolverine Restoration Plan

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Executive Summary

Wolverines (*Gulo gulo luscus*) were part of Colorado's native fauna until they were extirpated during the early 1900's, likely due to unregulated killing and use of poison baits for predator eradication. A population has not existed in Colorado for a century and wolverines have been classified as a State Endangered Species since 1973. It is estimated that Colorado can hold as many as 100-180 wolverines, which is likely similar to its historical capacity and represents a significant portion of the potential population size in the contiguous United States. Restoration of wolverines to Colorado would satisfy the Colorado Parks and Wildlife (CPW) mission *"To perpetuate the wildlife resources of the state…"*

At a broader scale, wolverines in the contiguous U.S. were recently listed as Threatened under the U.S. Endangered Species Act (ESA); restoration of this species to Colorado would significantly benefit its persistence in that geography. This plan describes reasons why restoration is best served via a planned reintroduction program, delineates the suitability of Colorado as a focus for restoration, and then lays out details regarding how such a program can be executed. The plan concludes with specific benchmarks for success for each phase of the program, including a final endpoint when the program will be considered complete and state downlisting of the species could occur.

The structure of this document is based on principles outlined in the International Union for Conservation of Nature (IUCN) "Guidelines for Reintroducing Species and Other Conservation Translocations," and the proposed translocation procedures represent guidance and best estimates provided by a team of wolverine, translocation, and veterinary experts assembled from around the world. As such, CPW has diligently considered a host of biological and management issues related to restoration of this species. However, a formal wolverine reintroduction has never been attempted, and how translocated wolverines will react to some scenarios will only become apparent during the restoration effort. Success will depend on CPW's ability to learn and adapt as events unfold and new information becomes available. Therefore the approach outlined in this plan is one of strategic assessment designed to learn what works best and adapt where new information suggests ways to improve success. The release procedures are of particular importance for success, and will initially take an approach that will be more logistically challenging but will have the potential for greatest success. If those procedures do not yield more favorable results, the release strategy will adapt toward a less logistically challenging approach. A communications plan related to the restoration effort will be developed separately from this restoration plan, as will rules guiding compensation for livestock depredation. Any regulation governing 'take' of wolverines will be present in a U.S. Fish and Wildlife Service 10(j) rule.

Male wolverine "M56" in Rocky Mountain National Park, 2009. Photo courtesy of ©Ray Rafiti

Chapter 1 describes the background for why and how this plan was developed.

CPW contends that a planned reintroduction represents the most effective way to restore wolverines to Colorado. Natural recovery is inhibited and limited by wolverine biology, specifically: female dispersal patterns, limited capacity for population growth, and genetic factors. Natural recovery is highly unlikely, as evidenced by the fact that it has not occurred during the 90-year period when the species reoccupied its former range within Montana, Idaho, and northwest Wyoming. Additionally, a planned reintroduction allows for a strategic approach to alleviate the numerical and genetic perils of a new population initiating from what would most likely be a single breeding pair.

CPW has considered reintroducing wolverines since 1998 when a draft plan was assembled proposing to reintroduce them along with Canada lynx. Ultimately, CPW chose to reintroduce lynx first, and has since turned its focus to restoring wolverines once the Canada lynx reintroduction was deemed a success in 2010. This plan was developed based on principled guidance laid out by the IUCN for "conservation translocations." Specific details follow guidance from a team of wolverine, translocation, and veterinary experts assembled from around the world and the most recent science available. .

The primary goal of this Plan is to provide a guiding document for CPW to recover and maintain a viable wolverine population in Colorado.

Chapter 2 describes key components of wolverine ecology that are relevant to restoration in Colorado.

Wolverines are the world's largest terrestrial species of weasel (family Mustelidae), weighing 20-40lbs. They have a circumpolar distribution in the northern hemisphere and occupy cold, snowy biomes in Scandinavia, Asia, and North America. Their historic range included extensions from boreal Canada into the contiguous U.S. along the Rocky Mountains and the Cascade and Sierra-Nevada Ranges.

In North America, wolverines occupy tundra and taiga biomes, which manifest as alpine and subalpine zones in montane areas of the contiguous U.S. In these environments, wolverines largely subsist via scavenging and caching, although they are moderately adept at hunting small mammals and other prey, doing so mostly during summer months. Wolverines are territorial, excluding other individuals of the same sex. Their territories are extraordinarily large for a mammal of their size, yet they are capable of patrolling them regularly. Their utilization of large territories naturally results in extremely low densities and is accompanied by a low reproductive rate. Males are capable of dispersing large distances and commonly do so while females tend to establish home ranges closer to where they were born.

Wolverines breed during summer and display delayed implantation such that a fertilized egg does not begin to develop until the following winter. Young are born February–March in a den usually consisting of structure (for example boulders or avalanche debris) insulated by snow-cover. On average, females begin reproducing at age 3-4 and have 1-2 young every other year. The young generally begin to disperse to find a territory of their own at one year of age. Wolverines can live about 15 years. The leading documented causes of mortality for wolverines in North America are legal trapping, starvation, and predation by other carnivores. Avalanche, conspecific (killed by another wolverine), and road mortalities also occur. Conspecific mortality is a common cause of juvenile and subadult mortality in Scandinavia (the only place it has been monitored and assessed) and is an important consideration for reintroduction. Wolverines in the contiguous U.S. exhibit lower levels of genetic variation and more population structure than exists elsewhere in North America.

Chapter 3 describes the potential for wolverine restoration in Colorado along with conservation issues associated with such an action.

According to a model of wolverine habitat for the western U.S., Colorado contains approximately 30,000 km^2 of primary wolverine habitat, equivalent to 20% of the estimated habitat in the entire lower 48 states. Colorado is the largest block of unoccupied former range in this geography. Estimates suggest that if habitat models are accurate, all available habitat becomes occupied, and wolverines in Colorado exhibit similar traits as elsewhere in the Rocky Mountains, Colorado could hold as many as 100-180 individuals, which is likely similar to historical capacity. Restoring wolverines to Colorado would significantly improve the conservation outlook of the recently ESA listed "Distinct Population Segment," which includes all wolverines in the contiguous U.S.

Unregulated human-caused mortality that led to the extirpation of wolverines at the turn of the 20^{th} century is no longer a risk in the modern era of science-based wildlife management, and no longer poses a threat to wolverines in Colorado. Colorado has a higher density of people and roads than almost any other area of wolverine range. Road mortalities may occur, however the fact that two-thirds of wolverine habitat in Colorado is classified as designated wilderness, national park, wilderness study area, or U.S. Forest Service Roadless area should buffer this potential source of mortality. Colorado has abundant ungulate and marmot populations which should provide ample food resources for a restored population of wolverines in both winter (ungulate carcasses) and summer (marmots). Because wolverines naturally occur at very low densities, they are not expected to have discernible effects on livestock or other wildlife species. Possible negative effects of wolverines on either include depredation of domestic sheep inhabiting high elevation allotments during summer and depredation of nests of white-tailed ptarmigan, which is a species of conservation concern in Colorado. Neither event is expected to be common based on interactions between these species elsewhere throughout wolverine range in the western U.S. during the last 50-75 years. Other than newborn calves, cattle are not vulnerable to wolverine predation, and even calves are generally large enough to avoid predation by the time they are turned out in alpine areas where wolverines exist.

Climate change is expected to have a generally negative impact on wolverine populations worldwide owing to their adaptation to cold, snowy environments. Colorado's wolverine habitat will not escape the impacts of climate change, but its high elevation and topographically complex terrain is expected to buffer impacts as well, if not better, than lower elevation habitat elsewhere in the western U.S. Winter recreation activities may elicit avoidance behavior by individual wolverines, and the potential for den abandonment due to human presence is also a topic of ongoing deliberation. However, it is unknown whether there are population-level effects from recreation on reproductive rates, survival rates, or density. Overlap between modeled wolverine habitat and developed ski areas is inconsequential (<1% overlap). Overlap with areas modeled as suitable for dispersed winter recreation is higher (20%), and would normally necessitate ESA consultation for this federally listed species. However, the 10(j) experimental, non-essential designation necessary for reintroduction to Colorado and tools such as biological opinions and exemptions pursuant to section 4(d) as indicated in the 2023 listing decision can ease consultation requirements. Any impacts from recreation may be buffered by the fact that much of the wolverine habitat in Colorado occurs within areas with limited access such as wilderness, national parks, wilderness study areas or federally designated roadless areas.

Chapter 4 describes implementation of the reintroduction program in Colorado.

A population viability analysis was completed to assess the probable outcomes of a wolverine reintroduction to Colorado given vital rates, and levels of stochasticity in those rates, observed from other established populations. The analysis indicates that reintroducing 30 wolverines to Colorado over two years would establish a population that is expected to grow and fill available habitat over several decades. Furthermore, the viability analysis suggested little chance that the newly established population would succumb to chance events (stochasticity) and go extinct before nearing capacity. To buffer against uncertainty, CPW is proposing to translocate up to 45 wolverines to Colorado over three or more years. This number of wolverines, captured from a variety of sites, should also provide sufficient genetic diversity to moderate potential negative effects from inbreeding depression that can result from a small founding population.

All states and provinces that currently have wolverine populations are considered to be potential source populations for this conservation translocation. CPW ranked each potential source area based on ecological similarity to Colorado and genetic diversity of its population. Southern and central British Columbia and Alberta are the top 4 potential source populations based on these biological and ecological considerations. Ultimately, however, logistics, identification of willing partners, and the ability of source populations to sustain removals will factor heavily into the source areas for wolverines. CPW contends that successful wolverine restoration is not necessarily dependent on sourcing individuals from specific locations.

Capture of wolverines at source populations will occur in early winter. CPW may compensate cooperators, or provide personnel to complete the work as necessary. Translocated wolverines will be transported to and held at CPW's Frisco Creek Wildlife Rehabilitation Center after arriving in Colorado to undergo veterinary examination, be fit with GPS collars, and recover from capture and transportation.

Release procedures are critical for success. Because there has not been a formal reintroduction of wolverines anywhere previously, there are many unknowns regarding both adequate and optimal release techniques. The Wolverine Translocation Techniques Working Group (2013) suggested, as have other wildlife reintroduction specialists (e.g., Jachowski et al. 2016), that an approach that facilitates learning and adaptation will be best. This is the approach CPW will take, using a "Reproductive Focus" release strategy in a "learn and adapt" framework to determine procedures that are most effective. If this strategy or portions of it improve success, those techniques will continue to be utilized. If they do not improve success, CPW will move toward a simpler "Logistical Focus" strategy.

The Reproductive Focus strategy will attempt to capitalize on the fact that the majority of adult females will be pregnant (via delayed implantation) when captured during November-January. Site fidelity (remaining in Colorado) is key and *could* be greater if translocated females are accompanied by newborn young near the time of release. Retaining litters will depend on sufficient food availability, and because females will not have made caches over the winter, food will likely need to be provisioned. After being conditioned at Frisco Creek, approximately half of the translocated females that retain pregnancies will be released ~February 1 (about two weeks before giving birth) at a den-like structure provisioned with a carcass ("Wild Births"); additional food resources will be provisioned to these individuals as necessary until the time of marmot emergence. The other half of the females that retain pregnancies will be held in captivity where it is assured that they can be well-nourished in an attempt to successfully birth litters ("Captive Births"); these family groups will be released by ~June 1 when marmots have emerged and the young are capable of travelling with the female. Male translocations during the first year will be limited to those adult males captured at the same site as a translocated adult female (to insure some male presence but reduce chances of infanticide by males that are not mates of the pregnant females). These few males, along with successful litters, half of which will be male, can provide the male portion of the population, or, if needed, males can be translocated to Colorado in subsequent years. After year one of translocations, CPW will assess whether retention of pregnancies occurred at a high-enough rate, site fidelity was improved by the presence of litters, and recruitment was greater via wild vs. captive births. Sustained wolverine utilization of remote, provisioned den release sites will also be assessed, as will the influence of same-site captured males. Those techniques that appear to be more effective will continue to be utilized. If none are more effective, the Logistics Focus release strategy will be employed and could be as simple as releasing male and female wolverines into suitable habitat at the most accessible location.

There are 3 near-equally sized Release Zones in Colorado that occur 1) north of I-70, 2) in the central mountains, and 3) across the San Juan Range. The central mountains will be the primary release zone during year one because of its habitat quality, centrality related to other suitable habitats in Colorado, and fewer domestic sheep allotments. The location of releases during subsequent years will depend on where previously released wolverines settle.

Chapter 5 describes benchmarks of success for the two phases of reintroduction - the Establishment Phase and the Growth Phase - as well as criteria for down-listing wolverines in Colorado from the State Threatened & Endangered list.

The Establishment Phase of the project will encompass years 1-3 (potentially longer) when animals are actively being transported from source populations and released into Colorado. Benchmarks of success for this phase include wolverine fidelity to habitat in Colorado, adequate annual survival during the first year post-releases, and the establishment of home ranges in Colorado by at least 30 individuals. The Growth Phase begins as the Establishment Phase concludes, and will ideally be characterized by increases in population size and distribution. Benchmarks during this phase include continued adequate annual survival of individuals along with evidence of breeding and recruitment of young into the population. The final benchmark for the Growth Phase, and the ultimate determination of the success of the reintroduction program, will be indicated by a population model. Success will be achieved when such a model, informed by Colorado-specific estimates of survival and productivity gathered across several years, projects a stable or increasing population. Either phase of the project can be paused, or extended, as deemed necessary to achieve success.

As of November 29, 2023, wolverines in Colorado are listed as threatened under the ESA.

This Plan does not replace a federal recovery plan, nor does it outline federal recovery goals.

As this Plan is implemented, CPW will work in cooperation with the United States Fish and Wildlife Service (USFWS).

This Plan authorizes downlisting of wolverines from State Endangered (Stage 1) to State Threatened (Stage 2) when CPW determines that all benchmarks of success for the Establishment and Growth Phases of the reintroduction have been met. Furthermore, downlisting from State Threatened to State De-listed (Stage 3) can occur when monitoring indicates that wolverines occur in all 3 Release Zones, and that the distribution is estimated as reasonably stable for at least 10 years after transitioning to Stage 2 (threatened). We note that official change in state status can only occur via a regulatory process initiated by the Parks and Wildlife Commission.

Marking the entrance to a wolverine den in an avalanche chute. Photo ©R. Spence.

Chapter 1: Introduction and Background

Need

The North American wolverine (*Gulo gulo luscus*) was part of Colorado's native fauna until it was extirpated during the early 1900's, likely due to poisoning and unregulated killing (Aubry et al. 2007). A breeding population of wolverines has been absent from Colorado for a century and wolverines have been classified as a State Endangered species since 1973 (Seidel et al. 1998). Restoring wolverines to Colorado would help fulfill the Colorado Parks and Wildlife (CPW) mission "To perpetuate the wildlife resources of the state…" At a broader scale, wolverines in the contiguous U.S. were recently listed as Threatened under the Endangered Species Act (ESA, U.S. Fish and Wildlife Service 2023*a*). Restoration of this species into Colorado would significantly benefit its persistence in the contiguous United States by 1) directly increasing redundancy via re-creation of a population within the species' former range, 2) improving overall resilience of the species to stochastic events by augmenting population size, and 3) enhancing representation by creating a new, sizeable population with relatively diverse genetic composition (Inman et al. 2013, U.S. Fish and Wildlife Service 2016). Additionally, restoring wolverines to Colorado would reestablish a population into a large block of available habitat that is expected to resist negative effects of climate change as well or better than occupied habitat elsewhere (McKelvey et al. 2011, Marshall et al. 2019, Barsugli et al. 2020, Lute et al. 2022), which is critical for a cold-adapted species such as wolverine (Copeland et al. 2010, Inman et al. 2012*a* 2012*b*, U.S. Fish and Wildlife Service 2023*b*). Therefore, identifying a means to restore this species to its native range in the Southern Rockies is desirable both from a Colorado perspective and with respect to the contiguous U.S. metapopulation (Inman et al. 2013), which has been a source of conservation concern for decades https://ecos.fws.gov/ecp/species/5123

Natural Dispersal vs. Reintroduction

Compared to natural dispersal, restoration of wolverines to Colorado via planned reintroduction is most likely to lead to successful establishment of a new population; reintroduction will also benefit range-wide conservation of the species in the contiguous U.S. sooner and more fully. This is largely due to 3 factors - observed female dispersal patterns, limited capacity for wolverine population growth, and genetic considerations.

Restoration of wolverines via natural dispersal would require large-scale movements of individuals from other populations to Colorado. However, the likelihood that a female wolverine will disperse to Colorado is low and does not appear to have occurred in almost a century despite the presence of wolverines in suitable historical habitat in Montana, Idaho and Wyoming for decades (Newby and Wright 1955, Newby and McDougal 1964, Hoak et al. 1982, Groves 1988, Aubrey et al. 2007). This is due in part to female philopatry, which is well documented via field study and genetics (Flagstad et al. 2004, Aronsson and Persson 2018). Young, dispersing-aged females establish territories close to their mother's home range when possible. This limits the potential for females to begin the long-distance dispersal process necessary to recolonize Colorado. Even if a female did begin to disperse a long distance, the likelihood of her dispersal leading her into Colorado is low given the longer distances and lower suitability of habitat in-between compared with other potential dispersal paths (Schwartz et al 2009, Inman et al. 2013). Roads may also limit wolverine movements, especially females (Sawaya et al. 2019), and the high volume of traffic on Interstate-80 further reduces the likelihood of female dispersal to Colorado. Males may make it to Colorado occasionally (Packila et al. 2017). However, no population has established in Colorado during the nearly 100 years of wolverine recovery into their historical range of the contiguous U.S., suggesting that natural female dispersal to Colorado is rare, if it occurs at all, and not conducive to reoccupation of the state.

Even if a male and female dispersed at the same time to Colorado, they would need to locate each other, mate, and then successfully found a population despite perils owing to small populations. That is, a population of two is demographically fragile, especially considering the low reproductive rate of the wolverine. Chance events alone (e.g., lack of reproduction due to conditions, death of a mate) could drive the nascent population to extinction before it grows enough to resist such events. Additionally, close relatives would be the only potential mates during the early years of population growth, which would increase the probability of harmful effects due to inbreeding. Ideally, more than one pair would successfully disperse, which would help with these issues, but the probability of more simultaneous dispersals is exponentially smaller than a single dispersal. In summary, a series of very low probability events would need to align to start a new population via natural dispersal, and these events are unlikely to occur within a reasonable timeframe (e.g., within the next several decades). Further, if these events did occur within a reasonable timeframe, the resulting population would not grow quickly and would need to survive demographic uncertainties and a period of low genetic diversity until additional gene flow with other populations could occur. Thus, CPW does not recommend this option for restoring wolverines to Colorado.

CPW believes that restoration of wolverine to Colorado can be best accomplished with a planned reintroduction. Such an approach is more likely to establish a viable population compared to natural dispersal because it 1) overcomes impediments to dispersal posed by isolation from other populations, especially for females, 2) provides an opportunity to quickly establish a sizeable population over a short timeframe and 3) provides an opportunity to enhance genetic diversity of the new population to guard against inbreeding depression. Potential negative effects of a planned reintroduction include harming a source population by removing too many individuals or weakening social tolerance for the species at the release destination. However, CPW is confident that these potential negative effects can be alleviated via careful planning and outreach.

Background

On July 8, 1997, representatives from the U.S. Forest Service (USFS), U.S. Fish and Wildlife Service (USFWS), and the Colorado Division of Wildlife (CDOW, now Colorado Parks and Wildlife) met to discuss a cooperative program for the conservation and reestablishment of wolverine and Canada lynx (*Lynx canadensis*) in Colorado. On August 4, 1997, those agencies, plus the National Park Service (NPS) signed a letter agreeing to jointly prepare "A Candidate Conservation Strategy for Lynx and Wolverine in Colorado." CDOW and federal partners prepared a draft strategy for reintroducing both species in 1998 (Seidel et al. 1998). That same year, the Colorado Wildlife Commission (CWC) gave approval for the reintroduction of lynx and wolverine. However, due to the complexity of the program along with time, monetary, and biological constraints, CDOW elected to only pursue a lynx reintroduction at that time.

The lynx reintroduction was implemented from 1999-2006. By 2010, modeling efforts based on demographic data collected on the newly reintroduced lynx population indicated it was viable, and the reintroduction was deemed a success. Ongoing non-invasive monitoring continues to document a well-distributed lynx population and evidence of reproduction two decades later (Odell et al. 2023). Immediately after the conclusion of the lynx reintroduction, CPW began working to fulfill the wolverine portion of the strategy for reintroducing lynx and wolverine to Colorado (Seidel et al. 1998).

Wolverine Restoration Plan Development

The plan laid out in the following pages builds off of a *Draft Wolverine Restoration Plan* completed by CPW in 2010, as well as deliberations of the Wolverine Translocation Techniques Working Group convened that same year (Wolverine Translocation Techniques Working Group 2013). Details of the plan adhere to the International Union for the Conservation of Nature (IUCN) guidelines for wildlife reintroductions (IUCN/SSC 2013) and meet the IUCN definition of a Conservation Translocation: "the deliberate movement of organisms from one site for release in another intended to yield a measurable conservation benefit at the levels of a population, species or ecosystem." While the best available science is used in formulating this Plan, the Plan itself does not represent an exhaustive review of the literature on wolverine biology, ecology, management, and research. The reader is referred to Copeland and Whitman (2003), Fisher et al. (2022), and Mowat et al. (in press) for such reviews. Additionally, the reader can access the USFWS Species Status Assessment (U.S. Fish and Wildlife Service 2018) and associated addendum (U.S. Fish and Wildlife Service 2023*b*) for a summary of scientific information accumulated to date for this species in North America.

Plan Goals

The primary goal of this Plan is to identify the steps needed to recover and maintain a viable population of wolverines in Colorado.

Specifically, this Plan will:

- Provide relevant background information regarding the species' ecology and assess feasibility of a restoration.
- Outline a methodology to establish a population of wolverines using the best scientific data and expert assessment available.
- Outline a methodology for determining when the wolverine population is viable and when to remove the wolverine from the State List of Endangered or Threatened species.

Summary of Historical Distribution of Wolverines in Colorado

Prior to extirpation, the last verifiable record of wolverines in Colorado occurred in 1919 (Aubry et al. 2007, Armstrong et al. 2011). Aubry et al. (2007) exhaustively searched museum records, literature, and other archival materials across the contiguous U.S.; they documented 85 records in the Rocky Mountain states collected between 1827-1919, 34 of which were from Colorado. Twenty-eight such records had the requisite spatial resolution to accurately map. Locations were well-distributed throughout the high country of Colorado from the southern Park Range in the north to the southern San Juan and Sangre de Cristo Mountains in the south. No wolverines were recorded in Colorado from 1920-2005 (Aubry et al. 2007).

From 1979 through 1996, 12 surveys were conducted to search for the presence of wolverine (and lynx) within Colorado. Survey methods included snow tracking (5,834 miles), hair snags (62 locations), remote cameras (110 locations), and hair snares (686 trap nights; Seidel et al. 1998). Ten sets of tracks that appeared to have a high probability of being wolverine were found, but none were confirmed (Seidel et al. 1998). During 11 years of monitoring reintroduced lynx (1999−2010), which included over 4,000 km of snow tracking, 1 probable wolverine sighting and 1 probable track were observed. There were also 2 probable sightings of wolverine tracks reported by USFS during this time (A. Garcia, USFS, personal communication).

