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To:	cmcgowan@usgs.gov
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Here is Bob Inman's Doctoral Thesis from 2013.

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Betty J. Grizzle, D.Env.
Fish and Wildlife Biologist
U.S. Fish and Wildlife Service
Carlsbad Fish and Wildlife Office
2177 Salk Ave, Suite 250
Carlsbad, CA 92008
760-431-9440, ext. 215
760-431-5901 fax

Wolverine Ecology and Conservation in the Western United States

Robert Michael Inman
Faculty of Natural Resources and Agricultural Sciences
Department of Ecology
Uppsala

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Cover: F121 and two cubs of the year in the Gravelly Range of Montana, USA.
(photo: Mark Packila, WCS Greater Yellowstone Wolverine Program)

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Abstract

Successful conservation of rare species requires an understanding of the niche, knowledge of the scale over which a viable population exists, and a system that provides adequate funding to take the necessary actions. I radio-marked wolverines in the Yellowstone Ecosystem and examined spatial ecology and reproductive chronology from an evolutionary perspective to better define the wolverine niche. I used a resource selection function to map habitat suitable for survival, reproduction, and dispersal; make a rough estimate of population capacity; and develop conservation priorities at the metapopulation scale. I developed an index of metapopulation dispersal potential to identify areas most valuable for connectivity and discuss the steps needed to conserve wolverines through the 21st century. Wolverines were limited to high elevations where temperatures were low, structure was abundant, and deep snow exists during winter. Persistence in these relatively unproductive habitats required large home ranges that were regularly patrolled, a social system that provided exclusive access to resources, low densities, and low reproductive rates. These characteristics are prevalent across the species range, suggesting wolverines are adapted to exploit a cold, low-productivity niche. Caching during all seasons in cold, structured microsites to inhibit competition with insects, bacteria, and other scavengers is likely a critical behavioral adaptation. Habitat features that facilitate caching/refrigeration may be crucial for reproductive success and distribution. In the western U.S., primary wolverine habitat exists in island-like fashion and is capable of holding an estimated 580 wolverines distributed across a 10 state area. I estimated current population size to be approximately half of capacity. Wolverines exist as a small, inherently vulnerable metapopulation that is dependent on successful dispersal over a vast geographic scale. Priority conservation actions include: 1) maintaining connectivity, particularly in the Central Linkage Region of western Montana; 2) restoration to areas of historical distribution that are robust to climate change, e.g., Colorado; and 3) development of a collaborative, multi-state/province monitoring program. These actions will require significant funding. The viability of the wolverine in the contiguous United States, a candidate endangered species threatened by indirect, habitat-related impacts caused by all of society, depends on a fundamental shift in the way conservation of non-game wildlife and habitat are financed.

Keywords: connectivity, distribution, *Gulo gulo*, metapopulation, niche, wolverine.

Author's address: R. Inman, 222 Main St., Ennis, Montana 59729, USA, and SLU, Dept. of Ecology, Grimsö Wildlife Research Station, SE-730 91 Riddarhyttan, Sweden.
E-mail: binman@wcs.org

Dedication

For Ben, Tanner, Will, and all the other Viking Cubs. With Kris.

There are two spiritual dangers in not owning a farm. One is the danger of supposing that breakfast comes from the grocery, and the other that heat comes from the furnace.

Aldo Leopold, 1949

Talk is cheap, action speaks.

Coach R.L. Inman 1937–1999.

Contents

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Chairman:	**Tomas Pärt**, SLU, Uppsala
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Main Supervisor:	**Jens Persson**, SLU, Grimsö
Assistant Supervisor:	**Henrik Andrén**, SLU, Grimsö

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Inman, R.M., M.L. Packila, K.H. Inman, A.J. McCue, G.C. White, J. Persson, B.C. Aber, M.L. Orme, K.L. Alt, S.L. Cain, J.A. Fredrick, B.J. Oakleaf, and S.S Sartorius. 2012. Spatial ecology of wolverines at the southern periphery of distribution. *Journal of Wildlife Management* 76(4): 778–792.

II Inman, R.M., A.J. Magoun, J. Persson, and J. Mattisson. 2012. The wolverine's niche: Linking reproductive chronology, caching, competition, and climate. *Journal of Mammalogy* 93(3):634–644.

III Inman, R.M., B.L. Brock, K.H. Inman, S.S Sartorius, B.C. Aber, B. Giddings, S.L. Cain, M.L. Orme, J.A. Fredrick, B.J. Oakleaf, K.L. Alt, E. Odell, and G. Chapron. Developing a spatial framework and conservation priorities for a wolverine metapopulation. (Manuscript).

IV Inman, R.M., S. Bergen, and J. Beckmann. Wildlife as public domain: Endangered status, connectivity, and critical habitat of the wolverine. (Manuscript).

1 Introduction

1.1 The 3 Legs of Conservation – Niche, Scale, and Funding

Successful conservation of wolverines (*Gulo gulo*) in the contiguous United States requires an understanding of the species niche, knowledge of the scale over which a viable population functions, and a system that provides adequate funding to take the necessary actions. Understanding the species niche, or at least some key aspects of it, is necessary to provide the biological conditions required for persistence. This can include human influences. Knowledge of the scale over which a viable population functions is necessary from both the ecological and management perspectives. This factor defines the broadest geographical extent over which planning must occur to be biologically adequate, and it defines who needs to be involved with planning and actions. Moving from a theoretical understanding of what needs to be done to achieving it requires a system that provides adequate funding. This is vital for taking the actions necessary to maintain the niche at the scale of a viable population. Difficulties may occur if any of these 3 aspects are missing or misunderstood.