Wolverines have not been observed during non-invasive lynx monitoring efforts from 2014–present (Odell et al. 2023), which included over 240,000 remote-camera trap-nights. Further, there have been no observations during recent, large scale research projects on alpine species (e.g., brown-capped rosy finches [*Leucosticte australis*], white-tailed ptarmigan [*Lagopus leucura*], American pika [*Ochotona princeps*]) or subalpine species (e.g., snowshoe hares [*Lepus americanus*], pine martens [*Martes caurina*]) in Colorado (Ivan et al. 2014, 2018, 2023, Seglund 2015, Bernier et al. 2023, Seglund and Runge 2023). No detections occurred during a recent western U.S. wolverine survey that included northern Colorado (Gerber et al. in prep). Moreover, there have not been any road kills or accidental trapping or shooting of wild wolverines reported in Colorado for nearly a century (Aubry et al. 2007). For comparison, states with confirmed wolverine populations (Montana, Idaho, Wyoming, and Washington) have produced hundreds of confirmed records that include captured wolverines, dead wolverines, photos, and DNA evidence (Newby and McDougal 1964, Hornocker and Hash 1981, Copeland 1996, Aubry et al. 2007, Anderson and Aune 2008, Inman et al. 2012*b*, Lukacs et al. 2020). Thus, despite a substantial effort by CPW to document presence of the species in Colorado, no confirmed evidence of a resident wolverine population, however small, has been documented in Colorado since the species was extirpated.

Colorado's limited number of probable (but unconfirmed) records over decades could be instances of dispersing individual males. A single GPS-collared male wolverine, "M56", was radio-tracked as he dispersed from northwest Wyoming into Colorado in 2009 (Packila et al. 2017). M56 was the first confirmed evidence of a wolverine in the state in nearly a century; he was photographed by a Colorado citizen within 24 days of entering the state. The near immediate and independent confirmation of the presence of a wolverine in the state lends credibility to the apparent absence of a population in the state for most of the last century. Similar dispersals by unmarked, lone males into Colorado could have occurred in the past, which may explain occasional, unconfirmed sightings. CPW has concluded that if any wolverines were present in Colorado after the early 1900s, their numbers were so small that they did not represent a viable population.

Legal Status

Federal

Wolverines have been petitioned for listing under the U. S. Endangered Species Act (ESA) on numerous occasions over the past several decades. The first petition to list the wolverine in the contiguous U.S. as federally Threatened or Endangered was filed in 1994. From 1994 to 2020, the USFWS reviewed and rejected 5 petitions to list the species. In November, 2023, wolverines were officially listed as Threatened under the ESA (U.S. Fish and Wildlife Service 2023*a*). The U.S. Fish and Wildlife Service also adopted an interim rule under section 4(d) of the ESA prohibiting take of wolverines in the U.S.; this rule has limited exceptions. Notably, the interim 4(d) rule does not allow take of depredating wolverines or take resulting from backcountry winter recreation. The principal exceptions to the prohibition on take in Colorado are for take resulting from forest vegetation and fire management activities, incidental trapping, and take by CPW for conservation purposes (U.S. Fish and Wildlife Service 2023*a* at 83769; 50 C.F.R. 17.40(u)(2)). A final 10(j) rule governing the experimental population in Colorado may provide additional management flexibility via additional exceptions to the take provisions.

Tribal

The geographic focus of the State's wolverine restoration efforts in western Colorado impacts a region that is of current, historical, and cultural importance to the Southern Ute and the Ute Mountain Ute Indian Tribes. Additionally, the anticipated release areas and preferred habitat for wolverine overlap with areas in which the Tribes maintain wildlife authority and jurisdiction, including the Brunot Area and the Tribes' Reservations (Fig. 1).

Brunot Area

The Tribes and State also work cooperatively to manage wildlife resources in the Brunot Area, where the Tribes retain protected off-Reservation hunting, fishing, and gathering rights on ceded lands over which the Tribes retain wildlife management authority. The following map depicts the Brunot Area, which consists of approximately 3.7 million acres in southwest Colorado that includes parts inside the San Juan Mountain region in the State of Colorado.

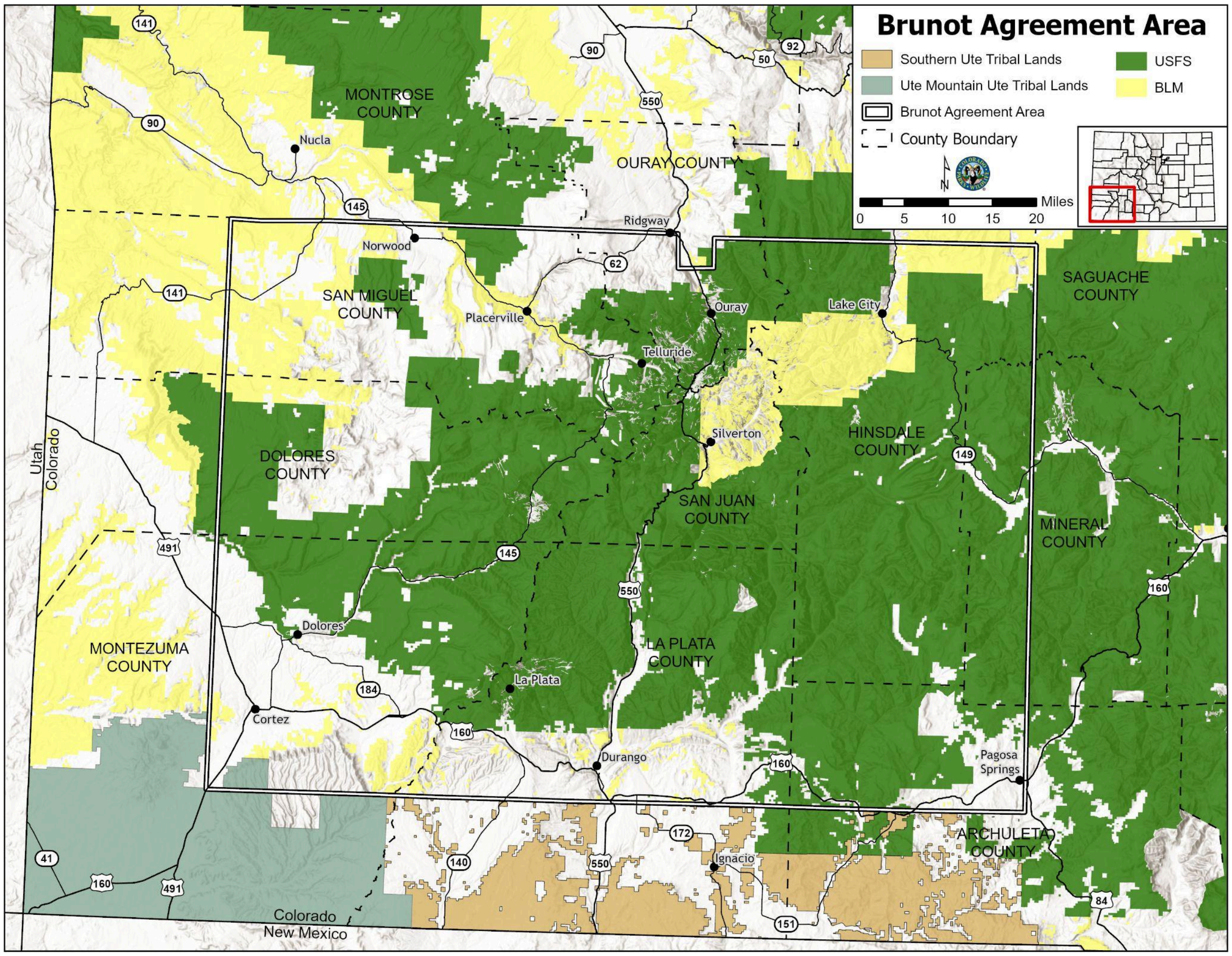


Figure 1. Southern Ute and Ute Mountain Ute Tribal Lands and the Brunot Agreement Area in southwest Colorado.

A Memorandum of Understanding (MOU) by the Southern Ute Indian Tribe in 2008 and by the Ute Mountain Ute Tribe in 2013 with the State of Colorado addressing each of the Tribal Nations' exercise of its hunting and fishing rights in the Brunot Area. These MOUs detail how the Southern Ute Indian Tribe, Ute Mountain Ute Tribe and State of Colorado approach Brunot Area hunting, fishing, and wildlife law enforcement, and express the intent of all three governments to work cooperatively toward long-term conservation of wildlife within the Brunot Area.

The Ute People

The Ute people (Nuchu) are the longest continuous residents in what is now Colorado, inhabiting vast areas of the state since time immemorial. The Southern Ute Indian Tribe and Ute Mountain Ute Tribe are both federally recognized Indian Tribes that have reservation trust lands located in southwest Colorado. These separate reservation lands that are held in trust for the benefit of the Southern Ute and Ute Mountain Ute Tribes were each established by a series of treaties and congressionally approved agreements.

The Utes signed a comprehensive treaty with the United States in 1868 that purported to guarantee to the Utes approximately the western third of what is now the State of Colorado – nearly 15 million acres of land that was “set apart for the absolute and undisturbed use and occupation” of the Ute people. Treaty with the Ute Indians, 15 Stat. 619 (1869). In 1873, the United States negotiated the cession of large portions of the Ute treaty lands. Agreement of September 13, 1873 (“Brunot Agreement”), ratified by Act of April 29, 1874, 18 Stat. 36 (1874). The area ceded, commonly called the Brunot Area, is approximately 3.7 million acres in southwest Colorado that includes parts of the San Juan Mountain region. As compensation for ceding the Brunot Area, the Tribe would be allowed to “hunt upon said [Brunot Area] so long as the game lasts and the Indians are at peace with the white people.”

Southern Ute Indian Tribe

Several years later after the 1873 Brunot Agreement was ratified, the Mouache and Capote bands of Utes, which today comprise the Southern Ute Tribe, were confined to a reservation that consisted of approximately 700,000 acres in portions of La Plata, Archuleta, and Montezuma counties. Following allotment, Congress opened portions of the Reservation to homesteading by non-Natives. Act of June 15, 1880, ch. 223, 21 Stat. 199; ch. 113, 25 Stat. 133. Subsequently, Congress restored Reservation lands that had not been disposed of during the allotment or the homesteading process to ownership by the United States held in trust for the Tribe. Indian Reorganization Act of 1934 (codified at 25 U.S.C. §§5101 et seq.); 3 Fed. Reg. 1425 (1938).

As a result of this complicated history, the Southern Ute Indian Tribe’s Reservation is “checkerboarded” in nature and many different land statuses exist within the Reservation boundaries, including Tribal and individual Indian trust lands, private fee lands, San Juan National Forest lands, and properties held by State and local governments. Jurisdiction on the Reservation is therefore complex. To help address jurisdictional confusion, in 1984, Congress confirmed the exterior boundaries of the Southern Ute Indian Reservation in Public Law 98-290 Act of May 21, 1984, Pub. L. No. 98-290, § 3, 98 Stat. 201, 202 (“P.L. 98-290). Notwithstanding this legislation, three sovereigns exercise jurisdiction within the Reservation boundaries: the federal government, the State, and the Tribe.

With respect to wildlife management authority, the Southern Ute Indian Tribe retains inherent authority over its lands. The Tribe manages wildlife and regulates hunting pursuant to this sovereign authority and pursuant to Article VII Section 1(n) of the Southern Ute Indian Tribal Constitution. Pursuant to this authority, the Tribe created its Wildlife Resource Management Division under its Natural Resources Department to lead the management and protection of the diverse and abundant wildlife resources on the Reservation. Additionally, the Southern Ute Indian Tribe enacted its Wildlife Conservation Code, which declares that "[a]ll matters relating to the conservation, regulation, control and management of the wildlife resources of the Reservation are subject to the jurisdiction of the Tribe," and reserves the Tribe's right to "establish the rules and standards to govern the action of members and non-members of the Tribe on the subject to wildlife regulation." Southern Ute Indian Tribal Code, Wildlife Conservation, §13-1-1-1(1)(b), (1)(c). Under the Wildlife Conservation Code, the Southern Ute Indian Tribe declares ownership of the wildlife within the Tribe's Reservation boundaries and is responsible for enforcement of the Code for all Native Americans within the exterior boundaries of the Reservation and for non-Natives who hunt on Tribal lands both with and without a valid Tribal hunting permit. The State of Colorado regulates the remainder of the non-Native population on private and federal lands within the exterior boundaries of the Reservation. The Tribe and the State work cooperatively to balance the needs of people with important Tribal wildlife resources.

The Tribe has a vested, sovereign interest in perpetuating the wildlife resources that Tribal hunters have relied upon since time immemorial on both Reservation lands and in the Brunot Area, as well as in managing wildlife consistent with the Tribal livestock industry. There are 18 livestock Range Units totaling approximately 124,000 acres on the Southern Ute Indian Reservation where Tribal member producers graze cattle, sheep, goats, and horses. Moreover, Tribal members annually procure hunting permits from the Tribe for the Brunot Area to hunt mule deer, elk, turkey, small game, big horn sheep, moose, and mountain goats. Given the Tribe's interests and its wildlife management authority, there is need to communicate and cooperate regarding the restoration of wolverines, to confirm the Tribe's intent to participate in the State's program to provide fair and timely compensation to the Tribe or Tribal members for any losses of livestock proven to be caused by wolverines, and to proactively collaborate with the Tribe on any rules CPW drafts and adopts to allow for compensation for livestock due to wolverine depredation.

Ute Mountain Ute Tribe

The modern-day Ute Mountain Ute Tribe originated from the Weenuche band of the Ute Nation of Indians. The Weenuche separated from the Capote and Mouache bands in 1897 and during allotment when the Weenuche band chose to continue to hold its land in common. The current Ute Mountain Ute Reservation encompasses approximately 578,500 acres, 460,000 of which are in the southwestern corner of Colorado, with 104,500 and 14,000 acres in New Mexico and Utah, respectively. The highest point on the Reservation is Ute Peak, which rises to 9,976 feet above sea level.

The Ute Mountain Ute Tribe has jurisdiction over wildlife within the exterior boundaries of its Trust Lands (Reservation). Ute Mountain Ute Tribal Council adopted the Wildlife Conservation Code in 1990 under Resolution 3681, which set forth a framework for regulating hunting and fishing, created protections for species of conservation need, and delegated authority for wildlife management to the Tribe's Wildlife Department.

Brunot Treaty Rights were not recognized by the State of Colorado until 1978, when both parties entered into a Consent Decree under the U.S. District Court of Colorado (Civil Action No. 78-C-0220). UMUT adopted a Hunting Code for the Brunot Area in 1990 under Resolution 3680, which created the Brunot Hunting Commission, made up of three Tribal members who are appointed by Tribal Council and serve three-year terms. The Commission has the authority to set hunting license parameters and issue hunting permits within the Brunot Area, although the responsibility to enforce the Hunting Code for the Brunot Area remains with the Wildlife Department. The Consent Decree was superseded in 2013, when the CPW and UMUT entered a Memorandum of Understanding to co-manage wildlife within the Brunot Area. Today, CPW and UMUT work closely together to ensure that the shared resource that has sustained the Nuchu since time immemorial continues to benefit current and future generations.

The objective of UMUT within both Reservation lands and the Brunot Area is to provide a resilient and sustainable resource that benefits its members by providing food security and yielding recreational, economic and intrinsic value. This includes supporting livestock producers, who graze horses and cattle on over 30,000 acres of private land and adjacent, leased State Trust Lands across Colorado. The Ute Mountain Ute Tribe expresses the need to communicate and cooperate regarding the restoration of wolverines, to confirm UMUT's intent to participate in the State's program to provide fair and timely compensation to UMUT or its members for any losses of livestock proven to be caused by wolverines, and to proactively collaborate with UMUT on any rules CPW drafts and adopts to allow for compensation for livestock due to wolverine depredation through formal consultation.

State

Wolverines are currently classified as State Endangered in Colorado and have held that status since 1973. A State Endangered Species is defined as "any species or subspecies of native wildlife whose prospects for survival or recruitment within this state are in jeopardy as determined by the Commission" (CRS § 33-1-102 [12]). "Unauthorized take (i.e., killing or acquiring possession except by accident such as killing by vehicle) of an endangered or threatened animal is punishable by a fine of not less than two thousand dollars and not more than one hundred thousand dollars, or by imprisonment for not more than one year in the county jail, or by both such fine and such imprisonment, and an assessment of twenty points towards restrictions of hunting and fishing privileges. Upon conviction, the Colorado Parks and Wildlife Commission may suspend any or all license privileges of the person for a period of from one year to life" (CRS § 33-6-109 [3a]). The Commission has statutory authority to add or remove species from the lists of Endangered, Threatened, and Nongame wildlife.

Colorado's State Wildlife Action Plan states that the primary conservation action for wolverines is to "develop the tools and social and political support necessary to undertake a restoration with the ultimate goal of reestablishing a self-sustaining population of wolverines to the state" (Colorado Parks and Wildlife 2025). Constitutional Amendment 14, approved by the voters of Colorado in November 1996, restricted the use of poisons, foot-hold, kill-type, and snare trapping devices in the State of Colorado. Such restrictions reduce the potential for non-target trap mortality, which would benefit wolverines should a restoration occur. It also formally restricts poisons, which are thought to be a primary factor that led to the extirpation of wolverines in Colorado a century ago.

In 2024, the Colorado General Assembly adopted a bill authorizing reintroduction of wolverine, with a number of prerequisites. *See* 33-2-105.9, C.R.S. Specifically, reintroduction may not begin until a final 10(j) rule has been adopted by the U.S. Fish and Wildlife Service designating wolverine as a nonessential experimental population under the ESA; and until the Parks and Wildlife Commission has adopted rules providing for compensation to livestock owners in the event of depredation by wolverine.

Other states within historical wolverine range in the contiguous U.S. (i.e., Wyoming, Montana, Idaho, Washington, Oregon, California, and Utah) consider wolverines to be a Species of Greatest Conservation Need in their State Wildlife Action Plans (California Department of Fish and Wildlife 2015, Montana Fish Wildlife and Parks 2015, Utah Wildlife Action Plan Joint Team 2015, Washington Department of Fish and Wildlife 2015, Oregon Department of Fish and Wildlife 2016, Idaho Department of Fish and Game 2017, Wyoming Game and Fish Department 2020). Additionally, some states further designate the wolverine as S1 Critically Imperiled (Washington Department of Fish and Wildlife 2015, Idaho Department of Fish and Game 2017), S2 Imperiled (Utah Wildlife Action Plan Joint Team 2015), or State Threatened (California Department of Fish and Wildlife 2015). Wyoming further classifies wolverines as Nongame Wildlife and defines them as a protected animal by state statute (Wyoming Game and Fish Department 2020). Wolverines are classified as a furbearer in Montana, but there has been no open season for trapping or hunting wolverines in the state since 2013 (Montana Fish Wildlife and Parks 2013, 2023). New Mexico does not consider the wolverine to be part of their native fauna; only one historical record exists (from 1860; Aubry et al. 2007), and the amount of suitable habitat in New Mexico is negligible from a population perspective (Frey 2006, Inman et al. 2013).

The most typical 2-2 mustelid (weasel) gait pattern. This "bounding" gait pattern or way of travelling is the most common track pattern and almost always found if a wolverine or suspected wolverine track is followed for a little while. Photo ©R. Inman

Chapter 2: Wolverine Ecology

Taxonomy & Description

The wolverine is the largest terrestrial member of the family Mustelidae. Although more closely related to badgers (*Taxidea taxus*) and other weasel species, the wolverine resembles a very small bear with a bushy tail: it has a broad, rounded head; short, rounded ears; and small eyes. Wolverines are brown to dark brown in color, with a faint to distinct yellowish stripe from shoulder to top of tail and across the forehead. Often there are white markings on the chest. Wolverines have five toes on each foot, non-retractable claws, and can climb trees. The feet are large relative to body size, making wolverines well-adapted to travel over snow. Across their range in North America, adult females weigh 8−12 kg (17−26 lbs) and adult males weigh 11−18 kg (26-40 lbs; Banci 1994). Males are 30-60% larger than females (Copeland and Whitman 2003).

Distribution

Wolverines have a circumpolar distribution in the Northern Hemisphere that includes portions of Scandinavia, Asia, and North America (Pasitschniak-arts and Lariviere 1995, Copeland and Whitman 2003). Wolverine populations were greatly reduced in Scandinavia (Landa et al. 2000) and extirpated from the contiguous U.S. (Aubry et al. 2007) and eastern Canada (Pasitschniak-arts and Lariviere 1995) by the early 1900s. These declines were due to human-related mortality, such as unregulated trapping, predator poisoning campaigns, and killing for bounty in areas with semi-domesticated reindeer (Landa et al. 2000, Aubry et al. 2007). In other portions of their range, such as Alaska and northern Canada, distributions appear to have remained stable over time, largely due to minimal human presence and regulation of take for several decades (Pasitschniak-arts and Lariviere 1995).

In North America, wolverines currently occur throughout Alaska and in all of the Canadian provinces west of Quebec (Dawson et al. 2010, Zigouris et al. 2013, Krejsa et al. 2021). The southern portion of their current range extends into the contiguous United States and includes Washington, Idaho, Montana, and Wyoming (Aubry et al. 2007, Lukacs et al. 2020). Recovery to these more southern portions of their historical range (Figure 2) began around 1930, most likely due to dispersal from Canadian populations (Newby and Wright 1955, Newby and McDougal 1964, Cegelski et al. 2003, Aubry et al. 2007, McKelvey et al. 2014). Reproduction has been documented in all four of these states in recent decades (Copeland 1996, Inman et al. 2007*a*, 2008, Anderson and Aune 2008, Rohrer et al. 2008, Heinemeyer et al. 2017). The southern Rockies and Sierra-Nevadas, historically part of wolverine range in the western U.S., have been devoid of verifiable records for nearly a century (Aubry et al. 2007) outside of an occasional dispersing male (Moriarty et al. 2009, Packila et al. 2017, Utah Division of Wildlife 2022). These areas do not currently appear to have viable populations.

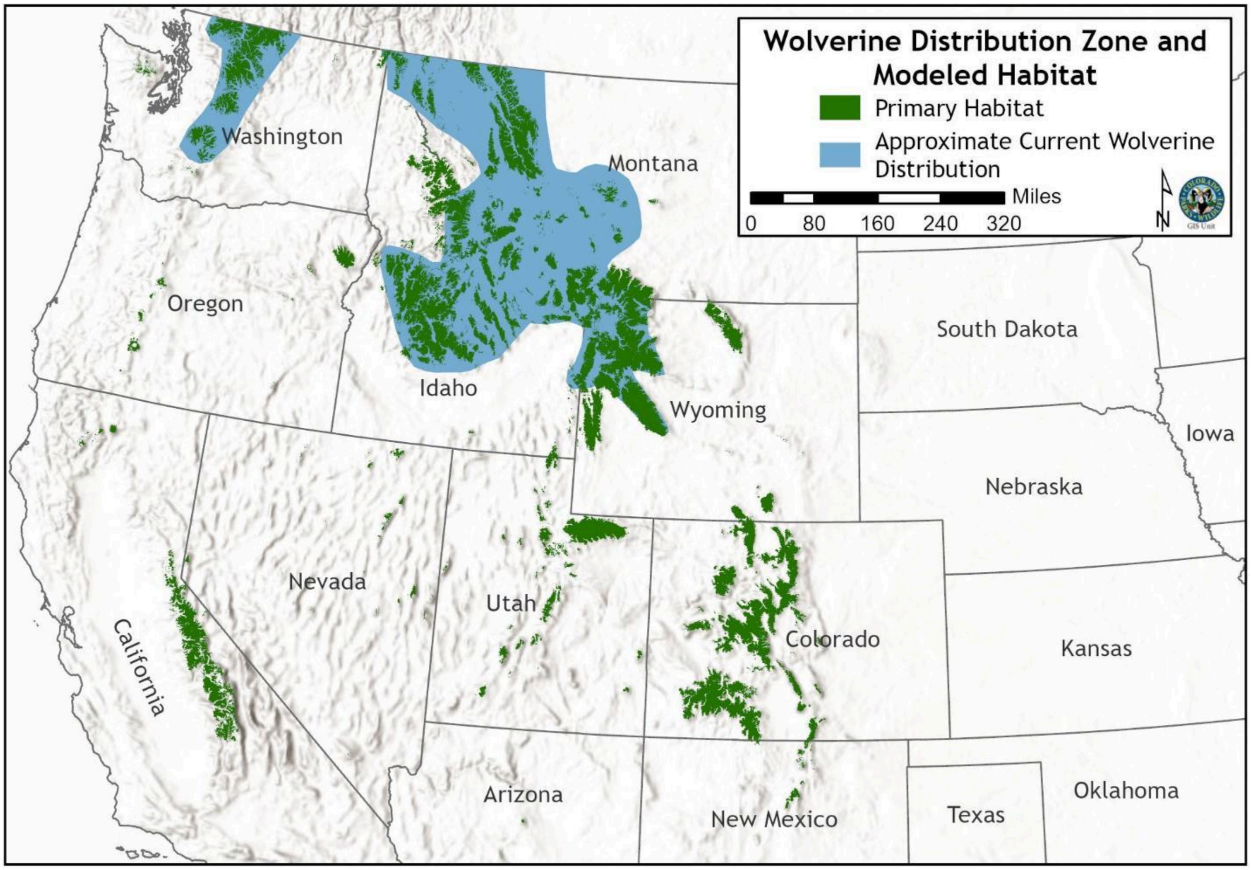


Figure 2. Primary wolverine habitat (Inman et al. 2013) and approximate range of current occupation (Lukacs et al. 2020).