1.2 The Wolverine's Niche

A fundamental niche is the full range of resources and conditions a species is capable of utilizing in the absence of competition from other species; a realized niche is the set of resources and conditions for which a species is adapted and from which it competitively excludes other species to a degree that allows it to persist over the long-term (Gause 1934, Hutchinson 1957). It follows that the distribution of a species is an expression of where its realized niche exists. Similarly, comparative differences in measureable traits such as home range size, activity pattern, spatial organization, and reproductive rate are expressions of how a species has adapted to gain competitive advantage within the specific set of conditions that are its niche. By understanding which resources different species have adapted to exploit along with the specific combination of traits necessary to successfully exploit them, we gain a fuller understanding of individual species' competitive advantages. This, in turn, allows us to better provide the conditions necessary for continued occupation of the niche. In the absence of this complete picture, management strategies could be misdirected and fail to provide for the full set of needs of a species.

The wolverine is a large, terrestrial Mustelid weighing 8–18 kg. It has large feet that allow it to travel easily over snow. The wolverine has typically been viewed as an uncommon, arctic/boreal scavenger (Hall 1981, Banci 1994). This general view of the species and its niche arose from its circumboreal distribution (Krott 1960, Pulliainen 1968, Nowak 1973), a paucity of sightings and records relative to other species (e.g., Murie 1944), and reports of food habits that emphasized ungulate carrion (Skinner 1927, Haglund 1966, Myhre and Myrberget 1975). Subsequent work supports much of this description and provides some refinement. However, a holistic view of the wolverine's niche and the strategies it has adapted to occupy this niche has not yet been described.

Wolverine distribution is limited to the northern Hemisphere in areas where cold, snowy conditions exist for much of the year. There is a correlation between wolverine den locations and areas with snow cover that persists through mid-May during at least 1 of 7 years (Copeland et al. 2010). This correlation has led to an 'obligate snow-denning hypothesis' that suggests distribution is limited by availability of deep snow for reproductive dens (Copeland et al. 2010). One implication of this hypothesis is that climate change will negatively influence distribution via decreased cub survival because of a lack of snow to provide thermal advantage at den sites (Copeland et al. 2010, McKelvey et al. 2011). This hypothesis has led to the wolverine being classified as warranted for protection under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 2010). If the snow-denning hypothesis is true, either the fundamental niche is limited by sites suitable for reproduction, or the realized niche is limited by competition for suitable reproductive sites. Because hundreds of suitable den sites appear to be available within a female home range (Inman et al. 2007*a*), limitations due to competition for dens (realized niche) does not seem possible. The idea that wolverines did not occur in places such as the Great Plains because they could not find den sites under snow or warm enough for cubs (fundamental niche limitations) also seems implausible. Clearly wolverines are adapted for snow and cold conditions, but food-based explanations for the spring snow correlation have not been explored and could provide important insights into limiting factors for the wolverine niche. Identifying limiting factors is important for understanding where wolverines can occur now and in the future. It is also important for knowing how impacts from climate change will influence wolverines and what can be done to minimize negative effects.

Wolverines have primarily been studied in taiga, tundra, or boreal forests where the predominant ungulates were moose (*Alces alces*) and caribou (*Rangifer tarandus*; Magoun 1985, Banci 1987, Persson 2003, May 2007). Wolverines in these areas have large spatial requirements, occur at low densities, and have low reproductive rates (Magoun 1985, Persson et al. 2006, Persson et al. 2010). However, the contiguous U.S. lies at the southern periphery of distribution, and fundamental differences in vegetation, predator, and prey composition could result in different spatial use and demographic characteristics. Wolverine data from the contiguous U.S. are sparse. Published accounts of even basic metrics such as home range size remain limited to a single estimate that is somewhat confounded by combining subadults and adults into one average (Hornocker and Hash 1981). Thus fundamental information on home range size, movements, social organization, density, and dispersal is absent or minimal. In addition, telemetry data from the contiguous U.S. was obtained in areas that did not contain the full suite of native large carnivores, i.e., grizzly bears (*Ursus arctos*) and/or wolves (*Canis lupus*) were absent (Hornocker and Hash 1981, Copeland 1996). Populations of these species have expanded in recent years (Schwartz et al. 2006, Smith et al. 2010) and may influence wolverines via competition for resources, provisioning of resources, or direct mortality. In addition, even though they are fundamental to niche occupation, our current understanding of wolverine food habits and behaviours that may be key in competing for food is limited. For instance, while it is clear that wolverines utilize a wide variety of foods (Hash 1987, Magoun 1987, Banci 1994, Lofroth et al. 2007), no attempt has been made to discern which foods specifically fuel the most energetically demanding periods of reproduction. And although caching is a common behavior (Magoun 1987, Landa et al. 1997, Samelius et al. 2002, May 2007, Mattisson 2011), there has been no effort to determine how or why it could be key in the reproductive process. Assimilating information on these fundamental ecological metrics at the southern edge of distribution will allow a fuller understanding of the adaptive strategies that enable the wolverine to occupy its niche.

1.3 The Scale of Wolverine Management in the Western U.S.

Understanding the scale that is adequate for management of a viable population requires knowledge of where suitable habitat exists, potential population capacity therein, and demographic data that can indicate how many individuals are required for a population to avoid vulnerability (e.g., IUCN 2000). Our understanding of where suitable wolverine habitat exists in the contiguous U.S. has improved over time but is capable of further refinement. No estimate of current or potential population size exists for the contiguous U.S.

The historical range of the wolverine included portions of the contiguous U.S., however the sparse nature of records along with their broad distribution led early ecologists to speculate that wolverine range could have included vast areas as diverse as the Rocky Mountains, Great Plains, and northeastern hardwood forests (Nowak 1973, Hall 1981). More recent work that included great efforts to discern reliable records from anecdotal reports suggest that wolverines were probably limited to mountainous areas of the western U.S. and potentially the Great Lakes region and northeastern U.S. (Aubry et al. 2007). In an attempt to refine distribution by understanding broad-scale habitat relationships, Aubry et al. (2007) compared locations of historical records to vegetation types, ecological life zones, and spring snow cover maps. They concluded that spring snow cover was the only habitat layer that fully accounted for historical distribution patterns. However, the spring snow layer did not account for all historical records and it also included vast areas where there were no historical records (Fig. 7 in Aubrey et al. 2007). Subsequent work showed that a refined definition of spring snow (areas where snow was present through mid-May in at least 1 of 7 years) at a finer resolution correlated well at a global scale with wolverine den and telemetry locations (Copeland et al. 2010). Spring snow also explained genetic relationships among mountain ranges of the Northern U.S. Rockies better than distance alone (Schwartz et al. 2009).

Clearly there is a relationship between wolverine distribution and cold, snowy conditions, and the spring snow layer has refined the understanding of where wolverines likely occurred. However, the spring snow layer is incongruent with other pieces of information. It failed to account for up to 25% of wolverine telemetry locations from studies within the contiguous U.S. (Table 1 in Copeland et al. 2010). Some large areas where spring snow exists produced very limited historical records, i.e., 2 records from the coastal ranges of Oregon in comparison to 29 from Washington and 57 from California (Aubry et al. 2007). And historical genetic data from California (Schwartz et al. 2007) suggests wolverines in the Sierra-Nevada Range were isolated for >2,000 years whereas the spring snow layer suggests that suitable habitat occurred in nearly continuous fashion from the Canadian border to the Sierra-Nevada in California (Fig. 8A in Copeland et al. 2010, and Fig. 2B in McKelvey et al. 2011). While spring snow shows some clear correlations with wolverine distribution, no single variable is likely capable of capturing all the factors that are a part of the wolverine niche. Therefore it is possible that further refinement of suitable habitat can be made and would be useful in determining the scale over which a viable population functions in the contiguous U.S. along with which agencies are responsible for management.

Population size of wolverines in the contiguous U.S. is unknown. A minimum effective population size (did not include samples from all areas of known and likely distribution) has been estimated at 35 (95% credible limits 28–52; Schwartz et al. 2009). Potential population size if areas of historical distribution were reoccupied is also unknown. This information is needed to better understand the scale over which a viable population does or can exist and therefore an effective area over which management should be coordinated. At present, each of the 11 western state wildlife agencies classifies and manages wolverines separately. In addition, while the state wildlife agencies have authority over regulations regarding intentional mortality of wolverines (hunting/trapping), numerous other agencies have authority to manage habitats and therefore influence reproductive rates etc. These entities include agencies from each state similar to the Idaho Department of Lands along with several federal agencies such as the U.S. Forest Service, Bureau of Land Management, National Park Service, and U.S. Fish and Wildlife Service. Management of Native American and private lands may also influence wolverine populations. Depending on the geography over which a viable wolverine population(s) exist in the contiguous U.S., the number of entities that would need to coordinate planning could range from <5 to >25. The expense and difficulty of effective planning and management likely increases when additional entities need to be involved in coordination. Therefore it is important to determine an appropriate scale/geography over which a viable wolverine population exists in order to be effective and efficient with personnel and financial resources.

1.4 Funding 21st Century Conservation: The Wolverine as a Case Study

Knowledge of the biology of a vulnerable species is of little consequence without the ability to act toward its conservation. Conservation in the United States is founded on the concept of the Public Trust Doctrine (PTD; Organ et al. 2010), which establishes that wildlife are a public resource, owned by no one, and held in trust for future generations (Bean and Rowland 1997). The obligation to maintain wildlife populations is backed by a legal framework that includes the Lacey Act, the Multiple-use and Sustained Yield Act, and the Endangered Species Act among others (Bean and Rowland 1997). The legal framework clearly plays a role in successful conservation. However, in practice this approach to conservation is somewhat reactive, and can become a desperate situation occurring at the brink of failure, as is often the case with endangered species.

In what could be called a more proactive approach to conservation, sportsmen-generated dollars contribute approximately $2.5 billion annually that makes up ~90% of state wildlife agency budgets (Association of Fish and Wildlife Agencies 2011, Loftus et al. 2011*a*, 2011*b*, 2011*c*). These funds are derived from the sale of hunting and fishing licenses by states along with federal excise taxes on the sale of equipment related to the hunting, fishing and shooting sports. This ‘North American Model’ for conservation (Organ et al. 2010) has proven vastly successful in restoring populations of many game species. For instance, by 1900, and prior to the model being in place, populations of white-tailed deer (*Odocoileus virginianus*) had been reduced to <2% of historical levels (Miller et al. 2003). By 1993, white-tailed deer had been restored to historical levels, nearly 5 million were sustainably harvested on an annual basis, and populations were continuing to increase in many areas (Miller et al. 2003). Many other species have also rebounded significantly under this proactive approach, and programs for monitoring population trend, conserving habitats, and conducting important research are in place. The successes of this system can all be linked to one fundamental aspect – a mandatory, user-based funding system that is specifically allocated to support the work necessary meet its goals.