Food Habits

Wolverines are opportunistic foragers that cache food regularly. They are widely known as efficient scavengers of large ungulates, and have an exceptional sense of smell that enables them to locate carcasses from long distances or buried deep in snow (Hornocker and Hash 1981, Copeland 1996). When a carcass is found, wolverines will spend considerable effort to cache the carcass, either by dragging it to a cache site or severing it into multiple pieces for transport (Inman and Packila 2015, van der Veen et al. 2020). Caching occurs year-round and is an important, innate behavior (Inman et al. 2012*a*, Aronsson and Persson 2018, van der Veen et al. 2020). Cache sites vary from boulder fields to forests to bogs and typically occur in places where snow, ice, or water create a cool environment (van der Veen et al. 2020). Caches, then, function to keep food away from large predators such as bears (in boulders inaccessible to larger carnivores) and to preserve food for extended periods (Inman et al. 2012*a*, van der Veen et al. 2020).

While scavenging and caching is the primary means of obtaining food, especially during winter, wolverines are moderately adept at hunting. When favorable conditions arise, such as a moose wallowed in deep snow, wolverines can take adult ungulates (Copeland and Whitman 2003). They regularly take adult reindeer (*Rangifer tarandus*) in the Scandinavian portion of their range (Mattisson et al. 2016). Hunting strategies for ungulates can include long pursuits until an ungulate is exhausted (Magoun et al. 2018). Wolverines occasionally raid beaver lodges (Scrafford and Boyce 2018). Remains of carcasses from human hunting of ungulates can also be a significant food source (Copeland 1996).

Elk leg that had been scavenged and cached for later use. Wolverines have an especially strong jaw structure and are capable of crushing bone to get at marrow. Photo ©J.Burrell

Summer foods are varied and can include, in addition to scavenging, small mammals, birds and bird eggs, medium to large-sized rodents, and at times newborn ungulates (Magoun 1987, Samelius et al. 2002, Gustine et al. 2006, Lofroth et al. 2007, Inman and Packila 2015, Dorendorf et al. 2018). Beaver (*Castor canadensis*) and fox (*Vulpes spp.*) are sometimes preyed upon and/or scavenged as well (Dorendorf et al. 2018, Scrafford and Boyce 2018). In North America, reproductive females often satisfy their energy needs during lactation with ground squirrels (*Spermophilus spp.*) and marmots (*Marmota spp.*). In the Rocky Mountains, marmots, in particular, are important to reproductive female wolverines, and are a staple food source for females rearing young in the spring (Lofroth et al. 2007, Inman and Packila 2015).

Habitat Requirements

From a biophysical perspective, wolverines are habitat generalists that can be found in varied ecosystems such as boreal forests and tundra. The use of alpine habitats is prevalent and consistent in the contiguous U.S., especially during summer; adjacent subalpine forests are frequented during winter (Hornocker and Hash 1981, Copeland et al. 2007, Inman et al. 2012*b*). This pattern of habitat use in montane areas of the contiguous U.S. may be related to the hunting of marmots and potentially neonatal ungulates as a food source during summer, followed by more extensive searching for carrion at lower elevations during winter (Lofroth et al. 2007, Inman and Packila 2015).

The presence of cold temperatures and snow are likely more influential for habitat suitability than vegetation of a particular type or successional stage. The wolverine's niche appears to be based on exploiting low-productivity environments where snow cover inhibits competitors and limited food resources are overcome via caching (Persson et al. 2006, Inman et al. 2012*a*, *b*, van der Veen et al. 2020). Most reproductive dens also include snowcover for at least some portion of time (Magoun and Copeland 1998, Copeland et al. 2010, Webb et al. 2016, Jokinen et al. 2019, Persson et al. 2023).

Within these cold, snowy, alpine and subalpine systems, large boulder fields are an important habitat element (Copeland 1996, Copeland et al. 2007, Inman et al. 2013). Such features often have ice underneath even late into summer, which provides cool, secure chambers wolverines use to rest and cache food. The aspect of a boulder field may influence its utility for wolverines as well, depending on season. Southern and eastern exposures with meadows nearby are often associated with high marmot use (Armitage 2003), and thus a potential prey resource. Northern aspects will retain snow and ice for longer and facilitate caching.

Home Range and Territoriality

Home ranges of adult female wolverines generally average 100-400 km^2 (Table 1). Compared to the home range size of other North American carnivores with similar body size, female wolverine home ranges are 8 times larger than Canada lynx (Anderson and Lovallo 2003); 21–104 times larger than those of the coyote (*Canis latrans*; Bekoff and

Gese 2003), badger (Lindzey 2003), and bobcat (*Lynx rufus*; Anderson and Lovallo 2003); and over 500 times that of the raccoon (*Procyon lotor*; Gehrt 2003). Adult males have larger home ranges than adult females (Copeland and Whitman 2003).

Wolverines display intra-sexual territoriality (Magoun 1985, Hedmark et al. 2007, Inman et al. 2012*b*), meaning territories are generally marked and defended from same-sex individuals, but overlap occurs between sexes. The territory of an adult male generally overlaps that of 2–3 adult females (Hedmark et al. 2007, Persson et al. 2010). Adult females in Sweden display high fidelity to territories year after year; 86% remained in the same territory they held the prior year, 6% expanded into a neighboring territory, and 8% vacated their territory (Aronsson and Persson 2018).

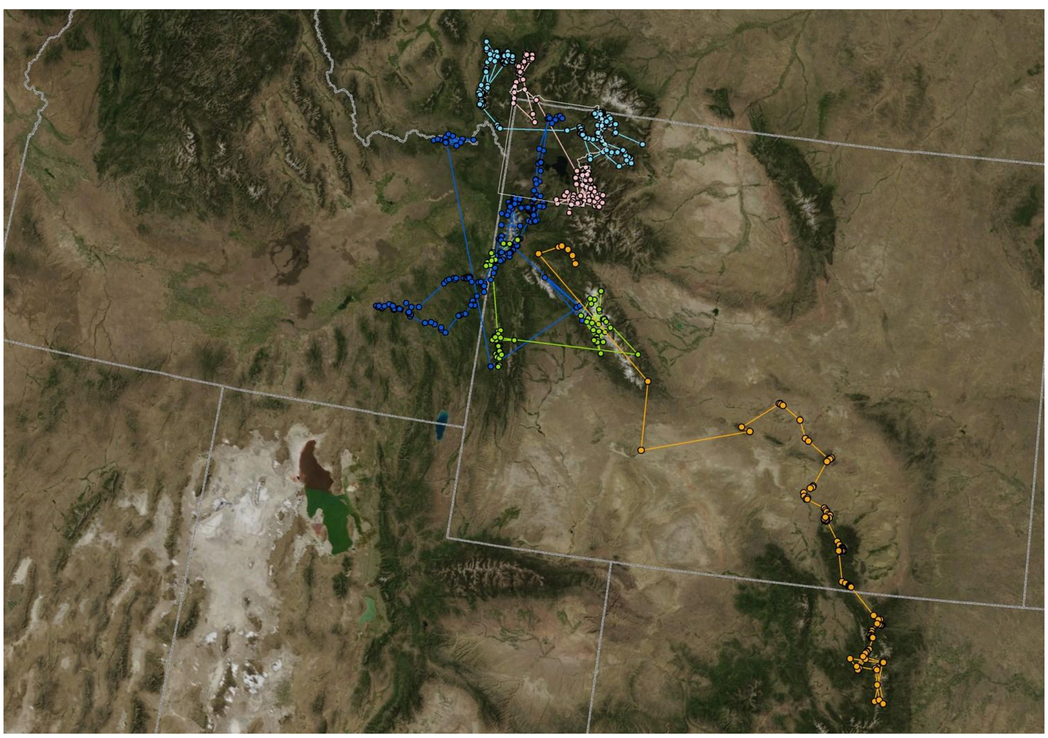
Source	Area	Method	*n*	Estimate (km^2)
Magoun (1985)	Alaska	MCP	6	112
Persson et al. (2010)	Sweden	MCP	24	131
Banci and Harestad (1990)	Yukon	MCP	3	228
Landa et al. (1998)	Norway	MCP	2	335
Krebs and Lewis (2000)	British Columbia	MCP	6	335
Krebs et al. (2007)	British Columbia (S)	Kernel	13	325
Krebs et al. (2007)	British Columbia (N)	Kernel	10	405
Hornocker and Hash (1981)	Montana	MCP	11	388
Copeland and Yates (2008)	Montana	MCP	7	139
Heinemeyer et al. (2019)	Idaho	LCH	10	289
Inman et al. (2012*b*)	Greater Yellowstone	MCP	8	303
Copeland (1996)	Idaho	95% MCP	5	304

Table 1. Estimates of adult female home range (i.e., territory) size for wolverines. Home range size has been estimated using a variety of methodologies including minimum convex polygon (MCP: Mohr 1947), kernel density (Kernel, Worton 1989), and local convex hulls (LCH; Getz et al. 2007). The number of sampled individuals is denoted as *n*.

Movement and Dispersal

Wolverines are widely renowned for their extensive movements (Copeland and Whitman 2003, Inman et al. 2004). Despite having very large home ranges, resident adults can cover >75% of their annual home range within a month's time (Inman et al. 2012*b*). Adult males can routinely travel up to 150 km in a week (Copeland and Yates 2008). Steep, rugged terrain may influence typical movements, but is not a barrier or at times even an obstacle; individuals have been observed traversing nearly 1,700 vertical meters (5,000 vertical feet) in less than 90 minutes (Copeland and Yates 2008). Wolverines are active both day and night, but display activity peaks during dawn and dusk (McCue et al. 2007, Thiel et al. 2019).

Genetic signatures indicate that dispersal is male-dominated; females tend to disperse less frequently and not as far as males (Wilson et al. 2000, Kyle and Strobeck 2002, Flagstad et al. 2004, Cegelski et al. 2006). Likewise, telemetry data suggest that while both sexes can disperse long distances (>170 km), males usually disperse farther and across less-suitable habitat (Inman et al. 2012*b*, 2013, Packila et al. 2017, Aronsson and Persson 2018). The availability of unoccupied territories (primarily due to mortality) influences the distance that females will disperse (Aronsson and Persson 2018). When local territories are available, females will generally occupy these first, dispersing longer distances only when habitat is saturated by resident adults. Peak periods of exploratory and dispersal movements seem to occur at 10–15 months of age but such movements may span a period of years (Magoun 1985, Copeland 1996, Vangen et al. 2001, Inman et al. 2012*b*). A portion of the population is often referred to as "transients," which are primarily subadults searching for a territory.



Long distance dispersal movements of wolverines captured in the Greater Yellowstone area, including M56. ©R.Inman

Reproduction

Wolverines are polygamous - males will mate with more than one female in a year (Hedmark et al. 2007). The intra-sexual territoriality of wolverine home ranges, strong site fidelity, and lack of multiple paternity suggests that familiarity between breeding pairs is common (Hedmark et al. 2007, Persson et al. 2010, Copeland et al. 2017, Aronsson and Persson 2018). Multiple paternity of a litter is rare (Hedmark et al. 2007).

Timing

Inman et al. (2012*a*) synthesized the timing and annual cycle of wolverine reproductive biology: Wolverine mating season extends from May through August and peaks in June. Wolverines exhibit delayed implantation where-in eggs are fertilized during mating season, but implantation into the uterine wall for development does not occur until late December through early February. Gestation is approximately 45 days. Birth occurs as early as late January and as late as mid-April. However, the bulk of births occur from February to mid-March. Young are dependent on females for lactation for at least 9–10 weeks. Weaning and use of solid foods begins by April and peaks in May. After weaning, females may leave their young for extended periods while foraging. The female either brings food to them, or caches and leads them out to feed. The young start travelling regularly with the female during July and begin to forage on their own during late July to August. They are nutritionally independent to some degree and make exploratory movements by September. Young are adult-sized by early winter. The majority of dispersal away from the natal range occurs in February and March at approximately 1-year of age, but the independence and dispersal process may take place over multiple years (Inman et al. 2012*b*, Copeland et al. 2017).

Reproductive Rates

The reproductive rate of wolverines is relatively low, marked by prolonged age until sexual maturity, relatively long inter-birth intervals, and small litter sizes. Females in Scandinavia were sexually mature at an average age of 3.4 years (Persson et al. 2006). While examination of carcasses suggests approximately 90% of adult females are pregnant each year (Rausch and Pearson 1972, Banci and Harestad 1988), only about 50% retain litters through May (Persson et al. 2006). The specific point of loss is unknown but could be a) prior to birth and related to female body condition, b) within the first couple of months after birth and related to the amount of food cached for fueling lactation, or c) non-parental male or female infanticide (Persson et al. 2003, Inman et al. 2012*a*). Supplemental feeding of females increases reproductive rate and success at raising young to the time of weaning (Persson 2005), indicating that food availability is usually a limiting factor for recruitment of young into the population. Annual birth rate was 0.74

young/adult female/year for females ≥3 years old in Scandinavia, with an average litter size of 1.9 (Persson et al. 2006). Similarly, females in Glacier National Park, an area with small female home ranges where food is thought to be relatively abundant, produced 0.75 young/adult female/year (Copeland and Yates 2008). Reproductive rates may be lower in Idaho and Greater Yellowstone (Copeland 1996, Inman et al. 2007*a*).

Dens

Wolverine dens, which are places where newborn young and juveniles occur, have been categorized into three types – natal dens, maternal dens, and rendezvous sites (Magoun 1985, Magoun and Copeland 1998). The natal den is the location where birth occurs. Maternal dens are places where the female moves young after the natal den but before weaning. Rendezvous sites are used after weaning and are places where the female leaves cubs (or kits) and from which they will not depart without her. The primary months that natal and maternal dens are used are February, March, and April. Use of rendezvous sites begins in April and peaks in May and June (Inman et al. 2012*a*).

One function of wolverine dens and rendezvous sites is security for vulnerable young, especially newborns. As such, dens and rendezvous sites are almost always associated with structural complexity, ranging from nearly impenetrable layers of avalanche debris (Figure 3) to boulders, snow tunnels, down logs, rock caves, beaver lodges, logging debris, and uplifted root masses (Magoun and Copeland 1998, Inman et al. 2007*a*, May et al. 2012, Scrafford and Boyce 2015, Yates et al. 2017, Jokinen et al. 2019). The degree to which structure is necessary for protection of young may depend somewhat on the prevalence of other winter-active carnivores in the area (Jokinen et al. 2019). Additionally, heavily structured den sites, along with the frequent movement among den sites (Aronsson et al. 2023), may help ward off conspecific predation by other wolverines. This was the main cause of juvenile mortality in Sweden (Persson et al. 2003) where male wolverines have been observed travelling from one den to another and killing young (J. Persson personal communication).

Figure 3a)

Figure 3b)

Figure 3. Wolverine natal den in the Gallatin Range of southwest Montana illustrating how snow and avalanche debris provide structural and thermal security that protects newborns. Photos were taken in (a) April and (b) September, 2006. *Photo 3a)©R. Inman; Photo 3b)©M. Packila and T. McCue*

In addition to security, dens provide insulation. This is likely most crucial during February and March when ambient temperatures are at their lowest, and small newborns are less capable of thermoregulation. Young develop an adult-like coat that keeps them warm after 3-4 weeks (Copeland and Whitman 2003). Because the wolverine's niche is limited to cold, low-productivity environments, snow cover is common at den sites and provides the benefit of increased thermal insulation for young (Magoun and Copeland 1998, Inman et al. 2007*a*, Copeland et al. 2010, May et al. 2012, Yates et al. 2017). The association between snow and dens led to the conclusion that persistent spring snow cover in late April through mid-May is obligatory for denning (Copeland et al. 2010), which has been the basis for several projections of the effects of climate change on future wolverine distribution (McKelvey et al. 2011, Peacock 2011, Barsugli et al. 2020). Other work, however, suggests that snow cover in late April through mid-May is not a requirement for wolverine dens or reproductive success (Webb et al. 2016, Magoun et al. 2017, Jokinen et al. 2019, Persson et al. 2023). Still, snow is very common at den sites and likely provides important insulative value to dens, especially during the early denning period.

Mortality Sources

Longevity of wolverines can approach 15 years in the wild (Banci 1987, J. Persson, personal communication). Mortality arises due to a variety of natural and human-related causes. Of 62 wolverine mortalities observed during telemetry studies in North America where 239 wolverines were radio-marked, 22 (35%) died from trapping or hunting, 18 (29%) starved, 11 (18%) succumbed to predation, 8 (13%) died of natural but unknown causes, and 3 (5%) were hit by vehicle or train (Krebs et al. 2004). To date, documented wolverine predators include cougars (*Puma concolor*), wolves (*Canis lupus*), and black bears (*Ursus americanus*; Copeland 1996, White et al. 2002, Persson et al. 2003, Krebs et al. 2004, Inman et al. 2007*b*). Wolverines also die in avalanches and from falls (Inman et al. 2007*b*, Copeland and Yates 2008). Intra-specific aggression (aggression by other wolverines, also referred to as conspecific mortality) can cause mortality in adults (Persson et al. 2009), and has been identified as the main source of juvenile wolverine mortality in Sweden (Persson et al. 2003). These mortalities occurred in two periods - while juveniles were at den sites where unrelated males killed the young, and during dispersal where defense of territories by same-sex resident adults was likely. Poaching has been identified as a leading cause of mortality in Scandinavia where semi-domestic reindeer are managed by indigenous people (Persson et al. 2009).

Genetics

Genetics 101

Nuclear DNA (nDNA) is present in almost every cell and affects the physical and behavioral features of an organism. Genes are specific stretches of nDNA, and variants of genes (alleles) may differ between the chromosomes inherited from each parent. A common measure of genetic variation is called "heterozygosity" which is the proportion of individuals in a population that have different alleles for a set of genes (Allendorf et al. 2022). Isolated populations can rapidly lose genetic variation due to genetic drift and inbreeding, which can have serious negative consequences for wildlife (Frankham 1995, 2009). Over long periods of time, loss of genetic variation can inhibit a population's ability to adapt to a changing environment. Over shorter periods of time, loss of genetic variation can allow recessive damaging gene variants to be expressed, resulting in reduced fitness or "inbreeding depression." Because loss of genetic variation is unavoidable, when founding new populations, it can be advantageous to purposely source individuals from areas that maximize the initial heterozygosity (Frankham 2009, IUCN/SSC 2013, Annex 5). This approach, however, must be weighed against using individuals from source populations that may be adapted to substantially different environmental conditions.

An emerging field in genetics uses genotype-environment associations (GEAs) to scan large numbers of gene sites (i.e., loci) on nDNA, looking for statistical associations between gene variants and environmental conditions such as elevation, temperature, etc. (Lasky et al. 2022). Gene sites that are highly correlated with a given environmental condition are hypothesized to potentially reflect adaptation to that environmental condition. Populations that are locally adapted to certain conditions could serve as a good source for translocations to other regions with similar conditions. However, thorough testing is usually required to validate links between genes and environmental conditions as false positive correlations are not uncommon (Lasky et al. 2022).

Mitochondrial DNA (mtDNA) occurs within cellular organelles that are responsible for energy production. It is distinct from nDNA, and does not directly control various physical or behavioral traits of an individual. Mitochondrial DNA is passed exclusively from mother to offspring and there is no paternal contribution to the offspring of mitochondrial DNA. This allows for tracing of long-standing female lineages. By examining the mtDNA of museum specimens it is possible to determine which haplotypes (i.e., combination of alleles on a single strand of mtDNA) were historically present in an area (e.g., McKelvey et al. 2014). Regions that share haplotypes are the most likely to have associated nDNA that was exposed to selective pressures in the area of interest. Therefore, haplotype matching to a source area, similar to the GEAs approach, can provide a means of attempting to incorporate local adaptation should any have occurred historically (Schwartz et al. 2007).

Wolverine Genetic Structure in North America

The genetic structure of wolverine populations is reflective of female philopatry (the tendency of females to establish near their mother's territory) and more frequent long-distance dispersals by males (Flagstad et al. 2004, Schwartz et al. 2009, Inman et al. 2012*b*, Aronsson and Persson 2018). Examination of mtDNA haplotypes shows some geographic structuring (clustering) in North America (Wilson et al. 2000, Zigouris et al. 2013, McKelvey et al. 2014). Neither Canadian nor Alaskan wolverine populations show signs of genetic drift or inbreeding (Kyle and Strobeck 2002, Cegelski et al. 2006). Because of the large and contiguous nature of these more northern populations overall, and their relatively high genetic diversity (Kyle and Strobeck 2002, Cegelski et al. 2006), wolverine populations in this part of the range are considered less vulnerable to extinction pressures associated with a low population size.

Populations in the contiguous U.S. exhibit less genetic variation than those in Canada and Alaska (Kyle and Strobeck 2001). Additionally, wolverines here display only a fraction of the haplotypes found in Canadian populations (Kyle and Strobeck 2001, Cegelski et al. 2003, 2006, Schwartz et al. 2007, McKelvey et al. 2014). The reduction of haplotypes is likely a result of extirpations (Aubry et al. 2007) and the fragmented nature of wolverine habitat in the contiguous United States (Inman et al. 2013). This is consistent with an emerging pattern of reduced genetic variation at the southern edge of species' ranges as documented for a suite of boreal forest carnivores (Schwartz et al. 2007).

Historical Wolverine Genetics in Colorado

Samples collected from wolverines in the Rocky Mountains prior to their extirpation include Haplotypes Cali1, O, A, and F (McKelvey et al. 2014). In Colorado, 4 historical skull samples were analyzed and they were identified as Haplotypes Cali1 and O. Cali1 is no longer found in any current wolverine population (Zigouris et al. 2013, McKelvey et al. 2014, Sawaya et al. 2019, Lukacs et al. 2020, Krejsa et al. 2021). Haplotype O is currently only found in the Columbia Mountains area of Canada. In 2009 a single male wolverine ("M56") dispersed to Colorado and was found to be a Haplotype A, which is the near exclusive haplotype found in the U.S. Rocky Mountains today.

Chapter 3: Suitability of Reintroduction and Conservation Issues

Prior to restoration, it is critical to consider the suitability of Colorado's contemporary landscape for wolverines from both a biological and socioeconomic viewpoint (IUCN/SSC 2013). As a first step, CPW assembled a map of wolverine habitat for the state and estimated the number of individuals that might occupy this habitat to ensure that a reintroduction could conceivably support a viable population that would provide a meaningful contribution to wolverine conservation. Next, CPW considered important biological and socioeconomic issues that could impact the success of a wolverine reintroduction or impose hardships on various entities and industries already established in the state. Of note, over 94% of modeled wolverine habitat in Colorado occurs on public land (Figure 4a), and 68% occurs in federally designated wilderness, National Park, Wilderness Study Area, or U.S. Forest Service Roadless Area (Figure 4b). This correspondence alone should dampen potential impacts to socioeconomic activity while supporting biological needs of the species.