While the legal framework and adequate funding both play a role in successful conservation, the wolverine provides an interesting example for comparing the influence of the two factors. Wolverines have long been recognized as uncommon and at one point likely extirpated from the contiguous U.S. (Newby and Wright 1955). They are classified as a non-game, sensitive, or state endangered species in all of their historical distribution other than Montana (where they are a furbearer). Yet only 15 verifiable records of presence that did not arise from opportunistic telemetry studies were made within Idaho, Wyoming, and Washington during an 11-year period 1995-2005 (0.45 records per state per year; Aubry et al. 2007). This absence of information about the status of the population has occurred despite the legal framework requiring wolverine persistence and petitions to list the species as endangered beginning 19 years ago (U.S. Fish and Wildlife Service 1995). This lack of basic information about a rare species is largely due to inadequate funding for monitoring and research of non-game species.

In their most recent report on wildlife diversity funding, the Association of Fish and Wildlife Agencies (2011) recommend determining justifications for wildlife diversity conservation to inform and substantiate the funding need to

Congress, state legislatures, partners, and others. The work needed to be done to conserve wolverines through the 21st century provides a good opportunity to examine whether the current wildlife funding paradigm is adequate for conserving the growing range of biodiversity that society has said it wants to conserve in written law. It also offers the opportunity to discuss how to accomplish that goal.

1.5 Objectives

The goals of this thesis were to improve the ecological foundation for wolverine conservation in the contiguous U.S., identify conservation priorities therein, and develop tools for achieving species persistence. To do this I use wolverine telemetry data from the Greater Yellowstone Ecosystem and synthesize information from the literature to further our understanding of how the wolverine occupies its niche. I also develop a spatial framework for management planning at the scale appropriate for wolverines and identify population-level conservation priorities. Finally, I examine one aspect of the unique situation that is wolverine conservation in the contiguous U.S., connectivity at the landscape-scale, and suggest actions necessary to fund the conservation of this species. The main questions were:

Paper I — How do wolverines use space at the southern periphery of distribution in the presence of more species of ungulates, carnivores, and other organisms? What set of conditions gives them competitive advantage to exploit this environment?

Paper II — What does the timing of wolverine reproduction suggest are important foods for successful reproduction? Are there any behavioural adaptations or habitat features that are key for wolverines to occupy their niche?

Paper III — Where does suitable wolverine habitat exist in the western U.S? What is a crude estimate of potential and current population size? What are the major conservation actions of significance for this metapopulation?

Paper IV — Which areas are most important for maintaining connectivity among wolverine habitats in the western U.S. and how can protection of these areas be achieved?

2 Materials and Methods.

2.1 Study Area

My research occurred in and near the Greater Yellowstone Ecosystem (GYE, Fig. 1), a 108,000 km^2 area of the Yellowstone Plateau and 14 surrounding mountain ranges in Idaho, Montana, and Wyoming (Patten 1991, Noss et al. 2002). Elevations range from 1,400–4,200 m. Precipitation increases with elevation and varies from 32–126 cm per year (National Oceanic and Atmospheric Administration 2007, Natural Resources Conservation Service 2007). Snow usually falls as dry powder and depths at higher elevations are often in excess of 350 cm. A variety of vegetative communities are present (Despain 1990). Low-elevation valleys contain short-grass prairie or sagebrush communities. The lower-timberline transition to forest often occurs with lodgepole pine (*Pinus contorta*) or Douglas fir (*Pseudotsuga menziesii*). Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and whitebark pine (*Pinus albicaulis*) are more common with increasing elevation. The highest elevations are alpine tundra or talus fields where snow is typically present for at least 9 months of the year (Natural Resources Conservation Service 2007). The diverse fauna that is present (Bailey 1930, Streubel 1989) contains the vast majority of ungulates and carnivores that are found within wolverine distribution but includes several that typically are not, e.g., elk (*Cervus elaphus*), cougar (*Puma concolor*), and coyote (*Canis latrans*).

2.2 Animal Location Data

During 2001–2010 we captured 38 wolverines (23♀, 15♂) in log box traps (Fig. 1; Copeland et al. 1995, Lofroth et al. 2008) or by hand at den or rendezvous sites (Persson et al. 2006). We surgically implanted all wolverines with an intra-peritoneal VHF radio-transmitter, and we fit 18 wolverines (11♀,