Photo ©AB Photography/Adobe Stock

Figure 4a)

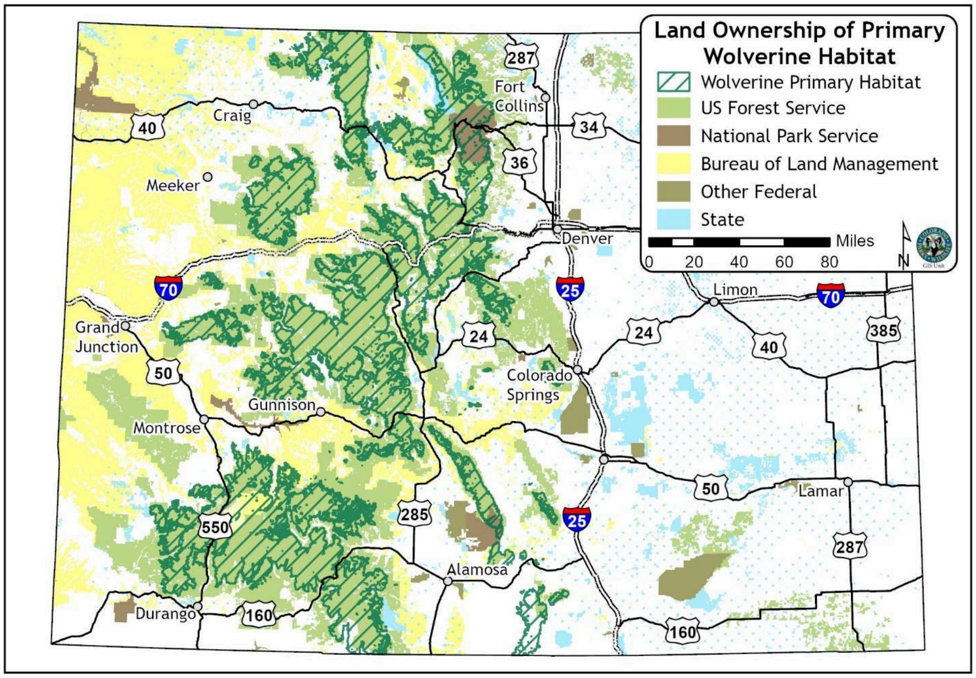


Figure 4b)

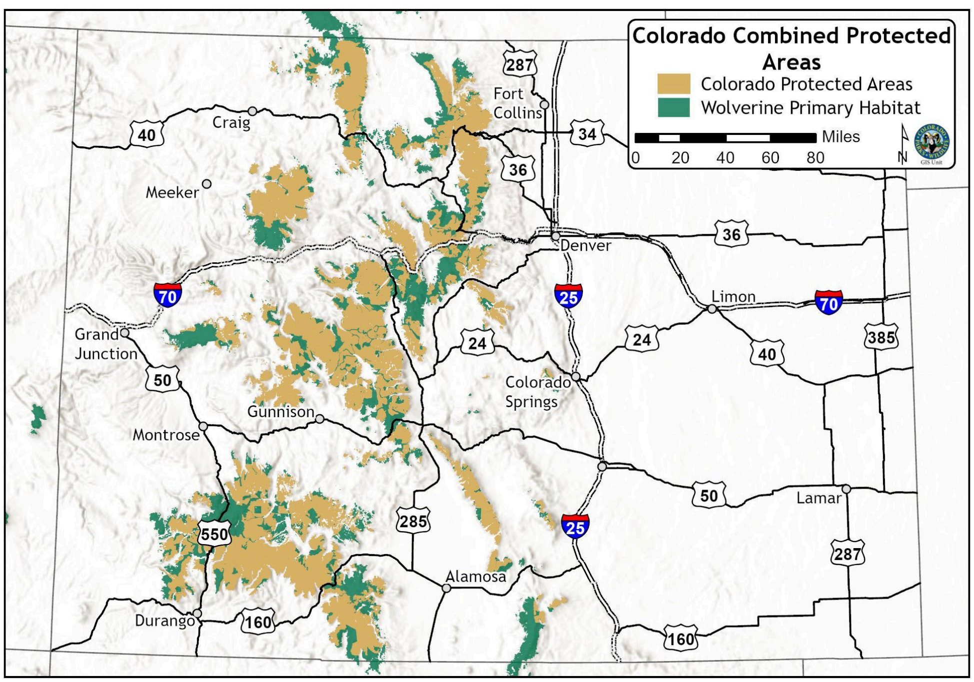


Figure 4. Modeled primary wolverine habitat (Inman et al. 2013) a) overlaid on land ownership, and b) overlaid with protected areas (i.e., federally designated wilderness, wilderness study area, National Park, or U.S. Forest Service Roadless Area). Only those protected areas that intersect primary wolverine habitat are shown, meaning that wolverine habitat underlies all protected area polygons shown in b).

Modeled Wolverine Habitat

Inman et al. (2013) modeled wolverine habitat for the western U.S. based on location data collected from individuals in the Greater Yellowstone Area (Figure 5). Their model partitions a continuous surface produced via standard resource selection function methodology (Manly et al. 2002) into 4 biologically meaningful categories: 1) “primary habitat”, which was projected to support routine use and survival of resident adults, 2) “maternal habitat”, which was that subset of primary habitat predicted to be of high enough quality to support reproductively active females, 3) “female dispersal habitat”, and 4) “male dispersal habitat.” The latter two categories represent lower quality habitat expected to support only intermittent, short term use as individuals move between larger blocks of higher quality habitat. Categorization of the continuous surface was based on cut points corresponding to observed behaviors of interest for a given category. Colorado contains over 30,000 km^2 of primary wolverine habitat, all of which occurs in the high country in the western half of the state. Much of the modeled primary habitat occurs as large, contiguous blocks, and virtually all blocks are connected by areas suitable for dispersal by both males and females (Figure 5).

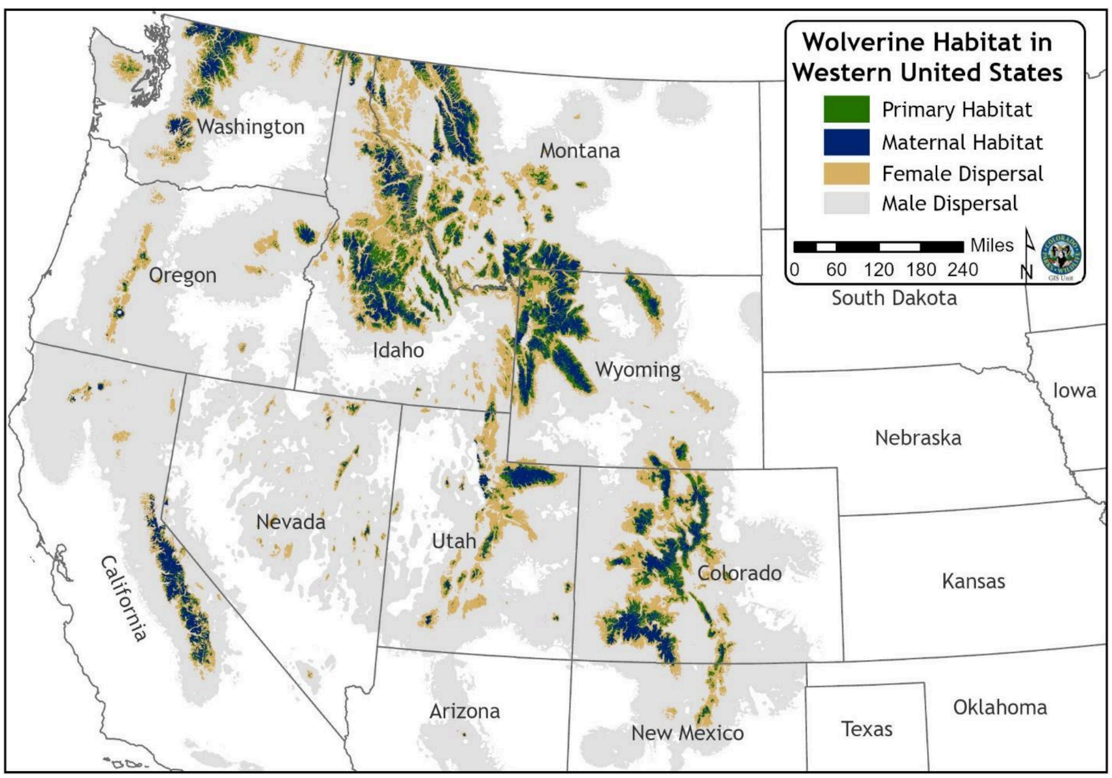


Figure 5. Modeled wolverine habitat in the western U.S. (Inman et al. 2013). Resident adults are expected to routinely use the green (Primary habitat) and blue (higher-quality Maternal habitat) areas.

Estimated Capacity in Colorado

The territory size, habitat use, and number of wolverines Colorado can support are largely unknown and will remain so until and if a population is restored and observed in the state. However, estimating Colorado's capacity to support wolverines, even though rough, is a useful exercise in order to assess the potential conservation benefit of restoration, and to provide an anchor point for modeling efforts aimed at determining the number of individuals to translocate. CPW considered several methods to estimate the number of wolverines that could be supported on the contemporary landscape of Colorado.

Inman et al. (2013) suggested a capacity based on a wolverine density estimate obtained via mark-recapture techniques in the Greater Yellowstone Ecosystem (GYE) that was then applied to mapped primary habitat in Colorado (Inman et al. 2012*b*, 2013). Patches that were deemed too small or disconnected for occupation were eliminated from the exercise (Boyce and Mcdonald 1999, Hebblewhite et al. 2011, Inman et al. 2013). This method, which included adults and subadults age 1+, yielded a mean estimate of 137 wolverines (95% CI: 108 – 390). Note that the upper CI of 390 individuals, though statistically valid, was not considered realistically possible (Inman et al. 2013).

Based on typical female territory size across wolverine range (~400 km^2) and typical sex ratios (2M:5F), the Wolverine Translocation Techniques Working Group (2013) suggested a target "stocking rate" of 7 adult wolverines per 2,000 km^2 of wolverine habitat in Colorado. The resulting density (3.5 wolverines/1,000km^2) falls near the low end of the range of observed wolverine densities at the southern edge of their distribution (3.5-5.8/1,000km^2; Copeland 1996, Lofroth and Krebs 2007, Inman et al. 2012*b*) and would indicate a capacity of 106 individuals given that Colorado is estimated to have 30,225 km^2 of primary wolverine habitat (Inman et al. 2013).

It is also plausible that female wolverines in Colorado could exhibit home range sizes more in line with those from northwest Wyoming (303 km^2; Inman et al. 2012*b*), the population closest to Colorado. A 300 km^2 grid of hexagonal cells overlaid on wolverine habitat results in approximately 80 cells having significant amounts of primary and maternal habitat. If there are 80 adult female territories and an adult male for every 2-3 adult females, this would correspond to 27-40 adult males and a total of 107-120 adults. If it is further assumed that each adult female gives birth to 1.5 young every other year, cub survival is 50% to age 1, 80% to age 2, and individuals are considered adults after age 2, that adds another 54 subadults for a total of approximately 161-184 wolverines.

Given the three rough estimation techniques above, CPW suggests that Colorado can hold up to about 100 wolverines and that more than 180 is highly improbable. A population of around 100 individuals is relatively small. However, for this species, a re-established population of this size would represent approximately 25% or more of the total estimated population in the contiguous U.S. and would therefore significantly enhance wolverine conservation in that geography. CPW notes that the primary wolverine habitat layer referenced in these estimates was produced prior to several large wildfire events in high elevation forests, and does not account for changes in human density on the landscape in the past decade. Therefore the derived estimates may represent the upper bounds of plausible numbers of wolverines that could be supported in Colorado.

Conservation Issues in Colorado

Livestock Depredation

Colorado's livestock industry underpins the local economies of many rural communities, and successful reintroduction may partially depend on society's willingness to consider and mitigate depredation where possible (IUCN/SSC 2013, Persson et al. 2015). However, there is little evidence suggesting that wolverines would create widespread or significant impacts to livestock relative to all sources of depredation. Cattle grazing has overlapped with wolverine range on public lands in Montana, Idaho, and Wyoming for decades, yet wolverine depredation on cattle has not been reported (C. Mosby, Idaho Fish and Game; N. Kluge, Montana Fish, Wildlife, & Parks; H. O'Brien, Wyoming Game & Fish; personal communication). Sheep depredation is common in Scandinavia as is wolverine predation on semi-domesticated reindeer (Landa et al. 2000, Persson et al. 2015). Most sheep depredation occurs in Norway where nearly 2.5 million sheep are free-ranging on public lands during summer. These sheep are mostly unattended, widely scattered, and directly in wolverine habitat (Landa et al. 2000). However, wolverines in North America do not appear to be a significant threat to domestic sheep. Only one incident of sheep depredation by a wolverine is known from the northern Rockies, where a wolverine killed a sheep in the Bighorn Range in northeastern Wyoming in the late 1990s (B. Oakleaf, Wyoming Game and Fish, personal communication). An additional incident occurred in Utah where a dispersing male wolverine killed 4 sheep and wounded another 14 (Utah Division of Wildlife 2022). No other instances of wolverine predation on domestic sheep have been reported in the contiguous U.S. (C. Mosby, Idaho Fish and Game; N. Kluge, Montana Fish, Wildlife, & Parks; H. O'Brien, Wyoming Game & Fish; J. Lewis, Washington Department of Fish & Wildlife; personal communication). This difference may, at least in part, be due to the types of foods that are available; there are no large rodents such as marmots in Scandinavia.

Active sheep and cattle allotments on USFS lands in Colorado overlap 7.5% and 26.5% of modeled wolverine habitat, respectively (Figure 6). An additional 2% of wolverine habitat is overlapped by grazing allotments on Bureau of Land Management or State Land Board properties. Pursuant to C.R.S. 33-2-105.9(5) (2024), prior to reintroduction the Colorado Parks and Wildlife Commission will adopt rules to allow compensation for livestock lost to wolverine depredation. Negative impacts of grazing activities on wolverines has not been documented, and changes to current use of grazing allotments are not anticipated.

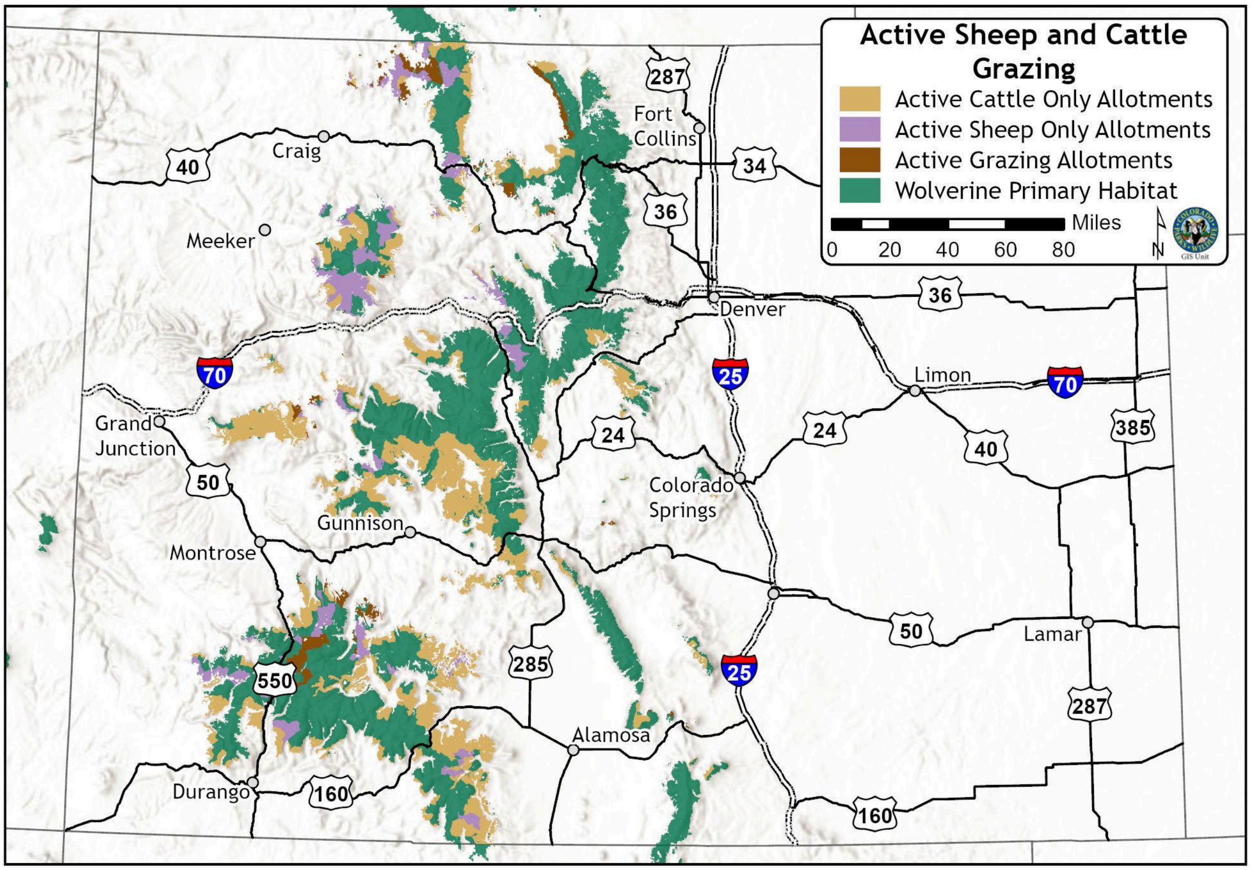


Figure 6. Overlap of grazing allotments with modeled primary wolverine habitat (Inman et al. 2013) in Colorado. Only those allotments that intersect primary wolverine habitat are shown, meaning that wolverine habitat underlies all allotment polygons shown here.

Human-caused Mortality

The extirpation of wolverines from the western U.S. (including Colorado) at the turn of the 20^{th} century occurred during a period when harvesting and killing of wildlife was unregulated. Predator species were often targeted and all means of take were allowed including bounties for killing predators and use of poison baits. These practices are thought to be the primary reason for wolverine extirpation (Aubry et al. 2007).

Wolverines began reoccupying their historic range in the contiguous U.S. during the 1930's and had made a substantial recovery by the 1960s (Newby and Wright 1955, Newby and McDougal 1964). During the 1970's, wolverines were given status as a furbearer with a limited season (Montana) or as a protected species (e.g., Colorado, Idaho, Wyoming). Most states within the historical range other than Colorado and California have had reproducing wolverines for several decades (Copeland 1996, Inman et al. 2007*a*, Anderson and Aune 2008, Rohrer et al. 2008). Intentional human-caused mortality is illegal in Colorado and unlikely to be a factor in the population viability of wolverines here.

Human Infrastructure and Roads

Humans and wolverines generally select very different habitats. This is especially the case at the southern edge of wolverine distribution where most human infrastructure occurs in warmer, drier, valley bottoms whereas wolverines are found in rugged mountainous terrain where it is cold and snowy much of the year (Inman et al. 2013, Barrueto et al. 2022). Therefore, even though Colorado has greater human densities and amounts of infrastructure than most of the wolverine's range, most of it will not affect the successful establishment of home ranges.

Once within wolverine habitat, roads and infrastructure do influence the species. Infrastructure in the form of forest roads has been shown to be negatively associated with wolverine density (Mowat et al. 2020), occurrence (Heim et al. 2017, 2019, Kortello et al. 2019), and habitat use (Schepens et al. 2023) in Southern Canada. Behaviorally, wolverines tend to avoid forest roads, and move past them quickly when they are encountered while traversing their home range (Scrafford et al. 2018). Major roads, such as the Trans- Canada Highway, may impede female movement and gene-flow (Sawaya et al. 2019).

Wolverines may be more tolerant of roads and general human infrastructure during dispersal events (Balkenhol et al. 2020, Carroll et al. 2020), and roads that apparently structure wolverine genetics are not absolute barriers to movement (Sawaya et al. 2019). Road and rail mortalities occur, but these types of mortality are rare, constituting <5% of known mortalities in North America (Krebs et al. 2004). Wolverines can also navigate road crossings successfully (Packila et al. 2007, Packila et al. 2017). Prompt removal of road-killed ungulates would likely reduce road mortalities of wolverines.

If road densities within wolverine habitat in Colorado are higher than other regions, females could require a larger home range, which could negatively affect the energetics of reproduction. However, higher road density could be buffered by the fact that two-thirds of wolverine habitat in Colorado is classified as designated wilderness, national park, wilderness study area, or U.S. Forest Service Roadless areas. This abundance of protected areas along with Colorado's existing underpasses (e.g., near Vail Pass) and overpasses (e.g., Eisenhower-Johnson Tunnel) associated with Interstate 70 can facilitate genetic exchange for a restored population. In addition, models of higher priority wolverine connectivity zones exist (Inman 2013, Carroll et al. 2020, 2021), and efforts to improve wildlife crossing infrastructure and remove roadkill that wolverines may feed upon in these areas could mitigate this potential impact (Packila et al. 2007). The potential for road mortalities may be elevated in Colorado more so than other areas within wolverine range and will be closely monitored during reintroduction efforts.

Food Availability

Despite significant settlement and land use changes over the last century in Colorado, much of the high-elevation habitat remains suitable for wolverines, and food resources here should be abundant. Colorado has large populations of elk, mule deer, and moose, many of which occupy subalpine forests (i.e., lower elevation portions of wolverine habitat) during some portion of the year. Wolverines will benefit from natural mortality of these species along with carcasses from harvested animals. Moreover, yellow-bellied marmots (*Marmota flaviventris*) are widely distributed throughout modeled wolverine habitat in Colorado (Seglund 2010); marmots are a staple food source for females rearing young in the spring (Lofroth et al. 2007, Inman and Packila 2015). Combined with occasional take of other small mammals and birds, food availability is not anticipated to be a limiting factor for reintroduced wolverines.

Effects on and by Other Wildlife

Natural densities of wolverines are so low that the species' presence is assumed to have little impact on other species (Banci 1994). Van Zyll de Jong (1975) summarized the wolverine's fundamental role in the ecosystem, maintaining that they are for the most part a seasonal scavenger at the top of the food chain. They are not obligate carnivores or efficient hunters such as lynx and wolves. Wolverines are capable of killing large ungulates including caribou (Magoun et al. 2018) and moose that become wallowed in deep snow (Haglund 1966) but these instances are rare. For example, during a 5-year wolverine study in Montana, no cases of predation on moose, deer, or elk were observed (Hash 1987). However, wolverines commonly fed upon kills of these species made by cougars (Hash 1987). Neonatal ungulates are vulnerable to wolverine predation (Gustine et al. 2006, Inman and Packila 2015), but wolverines have not been identified as a significant mortality factor for newborns that inhabit the alpine and subalpine areas of Colorado, i.e., bighorn sheep (*Ovis canadensis*), mountain goats (*Oreamnos americanus*), and moose (*Alces alces*; Guiguet 1951, Festa-Bianchet 1988, Côte et al. 1997, Scotton 1998, Cote and Festa-Bianchet 2003).

Wolverines interact frequently with Eurasian lynx (*Lynx lynx*) in Scandinavia, but these encounters largely occur at carcasses of reindeer killed by lynx (Mattisson et al. 2011*a*, *b*).

In contrast, Canada lynx in Colorado weigh about half of their Eurasian counterparts, and they feed almost exclusively on snowshoe hares and red squirrels; they rarely kill large prey or scavenge (Ivan and Shenk 2016). Therefore, interactions between the two species at kill sites is expected to be minimal. Furthermore, wolverines and Canada lynx have coexisted across boreal and montane Canada and Alaska for centuries. Direct interactions or indirect competition for small prey are not expected to be factors in the population dynamics of either species. In a recent study that examined the spatial relationship between these two, wolverine occurrence was unrelated to Canada lynx (Chow-Fraser et al. 2022).

Wolf populations likely influence wolverine populations, but not vice-versa. Wolves likely benefit wolverines via increasing the amount of carrion available due to wolf-killed carcasses (Wilmers et al. 2003, van Dijk et al. 2008, Nordli et al. 2024). Wolves do kill wolverines occasionally, at carcasses and at den sites (White et al. 2002, Krebs et al. 2004, Nordli et al. 2024). However, for the most part, wolverines and wolves are expected to spatially segregate themselves along elevational gradients. In the Canadian Rockies, wolverine distribution was not well-explained by wolf predation risk (Chow-Fraser et al. 2022). Instead, competition with coyotes, as mediated by linear features, such as roads and trails, had the strongest association with wolverine distribution (Chow-Fraser et al. 2022), and may explain the absence of wolverines in disturbed landscapes with abundant coyotes (Fisher et al. 2013, Heim et al. 2017). Coyotes are abundant in Colorado, and extensive networks of forest roads exist in portions of modeled wolverine habitat in the state. However, nearly 70% of modeled wolverine habitat is roadless, which should help minimize potential negative interactions between these species.

Brown-capped rosy finch, American pika, and southern white-tailed ptarmigan are native alpine species in Colorado that have been identified as Tier 1 Species of Greatest Conservation Need in the Colorado State Wildlife Action Plan (2025). The ranges of all three species overlap considerably with modeled wolverine habitat. Both pika and brown-capped rosy finch populations appear stable and well-distributed in Colorado (Seglund 2015, Bernier et al. 2023). Additionally, each species tends to reside in habitats (i.e., talus and cliffs) that should provide adequate protection from wolverine predation for both adults and young (Seglund 2015, Bernier et al. 2023). Wolverines are not projected to have any discernible impact on these species. Statewide occupancy of female ptarmigan and chicks has declined over the past decade (Seglund and Runge 2023). Previously, predation was identified as a primary driver of loss of both nests and chicks in Colorado, but population-level threats were identified as grazing, human recreation, climate change, and localized hunting pressure (Seglund et al. 2018). Wolverines occasionally consume birds and eggs during summer. It seems unlikely that a restored wolverine population could impose a population-level threat to ptarmigan, but perhaps their presence could exacerbate effects of other drivers.

Climate Change

Climate change is predicted to have a broadly negative impact on wolverines due to their affinity for cold, snowy environments (U.S. Fish and Wildlife Service 2023*a*). Although Colorado is at the southern edge of wolverine range, the state's high elevations are expected to somewhat buffer impacts of climate change. Much of the climate-modeling work with respect to wolverines has gravitated toward the idea that persistent spring snow (e.g., average snow depth on May 15 or similar) defines critical den habitat (Copeland et al. 2010). Other recent work indicates that persistent spring snow is not a requirement for denning to occur (Webb et al. 2016, Jokinen et al. 2018, Persson et al. 2023). Regardless, we review climate change literature below with an eye toward the notion that snow is an important component of wolverine habitat and at the least, spring snow may be a general indicator of cold snowy conditions where wolverines thrive.
By mid-late century, Colorado is expected to have larger pockets of cold temperatures (U.S. Fish and Wildlife Service 2023*c*), more days with snow cover (Peacock 2011), as much or more spring snow cover (dependent on model selection, McKelvey et al. 2011), fewer consecutive-year snow droughts (Marshall et al. 2019), and smaller changes in maximum snow-water equivalent compared to historical levels (Lute et al. 2022), than central Idaho, western Montana, and the Cascades of Washington. Barsugli et al. (2020) specifically modeled mid-century loss of springtime snowpack at elevations conducive to wolverine denning in Rocky Mountain National Park, Colorado and Glacier National Park, Montana. They projected losses of spring snow in both locales, but concluded that Rocky Mountain National Park was more resilient to loss of spring snow. However, a more recent and extensive analysis of spring-snow relative to wolverine denning habitat, carried forward to the end of century, indicated that percentage losses of spring snow in Colorado would be on par with other parts of the range (U.S. Fish and Wildlife Service 2023*b*). Still, in that same study, the absolute area of spring snow available at critical elevation bands was nearly as large as Montana, Idaho, and Washington combined (U.S. Fish and Wildlife Service 2023*b*). Additionally, rugged terrain, in conjunction with high elevation, is expected to provide an abundance of patches and microsites that will likely remain suitable for wolverine caching and dens for many decades (Decker and Fink 2014, Magoun et al. 2017, Barsugli et al. 2020). Thus, while climate change is likely to degrade wolverine habitat across its range, Colorado is expected to be as resilient, if not more so, than many other parts of current wolverine range. A re-established wolverine population in such a "refugium" would serve to improve resiliency, redundancy, and representation of the metapopulation in the contiguous U.S.

Winter Recreation

Winter recreation contributes significantly to Colorado's tourism economy. Related activities include developed ski areas, backcountry skiing and snowmobiling, and heliskiing. These activities have the potential to influence wolverine behavior and demography, and they occur within wolverine habitat on federal lands. This overlap invokes concerns regarding land use restrictions should a restoration occur and was a major factor in Colorado Senate Bill 24-171 requiring designation as a 10(j) non-essential experimental population prior to reintroduction.

Wolverines could be influenced negatively if they 1) fail to gain energetic resources because they avoid recreation, 2) if they sustain significantly increased energetic expenditure because of increased movement rates due to avoiding recreation, or 3) if disturbance at reproductive den sites leads to increased den-shifting and juvenile mortality. Presumably the cumulative effect of these factors could influence survival, productivity, or both. However, only a single study has been conducted to specifically assess biological impacts of winter recreation on wolverines; other studies have incorporated winter recreation variables among other potential factors that could influence wolverine distribution, density, or habitat use.

Heinemeyer et al. (2019) collected GPS data on both wolverines and recreationists occupying the same landscape to determine if dispersed winter recreation activity influenced wolverine habitat use. Wolverines selected against areas of both motorized and non-motorized winter recreation with off-road recreation eliciting a stronger response than road-based recreation. Wolverines also demonstrated a functional response (i.e., changes in selection as availability of resources changed) to recreational activity wherein the level of avoidance increased with increasing recreational intensity. Approximately 14% of female habitat and 11% of male habitat was estimated as being degraded by winter recreation in their study area (Heinemeyer et al. 2019). Heinemeyer et al. (2019) also remarked that over the long term, climate change could cause wolverines and dispersed winter recreation to converge more often in the same areas as cold, snowy environments shrink in extent.

In southern British Columbia, Krebs et al. (2007) used VHF telemetry locations to assess the influence of food, predation risk, and human disturbance on wolverine habitat use at multiple scales. Male wolverines appeared to be driven primarily by food-related habitat variables, but helicopter skiing was a negative influence during winter at an intermediate scale (i.e., within ~2–12 km of a wolverine). Habitat use by female wolverines was "complex," and driven by food and predation risk as well as human disturbance. Helicopter skiing at the landscape scale (i.e., within ~ 5–37 km of a wolverine) and backcountry skiing at the intermediate-scale (2-12 km) were negatively associated with female use in the most supported model. Areas used for snowmobiling did not appear to influence wolverine habitat selection in this study. However, Kortello et al. (2019) found that density of forest roads had a negative effect on wolverine distribution, especially for females, and postulated the effect was due to high snowmobile use on such roads. Barrueto et al. (2020) did not find that recreation negatively impacted wolverine distribution or density, but they did note that detection of wolverines declined with an increasing number of recreationists. The negative association between size of user groups and wolverine detection was observed during summer as well as winter.

Wolverines have also been purported to be sensitive to human presence at reproductive den sites (Copeland 1996, Hausleitner et al. 2025). However, recent data derived from intensive GPS collar locations indicate that movements among den sites occur regularly; females used an average of 9 and up to 28 den sites per reproductive season and began moving from natal dens on average by March 30 (Aronsson et al. 2023). All of the assumed abandonments (Hausleitner et al. 2025) occurred in mid-to-late April or later when den shifts are common.

While the above studies indicate that wolverines may respond to certain types and levels of recreation by altering their behavior to evade such activities, questions remain on the scale at which recreation is discerned by wolverines (Krebs et al. 2007), causes of observed negative correlations (Kortello et al. 2019), effects on statistical precision induced by non-independence of rapid telemetry fix rates (Heinemeyer et al. 2019), and disentangling den shifting due to human disturbance vs. a natural cadence (Hausleitner et al. 2025). Presumably, a threshold exists where behavioral alteration leads to demographic consequences such as reduced survival or reproduction, but no study to date has been able to assess the potential for impacts on these key vital rates. Of note, each study observed wolverines in recreated landscapes, and wolverines used areas where winter recreation also occurred. Heinemeyer et al. (2019) specifically point out that many individuals retained multi-year home ranges in highly recreated areas, including successful denning attempts, indicating that "…at some scale wolverines tolerate winter recreation." Thus, wolverines in these studies responded to areas with winter recreation by using those areas less than their availability on the landscape would suggest, but those areas were not completely avoided.

Developed ski areas overlap <1% of modeled wolverine habitat in Colorado (Figure 7). The level of human activity in these areas is likely high enough to preclude much wolverine use, but their overall footprint relative to total wolverine habitat is inconsequential.

The potential impacts of dispersed winter recreation are likely mitigated to some degree by the fact that 41% of Colorado's wolverine habitat is classified as Wilderness, Wilderness Study Area, or National Park. These areas are well-dispersed throughout wolverine habitat in Colorado; they preclude motorized winter recreation and limit non-motorized recreation (Figure 4b). An additional 27% is classified as U.S. Forest Service Roadless Area; these roadless areas are generally less accessible but can allow motorized winter travel (Figure 4b). The remoteness and limited accessibility of all of these areas may also reduce non-motorized use during summer and winter. Olson et al. (2017, see Appendix C) modeled habitat selection by backcountry skiers and snowmobilers in Colorado. From their continuous surface depicting probability of use by backcountry winter recreationists, CPW clipped out the most suitable 80% and found that this area overlapped 19.7% of primary wolverine habitat (Figure 7). Thus, there will be some overlap, and dispersed winter recreation could influence a reintroduced wolverine population. However, it should be noted that the Olson et al. (2017, Appendix C) model does not depict actual distribution of dispersed winter recreation, but rather the areas where conditions are most favorable for such activities. Therefore, if wolverines are affected by recreation, those effects will likely be concentrated within no more than 20% of wolverine habitat.

If wolverine vital rates are negatively influenced by human recreational activity, the potential for an impact in Colorado may be greater than in most areas of the species distribution. However, even if recreation fills all predicted recreation habitat in the state, and recreational impacts affect behavior dramatically enough to negatively impact vital rates or force avoidance of recreated areas (i.e., 20%, or 6,000 km^2, of mapped wolverine habitat is completely unavailable to wolverines), there is still enough remaining mapped habitat (24,000 km^2) to support >80 individuals (assuming 3.5 wolverines/1000 km^2), which is a substantial contribution to the conservation of this species. As such, it appears that Colorado has enough areas with limited human access that are well-distributed across the state such that CPW believes that wolverines can likely find suitable places to reside and reproduce even if recreation is a negative impact.

CPW notes that summer recreational use is increasing in Colorado, both at winter recreation sites and beyond, including the popular activity of summiting 14,000’ peaks. Much of this activity is focused on trails. Effects of this type of summer recreation on wolverine ecology are largely unknown, but could degrade habitat to some degree in highly used areas.

Overlap of primary wolverine habitat with ski resorts and areas of dispersed winter recreation may trigger ESA consultation where these activities require permits on federal land. However, tools such as a blanket Biological Opinion covering common activities, or a provision in the rule governing the establishment of a 10(j) experimental non-essential population could streamline the consultation process and ease concerns regarding ongoing land uses. CPW-led and supported research will provide additional needed understanding of the potential for coexistence between recreation and wolverines in Colorado.

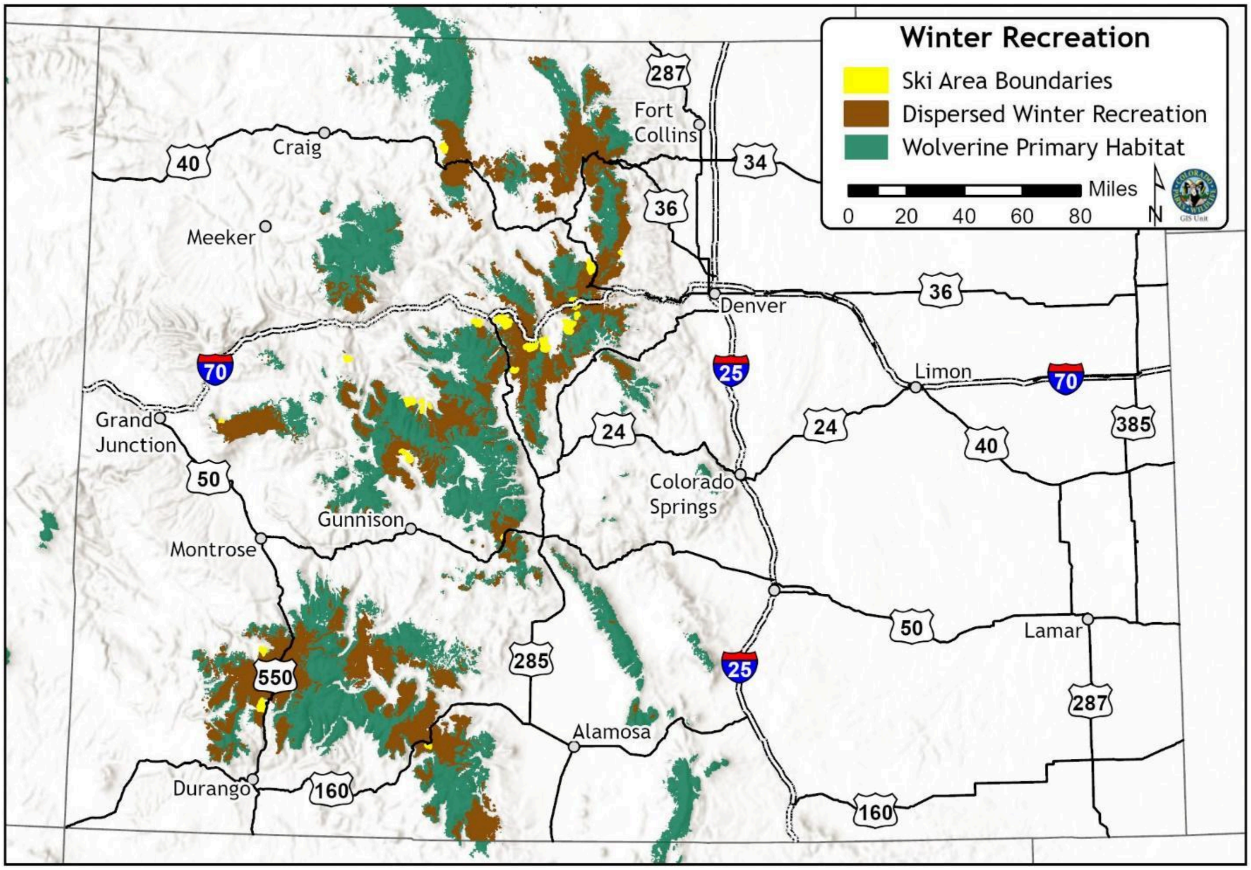


Figure 7. Overlap of permitted, developed ski areas and areas of potential dispersed winter recreation habitat (Olson et al. 2017) with modeled primary wolverine habitat (Inman et al. 2013) in Colorado. Brown polygons capture the most suitable 80% of predicted dispersed winter recreation "habitat". Note that these polygons indicate where dispersed winter recreation is likely to occur based on terrain and access but they do not necessarily indicate actual use. Only those winter recreation polygons that intersect wolverine habitat are shown, meaning that primary wolverine habitat underlies all yellow and brown polygons shown here.

Chapter 4: Reintroduction Implementation

Conservation translocation programs involve uncertainty. Several considerations should be addressed to minimize uncertainties and maximize the likelihood of a program's success (IUCN/SSC 2013). First, an assessment of the feasibility and design of a translocation should include some type of modeling to evaluate probability of success under various realistic translocation approaches (IUCN/SSC 2013, Annex 5). Second, the identification of suitable source populations is critical, paying special attention to ecological similarity of potential sources to the release area, genetic considerations, and demographic impacts to the source population(s). Finally, the timing, location, and strategy of releasing individual animals should be matched as closely as possible to the life history, ecology, and behavior of the species (IUCN 2013, Annex 7). These considerations are addressed in the sections below.

Population Viability Analysis and Number to Release

The Wolverine Translocation Techniques Working Group (2013) suggested that a reasonable goal for a wolverine reintroduction would be to release enough animals to occupy 20% of the available habitat. Equivalently, then, a reintroduction goal might be to translocate 20% of the estimated capacity in Colorado - roughly 25 individuals based on the midpoint of the expected capacity (see above) or about 35 individuals based on the high end of the range.

In addition to establishing a target number of individuals to introduce, the Wolverine Translocation Techniques Working Group (2013) developed a female stage-structured population model that was used to evaluate population viability and estimate the expected growth of a reintroduced population. Their simulation setup broadly matches the scenario of reintroducing 25-35 individuals over multiple years (i.e., their scenario modeled 10 female wolverines translocated in each of two years, which implies 5 males per year as well in order to reflect sex ratios typically observed). They assumed vital rate point estimates as observed from a population of wolverines in Sweden (Persson et al. 2006, 2009), and incorporated both demographic and environmental stochasticity. Each simulation projection started with 10 females in year one, and 10 more females during year two. This population was allowed to grow based on the survival and reproductive rates observed in Sweden, but with variability around each parameter such that there were both good (e.g., high survival with reproduction) and bad years (e.g., low survival with low or no reproduction), of varying magnitude, for each rate. Therefore, each projection of the starting population into the future was a different, but realistic, simulation of what could happen given the vital rate inputs. The median and upper 95% confidence bounds (i.e., excluding the most optimistic 2.5% of projections) of *n*=1,000 projections under this model indicates that full occupation, i.e., 50 adult females (along with 25 adult males and 25-50 subadults) in Colorado could be achieved in approximately 1-2 decades (Figure 8). The lower 95% confidence bounds of the population size (i.e., ignoring the poorest 2.5% of projections) was >0 for all years, indicating little chance of population extirpation over 5 decades, even under the most dire combinations of stochastic events (Figure 8).

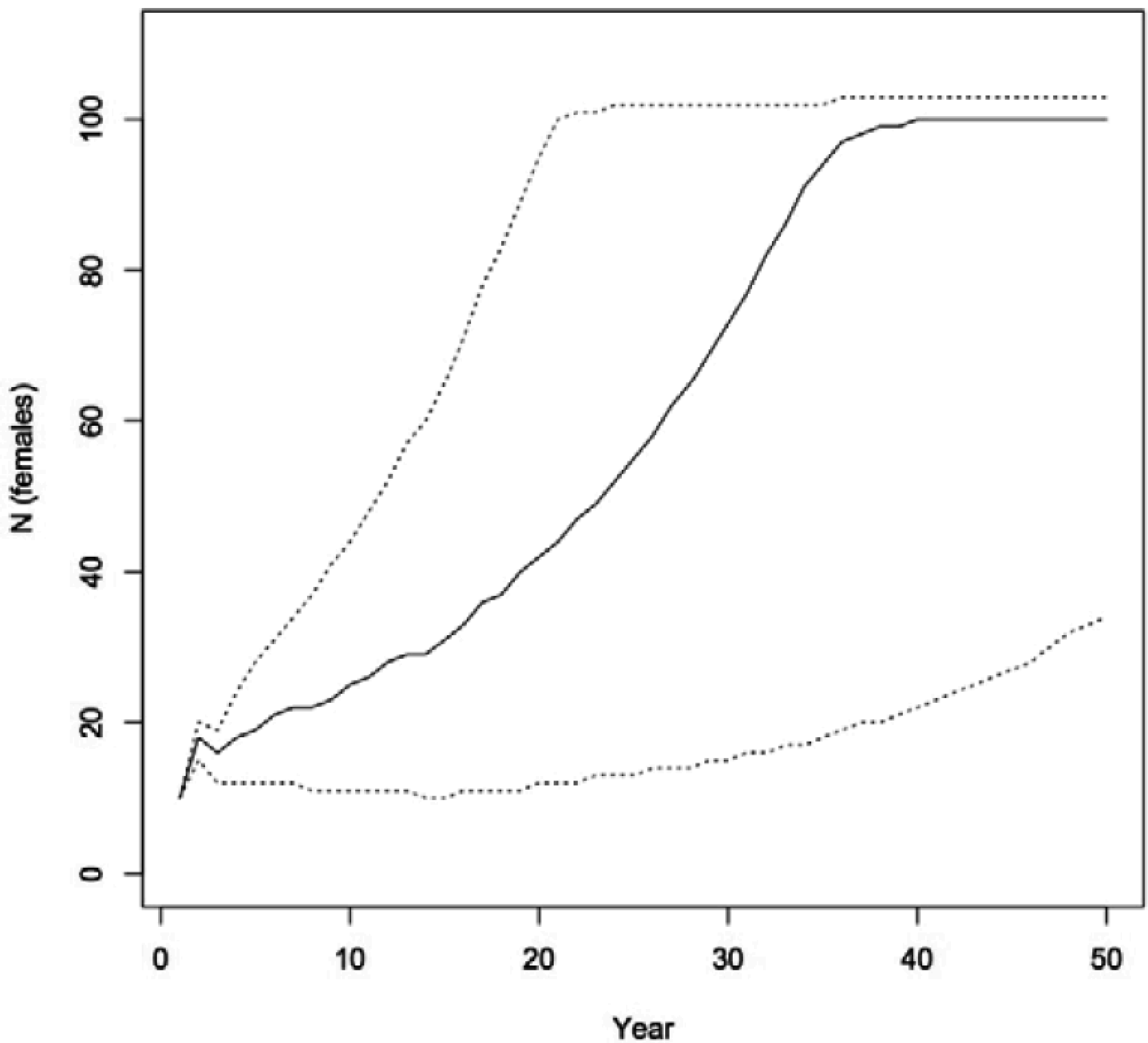


Figure 8. Median (solid line) and 95% confidence bounds (dotted lines) of *n*=1,000 population growth simulations starting from 10 female wolverines reintroduced in year 1, and 10 additional female wolverines reintroduced in year 2. Growth was capped at 100 females. Adapted from the Wolverine Translocation Techniques Working Group (2013).

The results from this population viability analysis indicate that release of approximately 20 females over 2 years (implying 10 males to replicate natural sex ratios) would be adequate to a) achieve a robust population, near expected capacity, within two decades, under the most likely and best-case scenarios, and b) keep the new population from going extinct under the worst-case scenarios. While this analysis suggests 30 wolverines would be sufficient, individuals departing from Colorado (<100% site fidelity) and the likelihood of slightly lower survival rates of translocated individuals were not included in this analysis. CPW will aim to translocate approximately 45 wolverines over 3+ years. The additional individuals would provide a buffer against the possibility that annual survival may be lower for translocated individuals, some number of translocated individuals may not stay in Colorado, or initial vital rates observed in Colorado may not match those that the population viability analysis was based on (i.e., a well-established population in Sweden). The extra year(s) would enable adaptation and improvement of techniques with each subsequent release, dampen effects of environmental variability such as a particularly harsh winter, and minimize logistical barriers and stress to source populations by spreading out translocations over time (IUCN/SSC 2013). This assumes that the total number of animals and desired sex ratios would be available and achievable from source sites (see below).

Female F121 and her 2 young at about 4 months of age in the Gravelly Range of SW Montana. Photo ©M. Packila.