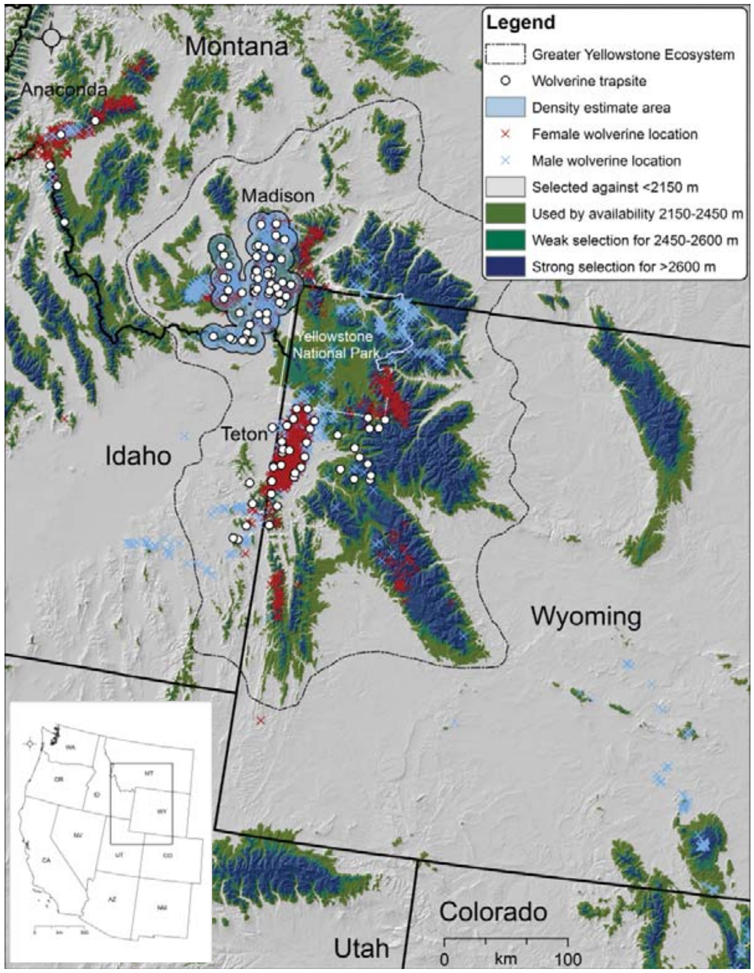

Figure 1. Map of the Greater Yellowstone Ecosystem and surrounding areas showing the three primary areas of wolverine capture and data collection (Madison, Teton, and Anaconda), 2001–2010. Trap locations, wolverine locations, and the density estimate area are displayed. Annual wolverine habitat selection by 150 m latitude-adjusted elevation band is also displayed.

7♂) with a global positioning system (GPS) collar for periods of ~3 months. We administered oxygen at a rate of 0.5 litres/min. We followed handling procedures approved by the Animal Care and Use Committee of the Montana Department of Fish, Wildlife and Parks. We attempted to collect aerial VHF telemetry locations at an approximate 10 day interval and estimated VHF telemetry error to be ~300 m.

2.3 Spatial Ecology

We used 2,257 VHF wolverine locations collected from 18 individuals (12♀, 6♂) to determine habitat selection (150 m elevation bands) by wolverines. We considered Nov–Apr to be winter and May–Oct to be summer. We calculated annual home range size by sex and age class using 100% minimum convex polygon and 95% fixed kernel (Mohr 1947, Silverman 1986, Worton 1989). We evaluated the degree to which wolverines are territorial with data on movement rates, the time period over which an area >75% the size of a multi-year home range was used, and the degree to which home ranges overlapped. We estimated wolverine density with mark-resight data from a 4,381 km^2 area of the Madison focal area during 6 encounter efforts (Huggins 1989, Huggins 1991, White and Burnham 1999, Burnham and Anderson 2002). We estimated the distance wolverines disperse by determining the distance between the locations of an offspring and the center of the mother's home range (Vangen et al. 2001).

2.4 Reproductive Chronology

We estimated the extent and peak periods of reproductive events based on similarities among studies and by weighting each study's contribution based on samples size, technique, and whether observations were based on wild or captive wolverines. We also used personal observations related to the timing of reproductive events obtained during wolverine field studies that we conducted. We also reviewed the literature to determine time periods during the year when different food items for wolverines are available; we considered information on their birthing periods, higher than usual levels of mortality (e.g., ungulate deaths due to winter kill), and entrance/emergence dates for hibernating species. We then discuss reproductive chronology in light of other information about wolverines in an attempt to develop hypotheses regarding which foods, behaviors, and habitat features may be influential for wolverines.

2.5 Habitat Suitability at Scale and Population Capacity

We used an approach similar to Hebblewhite et al. (2011) to train habitat models using 2,257 VHF radio telemetry locations collected from 12♀ and 6♂ wolverines resident to the Madison and Teton areas (Fig. 1). We developed a list of habitat features we considered important for wolverines (Table 1) and a set of GIS grids capable of representing these features in a first order analysis (Johnson 1980) across the western U.S. Prior to analysis, we disqualified highly correlated variables and limited our set of candidate models to those that

Table 1. *Habitat features we considered important for wolverines in the analysis of first order habitat selection within the Greater Yellowstone Region and subsequently modeled at a multi-state scale across the western United States.*

Key Component	Habitat Feature	Significance
Food	Alpine Meadow	Presence of marmots, bighorn sheep, mountain goats, elk, moose, mule deer.
	Cliffs	Vertical terrain for mountain goat and bighorn sheep presence.
	Talus/boulders	Presence of marmots.
	Proximity to forest	Presence of elk, moose, mule deer, grouse, hare, porcupine.
Competition	Deep snow	Wolverine adapted for travel in deep snow (where more difficult for other large carnivores).
	Structure	Cache food under boulders/logs away from birds and large mammals.
	Low ambient temps	Prolong caches due to reduced insect and bacterial activity.
	Duration of snow	Hide caches including reduced scent dispersion.
Escape cover	Structure	Escape larger carnivores under boulders and logs.
	Deep snow	Reduced presence of larger carnivores.
Birth sites	Structure	Security from larger carnivores under boulders and logs.
	Deep snow	Thermal advantage for young.
Dispersal	Trees	Familiar feature, escape cover.
	Talus/boulders	Familiar feature, escape cover.
	Presence of snow	Familiar feature, cooler temperatures.
Human presence	Roads	Potential avoidance.
	Human activity level	Potential avoidance.

were biologically relevant and explainable (Burnham and Anderson 2002). We used a forward and backward stepwise selection and the coefficients from the top logistic regression model to index habitat quality. We scaled our result from 0–1 and evaluated model fit with likelihood ratio chi-square test, residual diagnostics, and k-fold cross validation (Hosmer and Lemeshow 2000, Boyce et al. 2002, Hebblewhite et al. 2011). We then tested the model's ability to be successfully extrapolated using the k-fold procedure and 5 wolverine location datasets that were not used to train the model (Table 2; Boyce et al. 2002, Hebblewhite et al. 2011).

We binned relative habitat quality into biologically meaningful categories that were also informative for management. We defined primary wolverine habitat as areas suitable for survival (use by resident adults) by setting the decision threshold at a sensitivity of 0.95. We delineated areas suitable for use by reproductive females by determining the average habitat score within 800 m of 31 maternal sites (reproductive dens and rendezvous sites; Inman et al. 2007*a*) and then using the 10th percentile as our cut-off. We delineated areas suitable for use by dispersing wolverines (used briefly while moving between patches of primary habitat) to be those areas scoring higher than the lowest observed habitat value used during documented dispersal movements by each sex (4♀, 5♂).

Table 2. *Summary of wolverine locations used to A) develop a top resource selection function model of relative habitat quality at the first order, or B) test the predictive ability of the model with k-fold cross validation, western contiguous United States, 2001–2010.*

Dataset	Yrs collected	# Locations	r_s
A) Model development			
Resident VHF telemetry	2001–2010	2257	0.983
B) Model validation testing			
GPS collar locations of residents used to train model	2004–2008	2835	0.997
Disperser VHF and GPS locations	2001–2009	1165	0.964
Historical Records (Aubry et al. 2007)	1870–1960	157	0.646
	1870–1960	151 [a]	0.966 [a]
Contemporary Montana Records	1975–2005	321	0.951
Anaconda Range resident VHF and GPS locations	2008–2009	365	0.939

[a] Six historical records occurred inside modern cities. These were 2 records from 1870 that fell within the present city of Denver, Colorado; 3 records from 1871–1885 that fell within the present city of Ogden, Utah; and 1 record from 1954 that fell within the present city of Caldwell, Idaho. These areas were predicted to be low-quality habitat by our model due to the high road densities and human populations currently present. When these 6 records were removed from the original k-fold test of all historical records, r_s improved greatly.

We estimated potential and current distribution and abundance of wolverines by linking the resource selection function (RSF) to estimates of population size (Boyce and McDonald 1999, Hebblewhite et al. 2011). In order to facilitate discussion of landscape-level management strategies, we subjectively categorized patches of primary habitat >100 km^2 into regions based on position, degree of connectivity, and the nature of ownership (public/private).

2.6 Wolverine Connectivity

We utilized a wolverine habitat suitability model (Paper III) and Circuitscape software V3.5.1 (McRae and Shah 2009) to identify the relative value of lands for their potential contribution to wolverine dispersal/gene flow within the western United States. Circuitscape is based on electrical flow theory where dispersing animals (modelled as electrical charges) move between sources or core habitats (modelled as + and - poles) through a landscape modelled as a resistor network (McRae 2006, McRae et al. 2008). We included as source areas all patches of primary wolverine habitat within the western U.S. that were >241 km^2 (Paper I, Paper III). We defined the intervening resistance surface by taking the inverse of the scaled habitat suitability score (where initial values were between 0 and 100, 100 being the best), and then squaring the values (McRae and Shah 2009). We generated Circuitscape paths between each source patch and all other source patches that were a) within 250 km of each other based on observed dispersal movements of wolverines (Vangen et al. 2001, Paper I), and b) within direct line of sight of each other and shared at least one compass degree of direct exposure. We set the level of “charge,” or potential for producing dispersers, for each source habitat patch based on the relative number of female wolverine territories the patch could contain. We then allocated a source patch’s charge among the selected neighbouring patches in inverse proportion to their individually recorded resistances (Bergen et al. unpublished manuscript). We used pairwise mode to generate current and resistance. We then summed the values of all calibrated corridors to yield an estimate of relative metapopulation-level dispersal significance of each 360 m pixel. We then classified all pixels as percentiles of conductance, which approximates wolverine dispersal/gene flow potential.

3 Results and Discussion

3.1 Spatial Ecology and the Wolverine Niche (Paper I)

Wolverines selected for high elevations (>2,600 m) and against low elevations (<2,150 m; Fig. 1). Home ranges were large relative to body size, averaging 303 km^2 for adult females and 797 km^2 for adult males. Extensive movements throughout the annual home range occurred over brief time intervals for both sexes. Wolverines utilized an area ≥75% of their multi-year MCP home range size in an average of 4.6 weeks (32 days; range = 1–7 weeks). Overlap of home ranges between adult wolverines of the same sex was minimal and the shared area was <2% of either home range in all but one case. In two cases extensive GPS data did not reveal any significant forays into an adjacent same-sex territory, rather it confirmed the lack thereof (Fig. 2). Model weighted average population estimate within the study area was 15.2 wolverines (95% CI = 12.3–42.0) with individual estimates ranging from 13.9–18.2 wolverines. This yielded a density estimate of 3.5 wolverines/1,000 km^2 of area >2,150 m LAE (95% CI = 2.8–9.6). Average maximum distance per dispersal-related movement was 102 km for males (n = 10, SE = 16.4 km) and 57 km for females (n = 15, SE = 13.5 km). Maximum dispersal distance from the mother's home range centre was 170 km for males and 173 km for females.

Figure 2. GPS locations of 2 adult female wolverines with adjacent home ranges, Greater Yellowstone, USA, Feb–Apr 2007.