Ranking Source Populations

Logistical considerations will weigh heavily in deciding where individuals are sourced for the restoration effort, as will local knowledge of sustainable levels of removal. Furthermore, CPW believes that successful restoration can be achieved using individuals sourced under a number of different scenarios. That said, ranking potential source populations according to biological factors can be a useful exercise to determine where individuals should be obtained under an ideal setting in order to maximize the probability of success. At least 6 biological factors are important to consider when prioritizing source populations for a wolverine conservation translocation: 1) familiarity of wolverines with the general habitat available in Colorado (e.g., steep montane environment, subalpine forest), 2) familiarity of wolverines with potential mortality sources they will encounter in Colorado, 3) familiarity of wolverines with hunting strategies necessary for small prey that could be important in Colorado, 4) local adaptation as identified via Genotype-Environment Associations (GEAs) or matching mtDNA haplotypes that occurred historically in Colorado, which may reflect adaptions to local conditions, 5) genetic diversity (i.e., heterozygosity) of the founding, reintroduced population, and 6) sustainability of removals from the source area (IUCN/SSC 2013, Wolverine Translocation Techniques Working Group 2013). Collectively, factors 1–3 constitute “ecological similarity” and may have immediate, short-term impacts on translocated individuals. Factors 4–5 are “genetic considerations”, which may influence success over the long-term, but are also important because the translocation will necessarily begin with a small founding population, which warrants careful consideration of genetic information (IUCN/SSC 2013, Wolverine Translocation Techniques Working Group 2013, McKelvey et al. 2014). To prioritize potential source areas, CPW ranked each based on the ecological similarity and genetic considerations listed above. The following subsections outline the data and logic used in producing a prioritized list of potential source areas based solely on these biological considerations, except for sustainability of removals from the source. Those decisions will be left to jurisdictions charged with managing source populations. Individuals selected for translocation would come from a set of animals that would normally be harvested. Live capture and translocation of these animals will not result in any impact to the source population that would not occur in the absence of CPW’s reintroduction effort.

Ecological Similarity

Source populations that share similar habitat types to the translocation destination, or are geographically closer, may have certain adaptations or learned behaviors that improve fidelity, survival, or reproduction of translocated individuals. Wolverine range in North America includes steep montane environments such as those available in Colorado, as well as relatively flat tundra or taiga systems (Copeland and Whitman 2003). To hedge for the possibility that individuals already living in montane habitats would be better able to exploit them (e.g., they may already be accustomed to using cooler temperatures of north facing slopes for den and cache sites), potential source areas were first ranked based on this factor. Sources that broadly included montane environments were ranked 1; those with little topographic relief were ranked 5; areas of mixed or intermediate topographic relief were ranked 3 (Table 2).

Awareness of potential sources of mortality could influence wolverine survival immediately post-translocation. Many of the potential sources of predation in Colorado are similar to those found throughout the species range (Copeland and Whitman 2003). Black bears, grizzly bears (*Ursus arctos*) and wolves occur across the majority of wolverine range in North America and would likely be familiar to most wolverines. Mountain lions, however, are common in Colorado but absent across much of the current wolverine range. Mountain lion distribution (Pierce and Bleich 2003) overlaps with wolverine range in only two provinces and four states - British Columbia and western Alberta, Washington, Idaho, Montana, and Wyoming. Ranking of potential source areas for this factor followed a similar system as for habitat, with jurisdictions that included mountain lions ranked 1 (Table 2).

Familiarity with potential food sources in Colorado could also influence survival and reproduction after translocation. Wolverines are efficient scavengers, and locating carrion should be a familiar and similar process regardless of the source location. However, hunting small prey during summer may involve learned behavior that would benefit from familiarity. Yellow-bellied marmots in particular may be an important source of food for reproductive female wolverines translocated to Colorado (Krebs et al. 2007, Lofroth et al. 2007, Inman and Packila 2015). This species occurs in Wyoming, Montana, Idaho, Washington, and southern British Columbia and Alberta (Armitage 2003). Hoary marmots (*Marmota caligata*) are similar to yellow-bellied marmots, and their range includes western Alberta, and large swaths of British Columbia, Yukon, and Alaska (Armitage 2003). Arctic ground squirrels are a common food item in some locales (Magoun 1987) and may elicit a similar learned hunting strategy to marmots. This species is distributed across Yukon along with much of Alaska, Northwest Territories, and Nunavut (Yensen and Sherman 2003). Distributions of these prey species, prioritizing marmots, served as the basis for scoring the portion of ecological similarity due to prey availability, following the same system as above (Table 2).

The final ecological similarity rank for each potential source area reflected the mean of the habitat, mortality, and prey availability ranks (Table 2). Areas that are geographically closest to Colorado scored highest in ecological similarity. These areas were Wyoming, Montana, Idaho, Washington, and southern and central British Columbia and Alberta (Table 2). Northern British Columbia and Alberta along with Yukon and Alaska scored intermediately due to the lack of mountain lions in those areas. The central Canadian Provinces scored lowest due to a lack of both mountain lions and marmots.

	Ecological Similarity				
Potential Source Area	Factor 1: Habitat	Factor 2: Mortality	Factor 3: Prey	Mean Rank	**Ecological Similarity Rank**
Alberta, Central	1	1	1	1.00	**1**
Alberta, Southern	1	1	1	1.00	**1**
British Columbia, Central	1	1	1	1.00	**1**
British Columbia, Southern	1	1	1	1.00	**1**
Idaho	1	1	1	1.00	**1**
Montana, Crazy-Belts	1	1	1	1.00	**1**
Montana, Gallatin	1	1	1	1.00	**1**
Montana, Rocky Mountain Front	1	1	1	1.00	**1**
Washington	1	1	1	1.00	**1**
Wyoming	1	1	1	1.00	**1**
British Columbia, Northern	1	3	1	1.67	**2**
Alaska, Kenai	1	5	1	2.33	**3**
Alaska, North	1	5	1	2.33	**3**
Alaska, Northwest	1	5	1	2.33	**3**
Alaska, Southeast	1	5	1	2.33	**3**
Alaska, Southern	1	5	1	2.33	**3**
Yukon	1	5	1	2.33	**3**
Alaska, Central	3	5	1	3.00	**4**
Alberta, Northern	5	5	1	3.67	**5**
Northwest Territories	5	5	3	4.33	**6**
Nunavut	5	5	3	4.33	**6**
Manitoba	5	5	5	5.00	**7**
Ontario	5	5	5	5.00	**7**
Saskatchewan	5	5	5	5.00	**7**

Table 2 Ecological similarity rankings for potential wolverine source areas based on comparable habitat type, mortality sources, and availability of small prey between the source area and Colorado.

Genetic Considerations

Local Adaptation

Stacy (2024) recently used Genotype-Environment Associations (GEAs) in an attempt to identify evidence for local adaptation in wolverine populations in portions of western North America. This work identified a set of candidate genes that may be linked to adaptive traits (e.g., heat tolerance, thermal regulation, or fur growth) and climatic gradients (e.g., elevation, temperature, or precipitation). These links are preliminary and not experimentally validated, but this adaptive variation was still recommended when considering source populations for reintroduction to Colorado (Stacy 2024). Wolverine populations assumed to be experiencing environmental conditions most similar to Colorado would include Wyoming, Montana, and Idaho (Stacy 2025), and potentially others, although samples from the Canadian Rockies (i.e., Alberta and British Columbia) appear to have been limited to 5 samples from the far-northern portion of each province.

Genetic methods used to identify local adaptations rely on the assumption that the individuals whose DNA was sampled, and their ancestors, lived in a similar set of environmental conditions. Wolverines in the lower 48 states were largely extirpated by the mid-1900s and recolonized the southern Rocky Mountains from Canada in recent decades (McKelvey et al. 2014). This large-scale turnover at the southern extent of the range breaks the link between gene evolution and environment, challenging use of approaches to find evidence of local adaptation at the southern portion of the wolverine range. More fundamentally, if adaptation to local environments is important, this turnover suggests the assemblages of genes from southern mountainous regions most environmentally similar to Colorado no longer exist on the landscape today, i.e., the traits currently found and analyzed by Stacy (2024) were traits derived over the long term from further north in Canada.

With respect to mitochondrial DNA, haplotype O is the only extant haplotype that is known to have once occurred in the Southern Rockies. Currently, this haplotype is only known from Southern British Columbia (Sawaya et al., in prep). In theory, individuals possessing Haplotype O may be distantly related to those that once inhabited Colorado and may therefore exhibit some form of local adaptation to the region. However, as noted by McKelvey et al. (2014) historical haplotypes that existed in many parts of the Rocky Mountains do not match contemporary haplotypes. Furthermore, the majority of North American wolverine haplotypes are closely related to just a few common ones (e.g., 1 base pair separates Haplotype O from Haplotype A, which is the most widely distributed throughout North America). This indicates that populations radiated relatively recently from each other (McKelvey et al. 2014). Thus, in contrast to other species where long-term stability in haplotypes may be observed for a given area, it is unlikely that any given group of wolverines has accumulated specialized adaptations to a particular region, including the Southern Rockies. As a result, CPW will largely forgo attempts to match haplotypes when identifying appropriate source populations.

Heterozygosity

Because wolverine restoration will necessarily begin with a limited number of individuals, genetic drift (i.e., changes in allele frequency directed by random chance alone) is expected to outweigh selection and local adaptation as the most powerful force shaping evolution of the newly established population. Ensuring robust heterozygosity of the translocated individuals is the main tool available to help minimize the probability of inbreeding depression that can be exacerbated by drift. Heterozygosity, then, is the primary factor (as opposed to local adaptation as indexed by haplotypes or GEAs) that CPW considered for ranking source populations with respect to genetics. To this end, CPW assembled data on expected heterozygosity (H_e, Kyle and Strobeck 2002, Cegelski et al. 2006, Krejsa et al. 2021). H_e was ranked from 1 (highest heterozygosity) to 5 based subjectively on major cut-points in the data. Heterozygosity was highest in areas that scored at the bottom of the scale of ecological similarity (Table 4). The top six areas occurred in the central and northern Canadian Provinces. The next tier of diversity ranks included British Columbia and Alberta. The lower half of the rankings included Wyoming, Montana, Idaho, and Alaska.

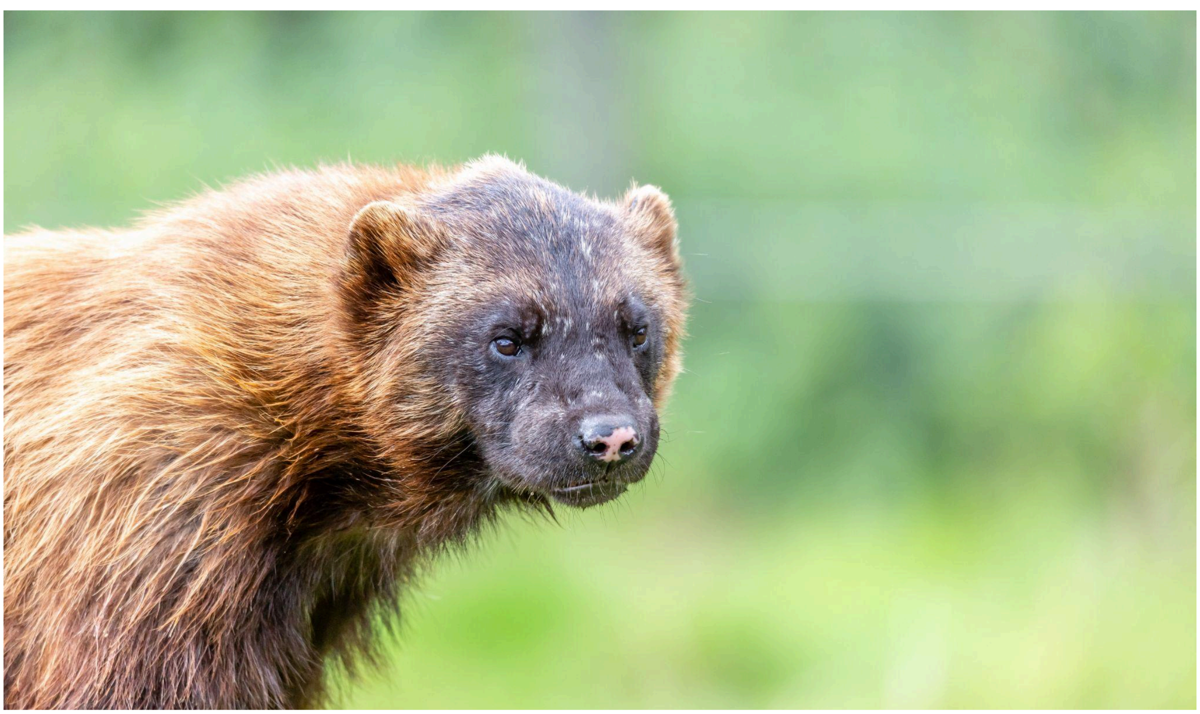


Photo ©SR7 Photo/Adobe Stock

Potential Source Area	Genetic Diversity	
	Expected Heterozygosity	Heterozygosity Rank
Manitoba	0.67	**1**
Northwest Territories	0.65	**1**
Yukon	0.65	**1**
Nunavut	0.64	**1**
Saskatchewan	0.64	**1**
Ontario	0.63	**1**
Alberta, Central	0.61	**2**
Alberta, Northern	0.61	**2**
Alberta, Southern	0.61	**2**
British Columbia, Central	0.61	**2**
British Columbia, Northern	0.61	**2**
British Columbia, Southern	0.61	**2**
Montana, Rocky Mountain Front	0.57	**3**
Alaska, Central	0.56	**3**
Wyoming	0.56	**3**
Alaska, Northwest	0.54	**3**
Alaska, Southeast	0.54	**3**
Alaska, Southern	0.54	**3**
Alaska, North	0.49	**4**
Montana, Crazy-Belts	0.49	**4**
Alaska, Kenai	0.45	**4**
Idaho	0.42	**4**
Montana, Gallatin	0.42	**4**
Washington	.	**5**

Table 3. Potential source areas ranked by expected heterozygosity values. Values were taken from Kyle and Strobeck (2002), Cegelski et al. (2006), and Kresja et al. (2021).

Summary of Priority Source Areas

Final source area ranks were calculated by averaging the final ecological similarity rank from Table 2 and the heterozygosity rank from Table 3 such that each component accounted for 50% of the final rank. Southern and central British Columbia and Alberta were the top four source populations (each with a Final Rank = 1), followed by a group that included northern British Columbia, Yukon, Wyoming, and a portion of Montana (Table 4). The ability of wolverine populations in these areas to sustain offtake and support restoration in Colorado will require consultation with wildlife agencies in these locales. CPW does not anticipate that any single source area will provide all individuals for the reintroduction, even within a given year. As described earlier, these rankings represent an ideal prioritization of potential sources for wolverine restoration based solely on biological considerations. Other factors will be important, and CPW believes that success of the restoration is not necessarily dependent on sourcing animals from certain locations.

Potential Source Area	Final Source Area Ranking (Biological)			
	Ecological Similarity Rank	Heterozygosity Rank	Mean Rank	Final Rank
Alberta, Central	1	2	1.5	**1**
Alberta, Southern	1	2	1.5	**1**
British Columbia, Central	1	2	1.5	**1**
British Columbia, Southern	1	2	1.5	**1**
British Columbia, Northern	2	2	2.0	**2**
Montana, Rocky Mountain Front	1	3	2.0	**2**
Wyoming	1	3	2.0	**2**
Yukon	3	1	2.0	**2**
Idaho	1	4	2.5	**3**
Montana, Crazy-Belts	1	4	2.5	**3**
Montana, Gallatin	1	4	2.5	**3**
Alaska, Northwest	3	3	3.0	**4**
Alaska, Southeast	3	3	3.0	**4**
Alaska, Southern	3	3	3.0	**4**
Alberta, Northern	4	2	3.0	**4**
Northwest Territories	5	1	3.0	**4**
Nunavut	5	1	3.0	**4**
Washington	1	5	3.0	**4**
Alaska, Central	4	3	3.5	**5**
Alaska, Kenai	3	4	3.5	**5**
Alaska, North	3	4	3.5	**5**
Manitoba	6	1	3.5	**5**
Ontario	6	1	3.5	**5**
Saskatchewan	6	1	3.5	**5**

Table 4. Final biological rankings of potential source areas for reintroducing wolverines into Colorado based on ecological similarity (50% of weight) and genetic diversity (50% of weight).

Mechanics of Obtaining Wolverines from Source Populations

The reintroduction effort will target translocating 15 wolverines per winter for 3+ winters for a total of 45 translocated individuals. The number of translocations in any year, or overall, will depend on capture success, continued participation by cooperators, and the degree to which relocated animals remain in Colorado and survive. Therefore, annual translocations could vary, and reintroductions could be extended for additional years depending on the outcome of initial efforts.

Capture Timing and Methods

The Wolverine Translocation Techniques Working Group (2013) concluded that early winter captures at source sites are the most practical for translocating wolverines, as well as the most likely to lead to translocation success. As such, captures will occur during November through January, which largely coincides with annual trapping seasons for those source sites that allow trapping. This timing also allows pregnant females to be captured, translocated, and released prior to giving birth. Capture of males could continue through April. Ideally, capture programs will be coordinated by wildlife agencies in cooperation with experienced local trappers. Additionally, CPW staff will be available to assist or lead capture efforts if needed. Cooperating agencies or trappers will be compensated for their efforts as necessary.

Capture methods will likely vary among source sites depending on logistics, available personnel, and resources. These could include legal restraining traps commonly used by fur harvesters, or stationary or portable box traps (Copeland 1996, Lofroth et al. 2008). Wolverines can also be darted from helicopter in open habitat (Persson et al. 2006, Fahlman et al. 2008, Arnemo and Evans 2017). Captured individuals will be anesthetized to facilitate a general health assessment and/or transfer to a transport container. Several groups (e.g., Fahlman et al. 2008, Wolverine Translocation Techniques Working Group 2013, Arnemo and Evans 2017) have provided recommended immobilization doses, safe handling protocols, and normal wolverine vital rates along with indicators, causes, and treatments of potential immobilization problems. During the general health assessment, sex, age, weight, and overall health will be determined and any individual that is of excessive age or poor health will be rejected for translocation. Criteria for rejection include excessive tooth wear, multiple missing teeth, emaciation, poor pelage condition, large parasite loads, disease, or obvious physical impairments.

CPW will likely contract with individuals capturing wolverines and specify sex and age of desired wolverines. In general, sexually mature females are preferred over subadult females because they will more quickly contribute to the breeding population upon arrival in Colorado. Sexual maturity in females is indicated by teats >10mm in length (Magoun 1985). Adult males captured at the same site as translocated adult females are preferred.

A female wolverine in a log box trap used to capture wolverines for research. This type of trap could be used at source areas for initial captures and also in CO to replace radio collars. ©R.Inman

Transportation of Wolverines to Colorado

Once an individual has satisfied the general health inspection and translocation criteria, and all requirements necessary for transport (including Colorado import requirements) have been fulfilled, it can be placed in a suitable transport crate and taken to the transport site. Animals will have a veterinary approved transportation plan followed throughout the process. All reasonable efforts will be made to minimize stress and the time between capture and delivery to the transport site.

Viable options for transporting captured individuals from the transport site to Colorado include but are not limited to commercial shipping companies, airlines, volunteer shipping organizations, and CPW vehicles. Translocated individuals will be provided appropriate food, water, and dry bedding, as necessary. Immediately upon arrival in Colorado, individuals will be taken to the CPW Frisco Creek Wildlife Rehabilitation Center (hereafter "Frisco Creek").

Care of Captive Wolverines in Colorado.

The holding facilities available at Frisco Creek have individual pens within a compound that can accommodate the number of animals anticipated for reintroduction (Wolverine Translocation Techniques Working Group 2013). These pens were constructed for the Canada lynx reintroduction, but were engineered to accommodate wolverines as well. Each pen will include a nest box for security and protection from elements, along with items for enrichment and exercise. Additionally, while at the facility, wolverines will be fed items that are likely to be their main food sources in Colorado, including elk, moose, deer, mountain goat, bighorn sheep, and marmots if available.

Personnel at the Frisco Creek Center will be responsible for monitoring captive wolverines for stress and health problems, coordinating collection and stockpiling game carcasses for feeding to captive wolverines, and fulfilling all other animal care requirements. A CPW veterinarian will be on call while wolverines are in the holding facility if an emergency arises. Human contact at the pens (visual, auditory and olfactory) will be minimized to reduce habituation of the wolverines to human presence.

After arrival at Frisco Creek, wolverines will be immobilized by CPW veterinary staff to complete a variety of tasks prior to releasing each individual. Qualified CPW personnel will:

1) Conduct a physical exam of each individual. Health issues will be addressed as deemed appropriate by CPW veterinary staff.
2) Estimate the age of each individual.
3) Collect morphometric measurements from each individual.
4) Determine the pregnancy status and stage as feasible.
5) Collect biological samples for health and genetic evaluation, and archival purposes.
6) Apply GPS/VHF telemetry device(s) as appropriate for determining survival, location, and movements.
7) Apply a microchip for unique animal identification.
8) Collect photos for unique animal identification and physical documentation.

Mechanics of Releasing Wolverines into Colorado

Release Zones, Release Units, and Distribution of Individuals

Modeled wolverine habitat was overlaid with a grid of 300-km^2 hexagons as a means to visualize potential female home ranges across Colorado. This grid was divided into three roughly equal-sized Release Zones (Figure 9). The Northern Zone is the mountainous region north of Interstate 70. The Central Zone is south of I-70 and north of Highway 50. The Southern Zone encompasses the San Juan Range of southwest Colorado, south of Highway 50. About 30% of primary habitat in the state is contained in the Northern Zone, and about 35% in each of the Central and Southern Zones.

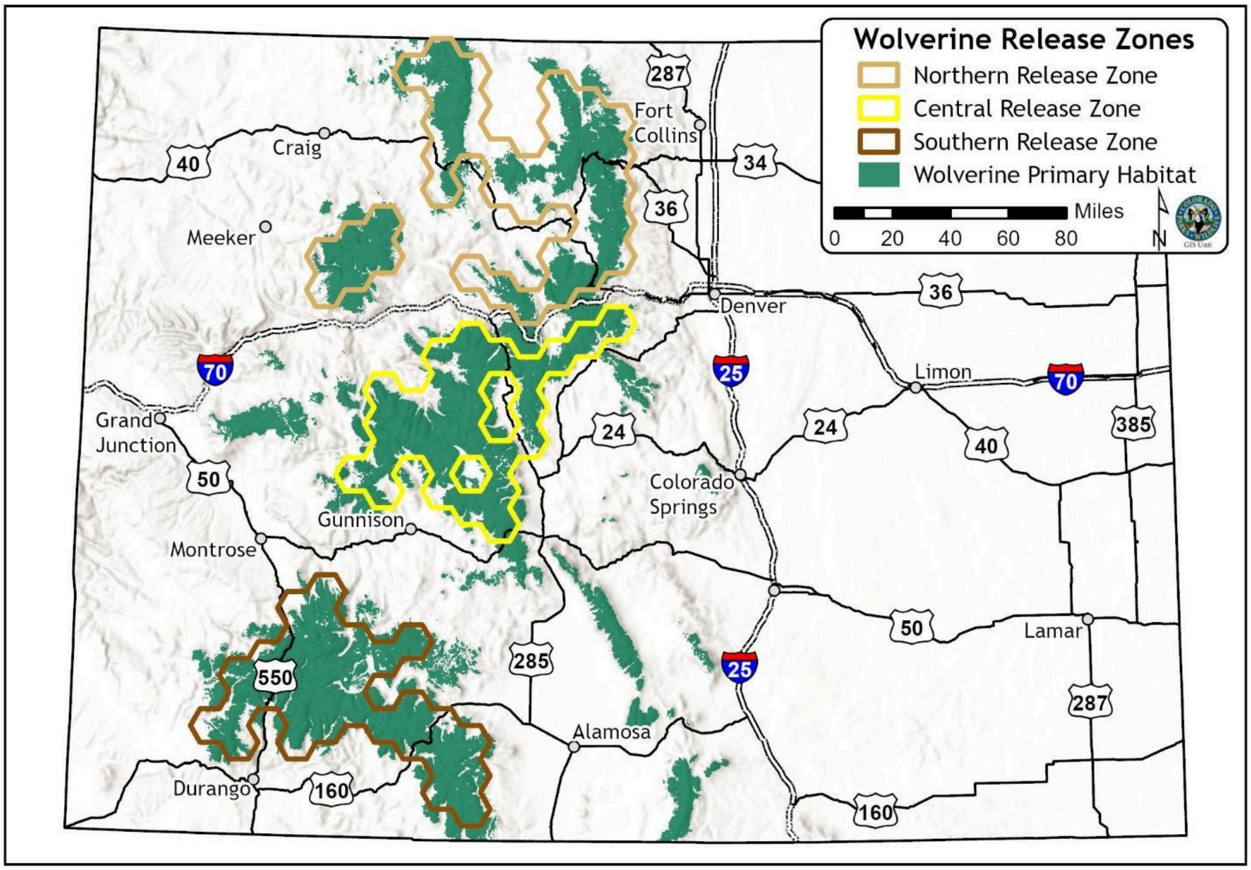


Figure 9. Release Zones overlaid on predicted wolverine habitat in Colorado (Inman et al. 2013). The three zones are approximately equal groupings of female home range sized (300-km^2) hexagons.