By synthesizing information on spatial ecology at the edge of distribution, where both suitable and unsuitable conditions exist

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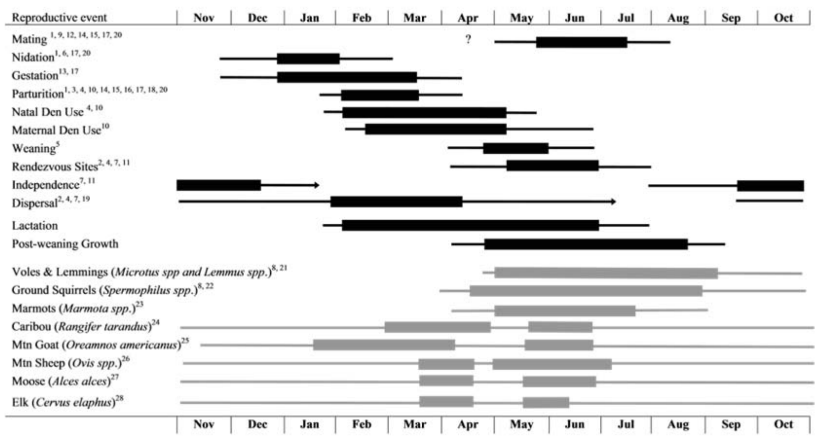
in close proximity, clear patterns emerge and help clarify the wolverine's niche. In the presence of a diverse assemblage of ungulates and carnivores at the southern periphery of their distribution, wolverines select high elevation habitats where there is deep snow during winter, the growing season is brief, and food resources are relatively limited. While most large carnivores (e.g., bears, wolves, and cougars) either hibernate or migrate along with elk and deer herds during winter, the wolverine remains active at higher elevations, utilizing its large feet to patrol a vast, frozen territory that is covered in snow. Successful exploitation of these unproductive environments requires large home ranges that are regularly traversed, territories that provide exclusive intra-specific access to resources, and low densities. These characteristics, along with low reproductive rates, are prevalent throughout the species range (Magoun 1985, Copeland 1996, Landa et al. 1998, Persson et al. 2006, Golden et al. 2007, Inman et al. 2007*a*, Lofroth and Krebs 2007, Persson et al. 2010, Royle et al. 2011). When viewed together, these characteristics indicate that wolverines are specifically adapted to exploit a cold, unproductive niche where resources are scarce and interspecific competition is limited.

3.2 Caching as Behavioural Key for Niche Occupation (Paper II)

We identified the chronology of wolverine reproductive events with a comprehensive literature review along with data from captive facilities and unpublished field studies (Fig. 3). Wolverines have evolved to time the energetically demanding periods of lactation and post-weaning juvenile growth to occur earlier than other non-hibernating northern carnivores. Our examination suggests this timing is adaptive because it allows wolverines to take advantage of a cold, low-productivity niche (Copeland et al. 2010, Paper I) by appending the scarce resources available during winter (Magoun 1985, Persson 2005) to the brief period of summer abundance (Fig. 3). The wolverine's bet-hedging reproductive strategy appears to require success in two stages. First, they must fuel lactation (Feb–Apr) with caches amassed over winter or acquisition of a sudden food bonanza (e.g., winter-killed ungulate), otherwise early litter loss occurs. Next, they must fuel the majority of post-weaning growth during the brief but relatively reliable summer period of resource abundance. The first stage is likely dependent on scavenged ungulate resources over most of the wolverine's range, whereas the second stage varies by region. In some regions the second stage may continue to be focused on scavenging ungulate remains that have been provided by larger predators. In other regions the second stage may be focused on predation by wolverines on small prey or neonatal ungulates. During all seasons and regions, caching in cold, structured micro-sites to inhibit competition with insects, bacteria, and other scavengers is likely a critical behavioral adaptation because total food resources are relatively limited within the wolverine's niche. Habitat features that facilitate caching, e.g., boulders and low ambient temperatures, are likely important and could be related to the limits of distribution. We propose a 'refrigeration-zone' hypothesis as a food-based explanation for the correlation between wolverine distribution and persistent spring snow cover (Copeland et al. 2010). This concept fits well with other characteristics that have been measured for wolverines, i.e. their spatial ecology (Persson et al. 2010, Paper I), low densities (Golden et al. 2007, Lofroth and Krebs 2007, Royle et al. 2011, Paper I), and low fecundity (Magoun 1985, Copeland 1996, Persson et al. 2006, Inman et al. 2007*a*)). Our examination of the wolverine's reproductive chronology suggests it is important to include summer foods and the influence of climate on competition for food as potential drivers of wolverine population dynamics. By doing so, the causes of projected declines due to climate change, should they occur, may be better understood and acted upon.



1. Banci and Harestad 1988
2. Copeland 1996
3. Davis 1967
4. Inman et al. 2007a
5. Iverson 1972
6. Liskop et al. 1981
7. Magoun 1985
8. Magoun 1987
9. Magoun and Valkenburg 1983
10. Magoun and Copeland 1998
11. May 2007
12. Mead et al. 1991
13. Mead et al. 1993
14. Mehrer 1975
15. Mohr 1938
16. Pulliainen 1968
17. Rausch and Pearson 1972
18. Shilo and Tamarovskaya 1981
19. Vangen et al. 2001
20. Wright and Rausch 1955
21. Pugh et al. 2003
22. Yensen and Sherman 2003
23. Armitage 2003
24. Miller 2003
25. Côtè and Festa-Bianchet 2003
26. Krausman and Bowyer 2003
27. Bowyer et al. 2003
28. Raedeke et al. 2002

Figure 3. Range (thin line) and peak (thick line) time periods of wolverine reproductive biology and availability of food items.