Each Release Zone has been further subdivided into 900-km^2 Release Units. Thus, Release Units are three times the size of anticipated adult female territories and encompass 3 adjacent 300-km^2 hexagons (Figures 10 - 12). Release Units were delineated based on the pattern of primary and maternal habitat within them along with major geographic boundaries such as valley bottoms and roads. They can be considered an initial, crude assessment of how adult female territories might align if the areas were to become saturated. The intent is to provide spatial context within each Release Zone so that animals can be released in a way that distributes them reasonably well, ***if*** they display fidelity to release sites or particular areas.

There is no expectation that wolverines will adhere to hexagon boundaries, and they may not remain in the unit where they are released. However, it is possible that some may show fidelity to the release site, and if they do, the release units may aid decisions on where subsequent releases should occur. Each Release Unit is large enough to accommodate at least one female, even if territory size is significantly larger in Colorado than anticipated, but small enough that a male can cover multiple release units that might collectively include 2–3 females. The units are also large enough that female offspring should be able to establish a territory adjacent to their mother, as is their habit.

During the first year of the translocations, CPW will focus on releasing wolverines into the Central Release Zone. Beginning the translocation in the Central Release Zone should help promote fidelity to Colorado by releasing individuals into the most interior blocks of habitat. It also promotes flexibility in the event that individuals disperse out of the Release Zone; large blocks of habitat to the North and South provide other opportunities for released individuals to settle into primary habitat. Ideally, releases in years 2 and 3 of the Establishment Phase would proceed in similar fashion in the Southern Release Zone, then the Northern Release Zone. However, some, or even many, translocated wolverines will move away from their initial Release Unit into other units or zones. Measures to promote site fidelity will be in place, but releases subsequent to the initial year will likely require flexibility and adaptation depending on where initially released individuals settle, which individuals survive, sex ratios available for release, etc.

The Central Release Zone includes 10,343 km^2 of primary habitat associated with 9 Release Units (Figure 10). The Central Zone is a more contiguous block of habitat than the Northern Zone and is largely comprised of the Sawatch Range, Elk Mountains, and West Elk Mountains. All Release Units contain some or a significant amount of designated Wilderness. These Release Units also contain higher proportions of primary habitat compared to the Northern Release Zone.

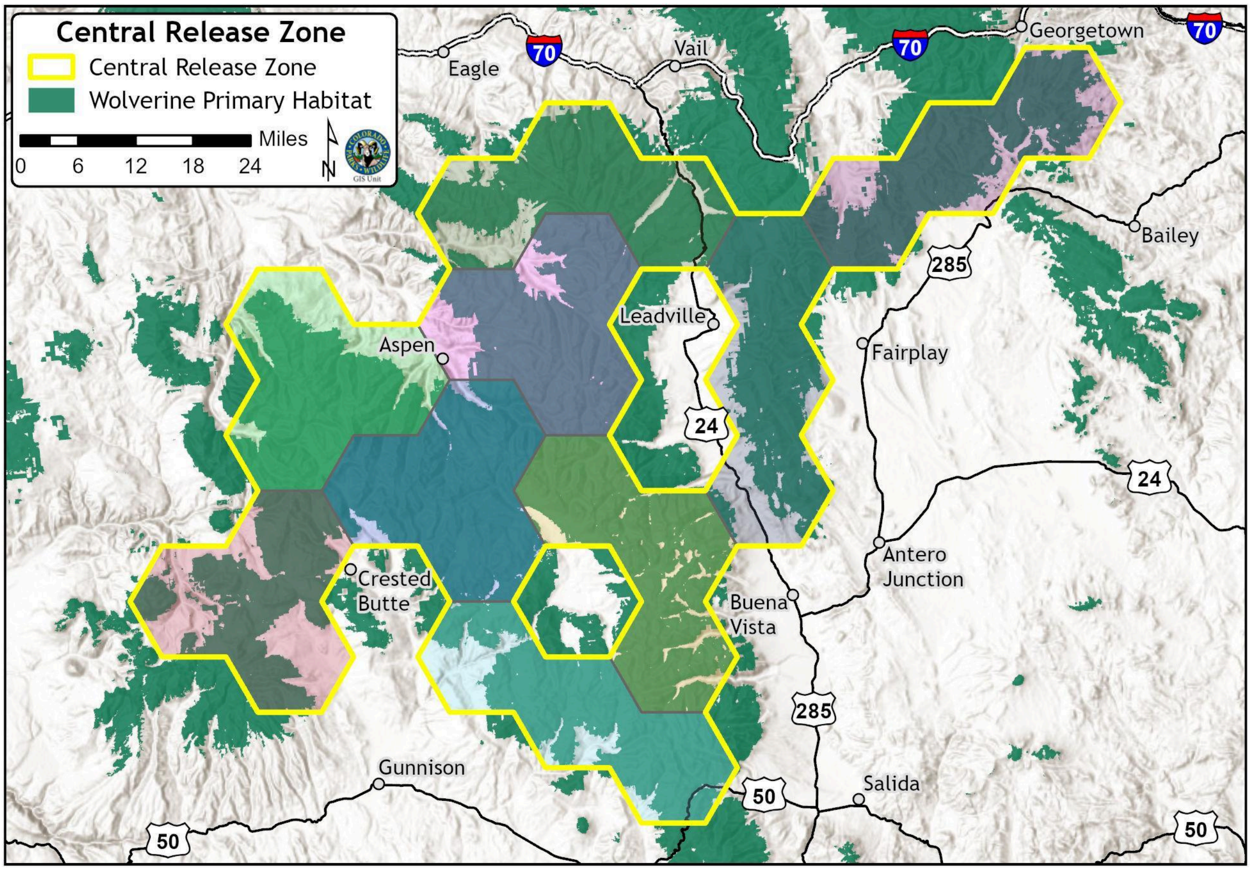


Figure 10. The Central Release Zone and 9 associated Release Units (groups of 3 hexagons that are adjacent and share the same color) occur in the central portion of Colorado, south of Interstate 70 and north of Highway 50.

The Southern Release Zone includes 9,625 km^2 of primary habitat associated with 10 Release Units (Figure 11). The Southern Zone is the most contiguous block of habitat in the state, and all Release Units have some or a significant amount of designated Wilderness. Most Release Units have high proportions of primary habitat.

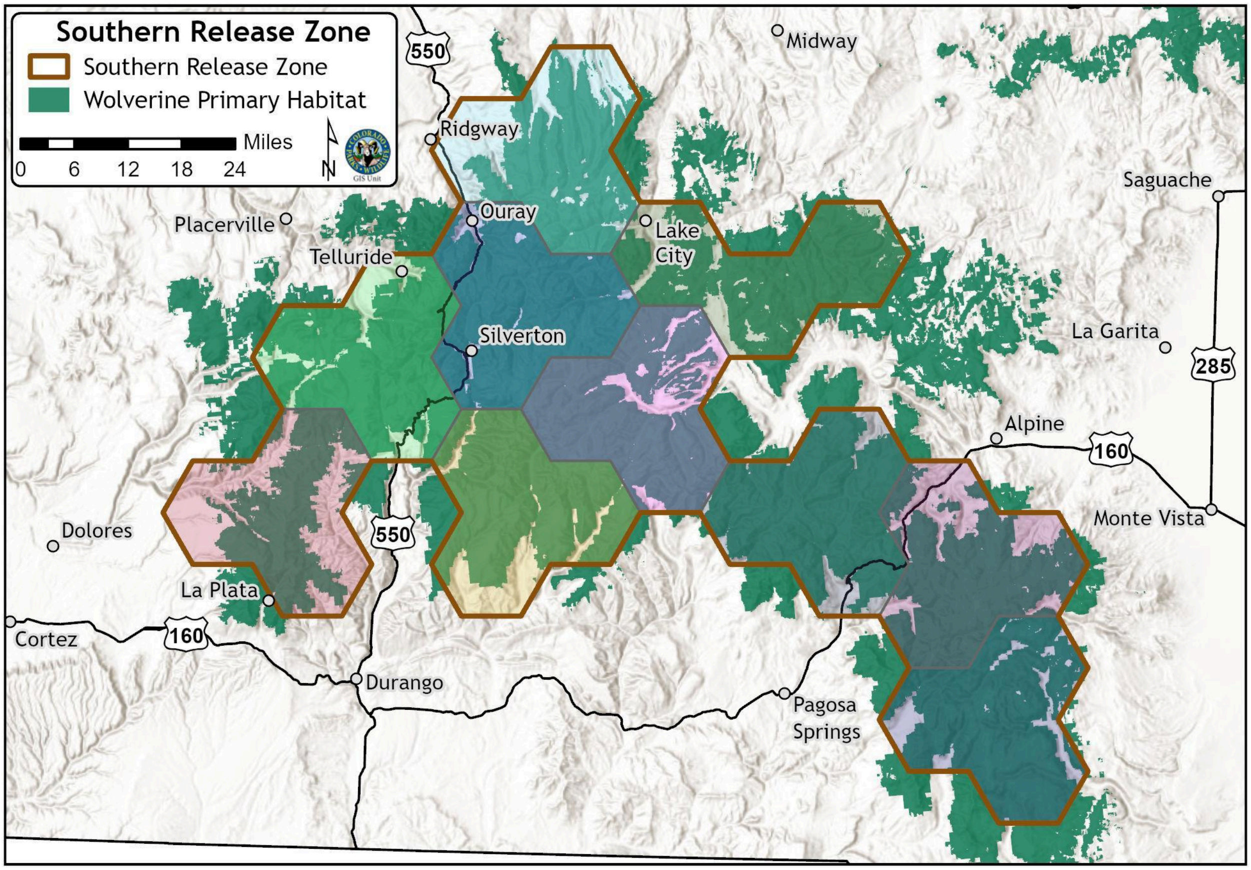


Figure 11. The Southern Release Zone and 10 associated Release Units (groups of 3 hexagons that are adjacent and share the same color) occur in the southwestern portion of Colorado in the San Juan Range.

The Northern Release Zone includes 8,475 km^2 of primary habitat associated with 13 Release Units (Figure 12). There are three major blocks of habitat that are somewhat disjunct: the Front Range, including Rocky Mountain National Park; the Park Range; and the Flattops. Virtually all Release Units contain significant areas of designated Wilderness or National Park. The percentage of each Unit that is primary habitat is lower in the Northern Zone than in the Central or Southern Zones, suggesting that fewer female territories may be realized in this Zone compared to the others.

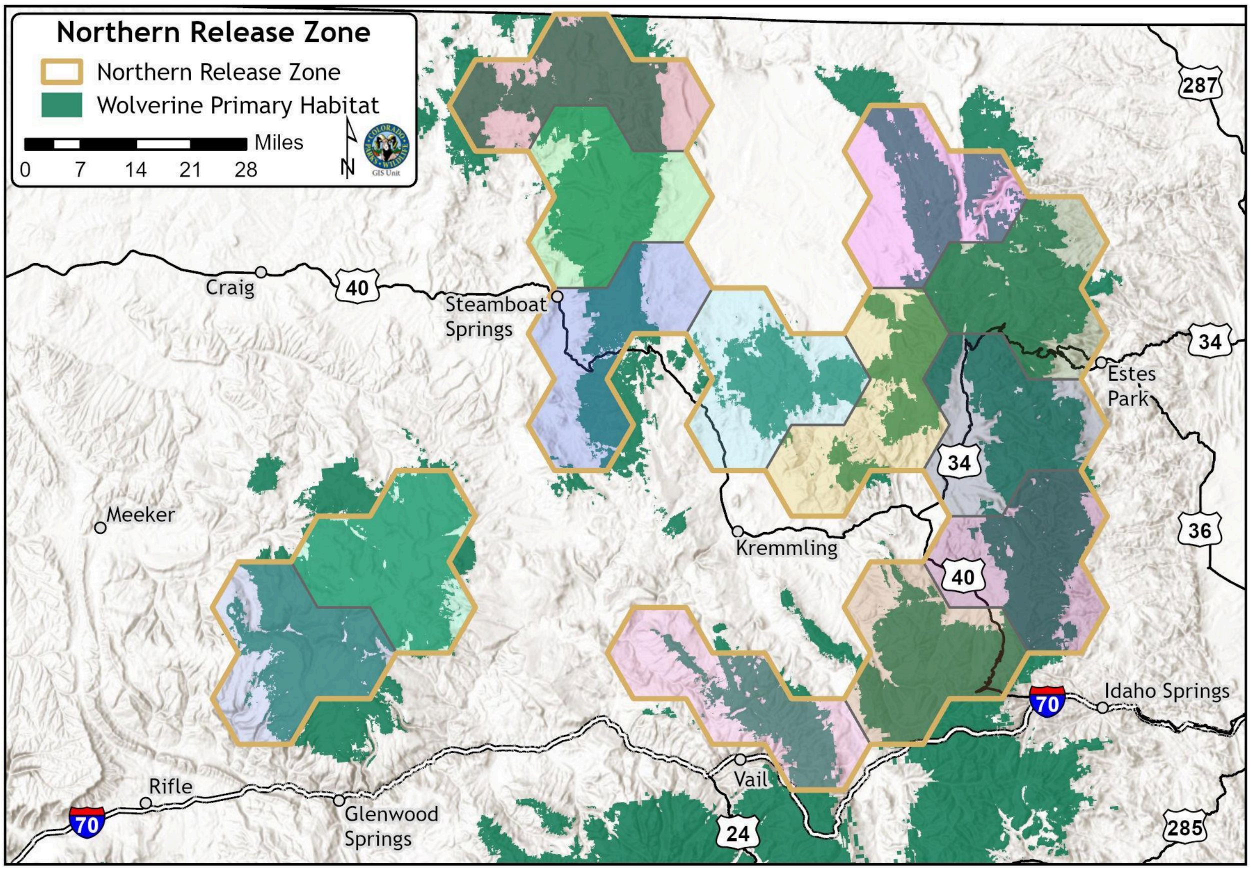


Figure 12. The Northern Release Zone and 13 associated Release Units (groups of 3 hexagons that are adjacent and share the same color) occur in the northwestern portion of Colorado, north of Interstate 70.

Release Methods

Moehrenschlager and Lloyd (2016) stated, “decisions regarding the release of animals are numerous and can make or break a reintroduction program.”

The releases of individual animals, and the compatibility of the species’ biology with the circumstances accompanying these releases, are a critical point affecting success or failure. The individuals either stay in the reintroduction area or do not, survive or do not, and recruit young into the population or not. These specific results govern the outcome. Given the significance of this element of the effort, CPW considered wolverine biology in depth to try and ensure adherence to the release area and a successful population trajectory moving forward.

The only known translocation of wolverines occurred in Finland where 6 females and 10 males were moved to a new area over a 20-year period (Pohja-Mykrä and Kurki 2008). During this fairly informal effort, the wolverines were removed from a reindeer husbandry area and were not monitored with telemetry; success appears to have been limited (Pohja-Mykrä and Kurki 2008, and see Figs. 1 and 2 in Lansink et al. 2020). Therefore, adequate and optimal release techniques for wolverines remain undefined.

The Wolverine Translocation Techniques Working Group (2013) developed guidelines and potential strategies for reintroducing wolverines, and those recommendations are generally followed here. One recommendation made by the WTTWG (2013) and that has been emphasized by other wildlife reintroduction specialists (Jachowski et al. 2016), is an approach that facilitates learning and adaptation during the effort. This is the approach CPW will take, initially attempting release techniques that are more difficult to execute, but if effective, could significantly increase success. If the initial attempts are not deemed to have improved the potential for success, CPW will fall back to a logistically simpler approach that should still be adequate given examples of other species' translocations. The goal will be to attempt and develop release strategies over the course of the project that maximize site fidelity, survival, and recruitment of young.

Numerous factors play into a wolverine release strategy and can influence site fidelity, survival, and recruitment. These include:

- capture period at the source sites
- pregnancy status at time of capture
- ability to capture the desired sexes and ages
- value of potential litters as a driver of site fidelity
- value of potential litters for population growth rate

- value of potential litters for genetic heterogeneity
- influence of female body condition on recruitment
- energetic sources that fuel lactation and successful recruitment in the wild
- availability (or lack thereof) of those foods in the release area at the time of release
- potential for mortality caused by conspecifics (other wolverines)
- role of adult males in juvenile survival
- habitat characteristics of an optimal release site
- logistics of releasing individuals at an optimal site
- human safety during releases (e.g., avalanche)
- animal welfare
- the need and logistical ability to provision food after release
- complexity of permitting related to release procedures, e.g., designated wilderness
- requirements of captive facilities, and
- costs and potential failure points.

CPW carefully considered these factors along with the recommendations of the WTTWG (2013) and more recent data on wolverine biology to deliberate several potential release strategies. Given the lack of previous wolverine-specific attempts and outcomes that can be used to identify a best approach, no option is clearly “best,” and there is a wide range of potential outcomes under any scenario.

In summary, during the first year of translocations, CPW will prioritize bringing at least 10 and up to 15 females along with as many as 5 adult males captured at locations where a translocated adult female was captured. This approach is gauged to have the greatest potential for site fidelity, survival, recruitment, and long-term population trajectory. Biological and logistical considerations related to this first-year approach are discussed below.

Timing of Capture & Pregnancy Status

For wolverines, the timing of capture in northern areas where significant populations exist begins in early winter (November). This is due to the timing of trapping seasons along with the accompanying local knowledge, skills, and willingness to capture wolverines. The presence of snow cover by that time also allows relatively efficient travel to and from capture sites, and, importantly, bears are generally in hibernation by this time and will interfere less frequently with baited capture sites. The capture season ends by February based on the initiation of the wolverine birthing period. Thus the capture season is best focused during November, December, and January.

Wolverines, like bears, are delayed implanters (Rausch and Pearson 1973). They breed during summer, the fertilized blastocyst remains dormant in the uterus for a period of months, and it finally implants in the uterine wall and begins development (nidation) during late December to early February (Inman et al. 2012a). About 90% of adult female wolverines become pregnant each year (Rausch and Pearson 1973, Banci and Harestad 1988). This means that most of the adult female wolverines captured for translocation purposes will be in or just prior to the early stages of active pregnancy at the time of capture.

A Logistics-Oriented Approach to Releases

The simplest way to translocate wolverines would be to assume pregnancies will not be retained during the winter of capture and transport, move females and males, let them establish and breed during the first summer after release, and rely on reproduction 1-year after translocation. This method would allow for logistically uncomplicated releases and less permitting. Individuals can simply be released from crates in suitable and easily accessible habitat where they can sort themselves into territories and breed the following season. This approach has proven adequate in reintroductions of several species.

While this approach is appealing for its relative ease and simplicity, and could be adequate, it may not be optimal. Site fidelity could be lower than possible with other approaches (see below). Releases mid-winter into a new and unfamiliar area could make obtaining sufficient food a challenge for survival. A lack of established caches and low food availability at the time of release could further reduce site fidelity, result in more movement, increase encounters with roads, and increase mortality. Any or all of these outcomes would serve to inhibit population growth and extend the time required to achieve success.

A Reproductive Focus Approach to Releases

The fact that most adult females will be pregnant when captured presents an opportunity to improve the success of the reintroduction effort. Pregnancies, and efforts to help maintain those pregnancies through to successful births and recruitment during the first year of translocations, could positively influence three factors that are key to overall restoration success.

First, site fidelity may be improved. Site fidelity is a concern for many species translocations, but could be a particularly difficult problem to overcome with wolverines. Even though they are relatively small animals, wolverines demonstrate frequent, persistent, and long-distance movement (Vangen et al. 1998, Moriarty et al. 2009, Inman et al. 2012b, Packila et al. 2017). The degree to which wolverines will move widely or even “home” back toward the location where they were captured is unknown, but the capability to move long distances in a short period of time is clearly evident. If translocated wolverines maintain pregnancies and successfully birth young in Colorado, that could positively influence site fidelity by providing females an incentive to remain where they are released. This has been demonstrated with other carnivores. Black bears have been translocated many times and frequently "home" back to their capture location. In an experiment to test whether homing by bears could be reduced, Eastridge and Clark (2001) moved pregnant females to a new area and found that pre- or post-parturient female bears moved less (average net distance of 7 vs. 63 km) and survived far better (0.88 vs. 0.20 annual survival rate) than females soft-released without cubs. The reduced movements and increased survival were likely the result of females being limited in their movements by the capabilities of young cubs and being instinctively driven to care for the young more than moving back toward their previous location. Because most adult female wolverines translocated to Colorado will be pregnant, making efforts to ensure that they successfully birth and recruit litters during their initial year in Colorado *could* aid in overall site fidelity and survival.

Second, population growth rate could be improved. If pregnancies are maintained and litters successfully recruited during the translocation process, that would provide a significant amplification to the initial population size and growth - each translocated individual could result in several individuals on the landscape. Successfully bringing the pregnancies of captured females to term in Colorado could therefore significantly increase the founding population size, which would benefit population growth rate and provide a buffer against mortalities that could impede the growth of this naturally small population.

Third, the genetics of litters born during the year of translocation could significantly improve the diversity of the founding population. Offspring bring with them the genes of fathers that may not be physically translocated. If 15 females are translocated and give birth in Colorado, their offspring would have genes from up to 15 males. Over 3 years, that could, at a maximum, provide the genetics of 45 males. On the other hand, if breeding is limited to 5 males translocated each year for 3 years, they would provide a maximum genetic contribution of 15 males. While these maximum potential contributions are not likely achievable, the relative level of contribution could be greater under the Reproductive Focus.

While it is possible that the reintroduction could be successful without any litter production during the initial year of translocations, there are clear and significant benefits *if* the litters of pregnant females can be successfully recruited into the population in Colorado. These benefits include the potential to overcome important and anticipated obstacles such as site fidelity, small population size, stochastic events, and limited genetic diversity. Given these potential benefits, during the first year CPW will pursue a focus on reproduction during the year of translocation and will do so within a "learn and adapt" framework.

A Learn and Adapt Framework

The learn and adapt framework will consist of groups of females that 1) give birth in the wild, 2) give birth in captivity, or 3) do not have litters.

After being conditioned at Frisco Creek, approximately half of the females that are pregnant will be released ~February 1 (about two weeks before giving birth) at a den-like structure provisioned with a carcass ("Wild Births"); additional food resources will be provisioned to these individuals as necessary through the time of marmot emergence.

The other half of the pregnant females will be held in captivity where it is assured that they can be well-nourished in an attempt to successfully birth litters in captivity ("Captive Births"); these family groups will be released by ~June 1 when marmots have emerged near alpine timberline and the young are capable of travelling with the female. Provisioning of this group after release is not expected to be needed.

Some, or maybe many, females will either not be pregnant or will not retain litters until they can be released. These females will be released into suitable habitat after acclimatization once the lack of potential for a litter is determined. Attempts to provision these females will occur until marmot emergence near alpine timberline.

Limited male translocation has been used successfully in reintroduction efforts (Jachowski et al. 2016). If retention of pregnancies and recruitment does occur during the year of translocation, about half of the offspring will be male and can provide much of the male portion of the population in Colorado. Because Colorado-born males can be the breeding male portion of the population, and due to the potential for infanticide by males that are unrelated to litters (Persson et al. 2003), during year one, CPW will forgo translocating the first 5 males captured, and instead will attempt to limit translocated males to those adult males captured at the same location as a translocated adult female. Capture of both adults at the same site is likely to be indicative of overlapping territories and a mated pair where the male is related to the offspring. Where this occurs, infanticide is less likely and paternal presence could potentially improve survival of the offspring (Copeland et al. 2017). If retention of pregnancies during the translocation year does not occur at a high enough rate, the ability of males from Colorado-born litters to become the male portion of the population will be limited and problematic. Inclusion of some same-site captured males will provide for some male portion of the new population. If year-one efforts are not successful in retention of pregnancies and male recruitment, additional males (not necessarily captured at the same sites as females) will be translocated to Colorado in subsequent years.

After year one of translocations, CPW will assess the release methods relative to site fidelity and recruitment. Those techniques that appear to be more effective will continue to be utilized. If none of the techniques lead to immediate recruitment of young, or only limited site fidelity, CPW may pivot to the Logistics Focus release strategy, or some variant thereof, to reduce complexity and effort while achieving similar results.

Techniques to Facilitate Successful Recruitment during Initial Translocations

An optimal release technique that attempts to provide wolverines with the best opportunity to reproduce and successfully recruit young during their initial year of translocation would:

- reduce stress during capture, transport, and release,
- acclimate individuals to higher elevations for at least 3-4 weeks,
- ensure a plentiful food supply until marmot emergence, approximately 1 June,
- ”train” individuals regarding foods and mortality sources during captivity,
- match release time with natural food availability and the capabilities of offspring,
- minimize the potential for conspecific mortality, and,
- release animals in remote areas with minimal human activity.

Notes on why these factors may be important and how they can be managed are below.

Reduce Stress

Reducing stress of translocated animals is an ethical requirement and will be beneficial to translocation success. CPW will make all reasonable efforts to reduce stress during captures and transport to Colorado. The transportation process will focus on providing animals with adequate food, water, and cool, quiet conditions to minimize stress. The degree to which these efforts will reduce potential stresses to the point that wolverines maintain pregnancies is unknown. However, there have been cases of wolverines transported from the wild and into captivity where pregnant females have given birth (D. Pedersen, personal communication).

Allow Altitude Acclimation

Most wolverines sourced from more northern areas will have lived at significantly lower elevations than where they will live in Colorado. High-altitude environments pose physiological challenges for mammals due to the reduced availability of oxygen. The process of adjusting to these changes is known as acclimatization, which involves both short-term and long-term physiological adaptations. Short term acclimatization occurs over a period of days or weeks and includes increased ventilation, cardiovascular adjustments, renal changes, and increased red blood cell production. Over days to weeks, the body produces more red blood cells to increase the blood's oxygen-carrying capacity. Full hematological adaptation (red blood cell increase reaching a plateau) can take approximately 11 days per kilometer of altitude ascended. In essence, initial acute adaptations occur within the first 3-4 days, and more significant performance-enhancing adaptations can take 3-4 weeks to fully develop. Full hematological adaptation, as measured by red blood cell levels reaching a plateau, can take even longer, potentially exceeding 45 days at 4,000 meters (~13,000 ft). Given these factors, a period of acclimation at the Frisco Creek facility in Colorado of at least 3-4 weeks will likely be beneficial for the translocated wolverines.

Provide Abundant Food

Wolverine reproductive success is clearly linked to food availability. Persson (2005) found that a female's reproductive success was affected by the duration of parental care she invested during the previous reproductive season. Average birth rates declined from 1.1/year for females that had not reproduced the previous year, to 0.8/year for those that reproduced but did not wean young, to 0.2/year for those that did wean young. Persson (2005) also conducted an experiment by supplementally feeding some females during winter. All food supplemented females reproduced in 3 consecutive years whereas only 18% of non-supplemented females did the same. Food and female body condition will be key for successful reproduction by translocated wolverines.

Inman et al. (2012a) examined the unique reproductive chronology of wolverines, who have an earlier birthing period (February-March) than any northern carnivore other than hibernating bears. They suggested caching of foods over the winter is one of two key stages of the wolverine's reproductive strategy. First, lactation (Feb-Apr) is fueled by caches amassed over winter or acquisition of a sudden food bonanza (e.g., winter-killed ungulate), otherwise early litter loss occurs. Second, the majority of post-weaning growth is fueled by the relatively reliable summer period of resource abundance. In Colorado, the first stage (winter caches) will likely have to be provided for the wolverines because they will not have had time to amass caches in the new area. Provisioning wolverines may not be necessary for survival, but provisioning will almost certainly benefit site fidelity and survival for all, and may be critical for successful reproduction by the translocated females. When food is available on a daily basis, captive male wolverines consume about 1-4 lbs of food per day; captive females consume 1-2 lbs per day (Wolverine Translocation Techniques Working Group 2013). Accordingly, a single deer carcass that yields 50 lbs of meat might sustain a male for nearly two weeks, or a female for nearly a month.

The second stage of fueling reproduction, post-weaning growth, occurs during summer when a variety of foods are generally available to wolverines. In southern Canada and the contiguous U.S., this stage appears to be focused on hunting marmots (Lofroth et al. 2007, Inman and Packila 2015). That is the expectation in Colorado too, where yellow-bellied marmots are abundant. During summer in Colorado food is expected to be abundant and easily obtainable. Provisioning during this season is not expected to be needed.

Time Releases in Relation to Significant Biological Events

The timing of events related to reproduction is relevant to developing options for release procedures. The first event of importance is the birthing date. Births generally begin during February and end during March. CPW will attempt to refine estimates of expected birth dates for each individual based on ultrasound as part of the initial assessment after arrival at Frisco Creek. The second important event is the weaning of cubs along with their ability to eat solid foods and travel with the mother. Weaning generally begins by mid-April. At this point in time the female generally transports the young to rendezvous sites or they follow her a short distance. By June 1, the young are capable of following the female longer distances. A third important event is marmot emergence dates at higher elevations where wolverines are expected to live in Colorado. Edic et al. (2020) studied marmot emergence at Gothic, Colorado over 14 years and found that emergence on average occurs on 7 May. The range of emergence date was from 12 April – 9 June and varied by average March temperature, local snowmelt date, and other factors.

Utilize Training

Reintroduction programs have often used "training" techniques to help improve success (Moehrenschlager and Lloyd 2016). "Training" can be as simple as feeding the animals foods they are likely to utilize in the new area. This will occur as much as possible for the wolverines in captivity in Colorado by providing them with ungulate carrion and possibly marmot carcasses. Training can also include providing live prey while in captivity. This may be more important for individuals sourced from areas where there are no marmots. Negative reinforcement can also be used to try and improve reintroduction success. This can be as simple as exposure to the scent of potential predators, e.g., mountain lions, followed by a negative stimulus such as loud noises.

Minimize Conspecific Mortality

Considering the potential for conspecific mortalities (wolverines killing other wolverines), could also be important for recruitment of young. Data collected over nearly three decades in Sweden and Norway indicate that conspecific mortality is the most significant cause of juvenile mortality (Persson et al. 2008). There appear to be two main periods when conspecific mortality occurs. The first period occurs when the young are altricial (infanticide), where males kill unrelated juveniles (often at dens) to increase reproductive success. The second period occurs after near-yearlings or subadults make exploratory movements outside of the mother's territory; these mortalities are likely the result of competition for resources (territorial defense). The potential for these behaviors have been accounted for in Colorado's reintroduction planning by 1) attempting to limit male translocations to those captured at the same site as adult females during year one (reducing the potential for infanticide), and 2) making attempts to distribute wolverines reasonably well across the landscape via the release units (Figures 10-12).

Release in Remote Denning Habitat

Wolverines are purported to be sensitive to human disturbance, especially at den sites (Hausleitner et al. 2024). If this is true, releasing females who are pregnant in an effort to recruit young would be more successful if released in remote areas with little human presence during winter and spring (Feb-May). Denning habitat in the contiguous U.S. generally consists of avalanche debris or large boulders covered by snow (Magoun and Copeland 1998, Inman et al. 2007a, Yates et al. 2017). Careful consideration to match pregnant females with release units that support optimal denning habitat characteristics could improve likelihood of success, in addition to maximizing likelihood of site fidelity more generally.

Release Locations and Procedures

Release sites will be selected based on knowledge of local habitat characteristics, access limitations, and other logistical considerations. In general, ideal sites will occur near timberline, have the potential for ungulate carcasses to scavenge during winter, facilitate personnel provisioning additional carcasses into the area during late winter and spring, and will be proximate to marmot colonies that will emerge during spring. To the degree possible, areas with less human activity are better, but wolverines can exist during winter in areas with human activity (Krebs et al. 2007, Heinemeyer et al. 2019). There are no particular vegetation types of significance to wolverines, but escape cover in the form of trees to climb or boulders to hide in-between is important.

When ready for release, animals will be transported to the release site in appropriate crates. Transportation to release sites could occur via helicopter or a combination of truck, snowmobile, and skiing with a pulk.

CPW plans to release females under the Wild Births protocol at a pre-identified den-like structure (large boulders with appropriately sized cavities covered by snow). Because most of these sites are on federal public land, cooperation by federal land management agencies will be needed. Food, likely portions of an ungulate carcass, will be placed near the site, and in the cavity if possible, to promote fidelity to the area. An attempt will be made to place the wolverine into the cavity and temporarily block the entrance to keep the individual inside for a brief period so that it locates the den-like structure and food. Food provisioning will continue periodically until marmot emergence. Females and offspring released later in the year under the Captive Births protocol will be released at a pre-identified site near emerging marmot colonies at alpine timberline in areas with large boulders. Females that are not pregnant or who have lost litters will be released after acclimatization into suitable habitat near alpine timberline. Adult males captured at the same site as an adult female will be released at the same location as the female unless antagonistic behaviors are observed during captivity.

Chapter 5: Monitoring, Benchmarks for Success, and State Status

Monitoring is an essential component for successful reintroductions as are specific goals and benchmarks of the monitoring program (IUCN/SSC 2013). In this section, the reintroduction program is divided into two distinct phases: The Establishment Phase "starts with the first release and ends when post-release effects are no longer operating" (IUCN/SSC 2013). The Growth Phase is "characterized by…rates of increase and/or expansion of range" (IUCN/SSC 2013). Benchmarks of success are defined for each phase. These benchmarks will serve to measure progress of the wolverine restoration program, provide clear transition points from one phase of the program to the next, and define when success has been achieved and the reintroduction program is complete.

For each phase, data obtained remotely from GPS collars on individual wolverines will provide the primary data stream for assessing benchmarks. However, batteries are not expected to power GPS collars beyond a year or two. Therefore, after the first year post-translocation, cohorts of translocated wolverines and their progeny will be targeted annually for collar replacement (via live-capture) in order to maintain the data stream required to assess benchmarks. VHF devices function longer than GPS collars, and may be used as a backup to GPS collars to facilitate re-capture efforts for individuals whose collars are nearing, or have exceeded, the end of their battery life. Remote cameras, hair snags, and/or snow tracking will serve as secondary data streams to augment collar data where appropriate or necessary.

Establishment Phase

The Establishment Phase of the wolverine restoration program is the period of time when wolverines are actively translocated from source sites to Colorado. Optimally, the translocation phase will encompass years 1-3 when 15 individuals per year are reintroduced to Colorado (see Chapter 4). An assessment will be made following translocations in year 3 to determine the program's position relative to the benchmarks for this phase. This phase could be extended up to several years in the event initial expectations are unmet (e.g., fewer individuals are available for translocation than expected, or fidelity or survival are lower than anticipated). Extension of the Establishment Phase would occur if CPW projected that such action would have a reasonable probability of achieving the benchmarks.

Benchmarks of Success for the Establishment Phase

The Establishment Phase will be considered successful and translocations will cease when all of the following benchmarks are achieved:

1) A minimum of 30 wolverines, including at least 20 females and 5 males, have developed site fidelity to areas within Colorado. Individuals may include any combination of collared animals released via translocation or new animals born in Colorado.
2) The 30 individuals with site fidelity in Colorado have survived for at least 1 year post-release, or post-birth, in Colorado.
3) Both male and female home ranges occur in at least 2 of the 3 Release Zones.

Monitoring Focus for Establishment Phase

Monitoring during this phase will inform subsequent releases and adaptation of release protocols as needed. For example, GPS data and remote cameras will be used to determine whether carcass provisioning sites are being used, and for how long, so that adjustments can be made as necessary. Mortality sensors on the collars, along with GPS data, will facilitate quick investigation of mortalities as they occur to ascertain the cause of death. GPS locations will be used to plot individual animal movements, determine fidelity, delineate home range size and territorial boundaries, and document interactions between collared individuals. Determining areas where males and females have settled will identify remaining gaps where additional individuals can be released during subsequent translocations; it will also inform efforts to establish mating pairs, reduce same-sex territorial conflicts, and reduce the potential for infanticide of newborns.

CPW will informally assess and evaluate all aspects of translocation and release protocols on an ongoing basis. Informal assessment is necessary because some population processes take time to occur and sufficient data to support formal analyses may not be available for many months, or even years. However, formal analyses that estimate survival (or mortality), post-release movements, site fidelity, and productivity as a function of release protocols (e.g., source area, release date, days in captivity, days released prior to parturition, age, sex, pregnancy status, heterozygosity, etc.) and habitat characteristics (e.g., food resources, human presence, road density) will be conducted periodically as soon as enough data accumulates to support such analyses.

Any unexplained mortalities or an unusually large number of mortalities during the first years of releases or following any modification to established protocols will prompt a review of procedures. Reintroduced wolverines that are injured or appear to be starving may be recaptured and rehabilitated at the Frisco Creek Wildlife Rehabilitation Center or euthanized on a case-by-case basis. The project may be suspended at any time as deemed necessary by CPW personnel, and may resume when likely cause(s) of problems are identified and solutions are implemented.

Growth Phase

The population Growth Phase is generally the period after translocations cease, and individuals in Colorado find mates, reproduce, and increase the population size. Presumably this phase of the program could begin in year 4 (or earlier), and could extend through year 10 (or longer). Assessments of survival and productivity will begin as soon as initial cohorts of wolverines are released, and will cease when evidence suggests the population is viable.

Benchmarks of Success for the Growth Phase

The reintroduction effort will be considered successful when all of the following occur:

1) Evidence of breeding by wolverines in Colorado.
2) Evidence of production of young in Colorado.
3) Recruitment of young conceived in Colorado and surviving to 1-year of age.
4) Wolverines born in Colorado survive, breed, and produce young.
5) Estimated annual survival and recruitment suffice to overcome mortality such that the long-term projection for the population is stable or increasing.

Canadian wildlife filmmaker Andrew Manske captures footage of wild wolverine kits while filming the documentary Wolverine: Ghost of the Northern Forest for the Canadian Broadcasting Corporation (CBC). Photo ©Andrew Manske

Monitoring Focus for Growth Phase

Once an adequate number of wolverines have been successfully translocated to Colorado, gauging success during the Growth Phase will depend on understanding wolverine survival, continued site fidelity, and reproductive success. Survival and cause of death will be monitored via a combination of locations and mortality sensors on collars, similar to the translocation phase. Similarly, continued assessment of site fidelity will be accomplished by remotely monitoring GPS or VHF locations of individuals. Monitoring reproductive success will likely prove more difficult.

GPS locations of females known or suspected to be pregnant can be monitored for clusters of locations during mid-late winter, which may indicate a den site (Aronsson et al. 2023). Collars will be programmed to increase intensity of data gathering during denning season to facilitate identification of clusters. Once birth occurs, females often do not leave the den for a week (Aronsson et al. 2023). Therefore, absence of GPS locations from potentially pregnant females during denning season will be interpreted as potential evidence for birth. At an appropriate time, crews will attempt to visit den sites and collect scats left by the litter, which may yield information regarding initial litter size and sex ratio (Mattisson et al. 2022). In May and June when females are moving offspring between rendezvous sites, crews will visit recent locations of females and attempt to verify the presence of a litter and collect genetic samples (hair or scat). Remote cameras, or drones, could be used at rendezvous sites or over baits to verify a litter and/or count young during this time. Crews will again attempt to observe family groups in August, before young potentially begin travelling independently. Young may be captured and radioed (Persson et al. 2006). Scat and hair samples will be collected opportunistically and remote cameras or drones may again prove useful. Ideally, verifying the presence of young at 1-year of age (March 1 or beyond) would be useful as that would facilitate an estimate of juvenile survival and thus recruitment. However, this information will be challenging to collect on a regular basis. More likely, information regarding recruitment will be collected opportunistically during efforts to capture individuals for (re)placement of collars or from incidental camera or snow tracking surveys.

Genetic samples from released individuals and those born in Colorado that are subsequently captured or non-invasively sampled will be analyzed periodically to estimate heterozygosity (or inbreeding). This will serve as a check to determine whether efforts to maximize H_e when translocating animals were successful. Additionally, it could trigger release of extra individuals if such an action is necessary to avoid inbreeding and potential inbreeding depression.

Monitoring specific to survival and reproductive success will continue throughout the Growth Phase (upwards of 10 years or more) in an attempt to capture annual variability in these important demographic parameters. Eventually, when enough data has been gathered to accurately estimate survival, productivity, and annual variability in each, a population model will be assembled to estimate population growth rate. A preponderance of evidence suggesting that the population is stable or increasing will indicate viability and trigger completion of the reintroduction.

Adaptations will be made as necessary in order to provide the best chance of achieving benchmarks and gathering evidence to support those achievements. This includes potentially augmenting the population with further translocations if necessary. The project may be suspended at any time as deemed necessary by CPW personnel.

Photo ©Adobe Stock

Recovery of Wolverines in Colorado

Definitions for State Endangered, Threatened, and Nongame Species are as follows:

- Endangered Species: any species or subspecies of native wildlife whose prospects for survival or recruitment within this state are in jeopardy as determined by the Commission (CRS § 33-1-102 (12));
- Threatened Species: any species or subspecies of wildlife which, as determined by the commission, is not in immediate jeopardy of extinction but is vulnerable because it exists in such small numbers or is so extremely restricted throughout all or a significant portion of its range that it may become endangered (CRS § 33-1-102 (44));
- Nongame Species: all native species and subspecies of wildlife which are not classified as game wildlife by rule or regulation of the commission (CRS § 33-1-102(29)).

Status	**Stage 1**[a] *(denotes State Endangered status)*	**Stage 2** *(denotes State Threatened status)*	**Stage 3** *(denotes State delisted, nongame status)*
Start	Current	All benchmarks of success for the Establishment and Growth Phases of the reintroduction have been met and the population is estimated to be viable.	Stage 1 and Stage 2 conclusion requirements are both met.
Conclude	All benchmarks of success for the Establishment and Growth Phases of the reintroduction have been met and the population is estimated to be viable.	Monitoring (monitoring plan to be developed later) indicates that wolverines are well-distributed throughout all 3 Release Zones, and that the distribution appears stable for at least 10 years after transitioning to Stage2 (Threatened) status.	No prescribed conclusion
Action upon conclusion	Downlist to State Threatened.	Delist from Colorado State list of Threatened and Endangered species	Not applicable
Criteria to move back into this stage	Monitoring (monitoring plan to be developed later) indicates the distribution of wolverines in the state is no longer stable and wolverines disappear from more than 1 Release Zone.	After delisting, evidence from long-term monitoring of the population indicates that the distribution is no longer stable or wolverines disappear from 1 of 3 Release Zones.	Not applicable

Table 5. Start and end points of Stages describing wolverine recovery in Colorado.

[a] *Stages will be dictated by information described in the table. While it is intended that state status will also correspond to these thresholds, there may be a time lag as the Parks and Wildlife Commission undertakes the regulatory process to change the state status.*

Stage 1 (State Endangered):

"Stage 1" of wolverine status and recovery refers to when the wolverine is classified by Commission rule as an Endangered species under state law. This stage will include the initial years of wolverine translocations when population size is small and new individuals are in the early stages of establishing home ranges and finding mates. During this stage, the initial wolverine population will be managed in accordance with state policy to conserve species listed as Endangered under Colorado's Nongame, Endangered, or Threatened Species Conservation Act (CRS § 33-2-101).

The species' status will remain in Stage 1 until CPW determines that all benchmarks for success for the Establishment and Growth Phases of the reintroduction have been met and the population is estimated to be viable. Once the criteria are met to move from Stage 1 to Stage 2, the regulatory process to downlist to State Threatened can begin. The Commission would be presented with the opportunity to conduct the downlisting processes to State Threatened through the CPW Chapter 10 regulation process.

Stage 2 (State Threatened):

"Stage 2" refers to when the wolverine is classified by Commission rule as a Threatened species under state law. Stage 2 is characterized by a period of stable or increasing distribution in the state. Stage 2 could begin after CPW confirms that all benchmarks for success for the Establishment and Growth Phases of the reintroduction have been met and the population is estimated to be viable. Stage 2 could conclude when monitoring (formal monitoring plan to be developed later) indicates that wolverines are well-distributed within the state and occur in all 3 Release Zones, and that the distribution appears stable (or increasing) for at least 10 years after transitioning to Stage 2 (threatened) status. This will correspond to a time when wolverines could be removed (delisted) from the State Threatened and Endangered Species List. At that time their status will be Nongame Wildlife. As in the transition from Stage 1 to Stage 2, there may be a regulatory lag moving between Stages depending on when or if the Commission initiates the process .

Stage 3 (Delisted/Nongame species status):

"Stage 3" refers to when the wolverine is classified as a Nongame Species under state law and is no longer on the list of Threatened or Endangered species. This Stage is characterized by a sustained wolverine population, as indicated by extensive and stable distribution throughout primary habitat in the state.

Stage 3 could begin after monitoring indicates that wolverines are well-distributed and occur in all 3 Release Zones, and that the distribution appears stable for at least 10 years after transitioning to Stage 2 (threatened) status. Once this threshold is met, the species could be reclassified to delisted, Nongame status.

Federal Status

Downlisting and de-listing under the State's statute does not impact federal status. Wolverines will remain federally listed until the USFWS determines that the DPS no longer meets the federal (ESA) definition of a threatened species. Upon federal de-listing, the 10(j) will no longer govern management of wolverines in Colorado.

Conclusion

This Plan is fundamentally based on principles outlined in the IUCN "Guidelines for Reintroducing Species and Other Conservation Translocations" (IUCN/SSC 2013). The proposed translocation and release procedures represent guidance and best estimates provided by a team of wolverine, translocation, and veterinary experts assembled from around the world (Wolverine Translocation Techniques Working Group 2013). CPW has incorporated additional planning based on newly available science and the current understanding of wolverine biology. As such, CPW has diligently considered a host of issues ranging in scale from conservation impacts to the population in the contiguous U.S.; to individual animal trapping, transport, and captive care; to wolverine biology-specific release strategies; to genetic signatures of potential sources. However, a formal wolverine reintroduction has never been attempted, and success will likely depend not only on the issues identified here, but on CPW's ability to determine those techniques that are most effective along with continued public support as unanticipated events occur. CPW will continually evaluate new information as it becomes available and will make every attempt to leverage such information toward successful restoration of wolverines to Colorado.

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