3.3 Mapping the Metapopulation's Niche and Developing Conservation Priorities (Paper III)

Wolverines selected areas of higher elevation, where there was steeper terrain, more snow, fewer roads, less human activity, and which were closer to high elevation talus, tree cover, and areas with April 1 snow cover. The k-fold cross validation score for the training locations indicated an excellent model fit (r_s = 0.98, SE = 0.005). The model also tested well using k-fold cross validation and various wolverine location datasets that were not used for training (Table 2), suggesting it is robust to extrapolation and useful for developing collaborative conservation strategies at the multi-state scale necessary for this species. Predicted habitat scores ≥0.982 represented primary wolverine habitat, i.e., areas suitable for survival and use by resident adults (Fig. 4). Ninety-one percent of primary habitat existed in 132 patches >100 km^2 that were distributed across 10 of the 11 western states. Six patches were >5,000 km^2 and occurred in the Northern Continental Divide, Salmon-Selway, Greater Yellowstone, and Southern Rockies regions (Fig. 5). We classified areas scoring ≥0.983 as maternal habitat (Fig. 4), the total area of which was 31% of the area classified as primary habitat. The lowest habitat value used by dispersing wolverines was 0.981 for females and 0.943 for males, and we used these to map areas suitable for dispersal for each sex (Fig. 4). Areas we predicted suitable for male dispersal linked all primary habitat patches >100 km^2. Habitats predicted suitable for female dispersal were distributed such that virtually all primary habitat patches in Montana, Idaho, western Wyoming and Utah are linked or very nearly so (<3 km) for female interchange. Large patches of primary habitat that appear isolated for females included the Sierra-Nevada of California, the southern Rockies of Colorado, and the Bighorn Range of northeastern Wyoming (Figs. 4 and 5). We estimated potential population capacity in the western contiguous U.S. to be 580 wolverines (95% CI = 454–1724) in the hypothetical case where all available primary habitat patches >100 km^2 were occupied (Table 3, Fig. 5). Sixty-one percent of this population capacity occurred in the combined Greater Yellowstone, Salmon-Selway, Central Linkage, and Northern Continental Divide ecosystems (Table 3, Fig. 5). We estimated that the Southern Rockies represent approximately 23% of total population capacity. We estimated current population size to be 310 wolverines (95% CI = 242–908; Table 3, Fig. 5) in the western contiguous U.S.

Our analysis suggests suitable habitat for resident adults and reproduction exists in island-like fashion distributed across 10 states (~2.5 million km^2) and has the capacity for approximately 600 individuals. The small wolverine metapopulation of the western contiguous U.S. is subject to the cumulative

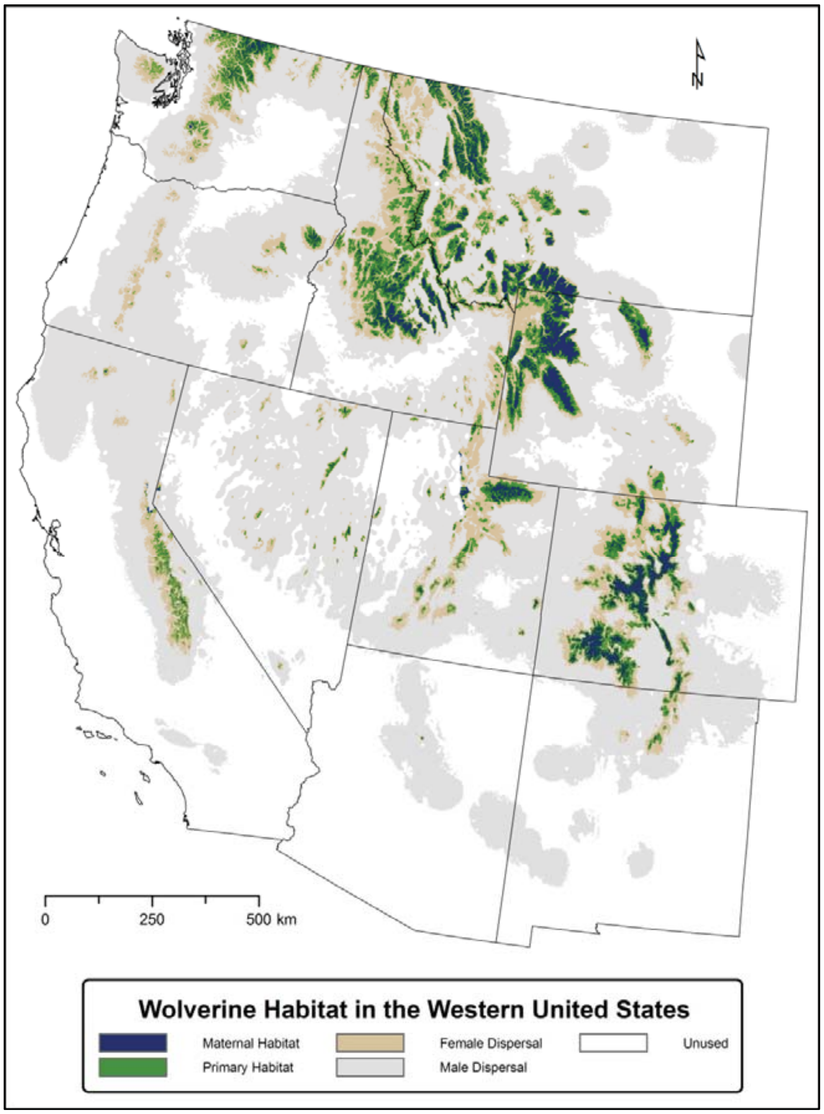


Figure 4. Areas of the western United States predicted to be maternal wolverine habitat (suitable for use by reproductive females), primary wolverine habitat (suitable for survival, i.e., use by resident adults), female dispersal habitat (suitable for relatively brief female dispersal movements), and male dispersal habitat (suitable for relatively brief male dispersal movements) based on resource selection function modeling developed with wolverine telemetry locations from the Greater Yellowstone Ecosystem, of Montana, Idaho, and Wyoming, USA, 2001–2010.

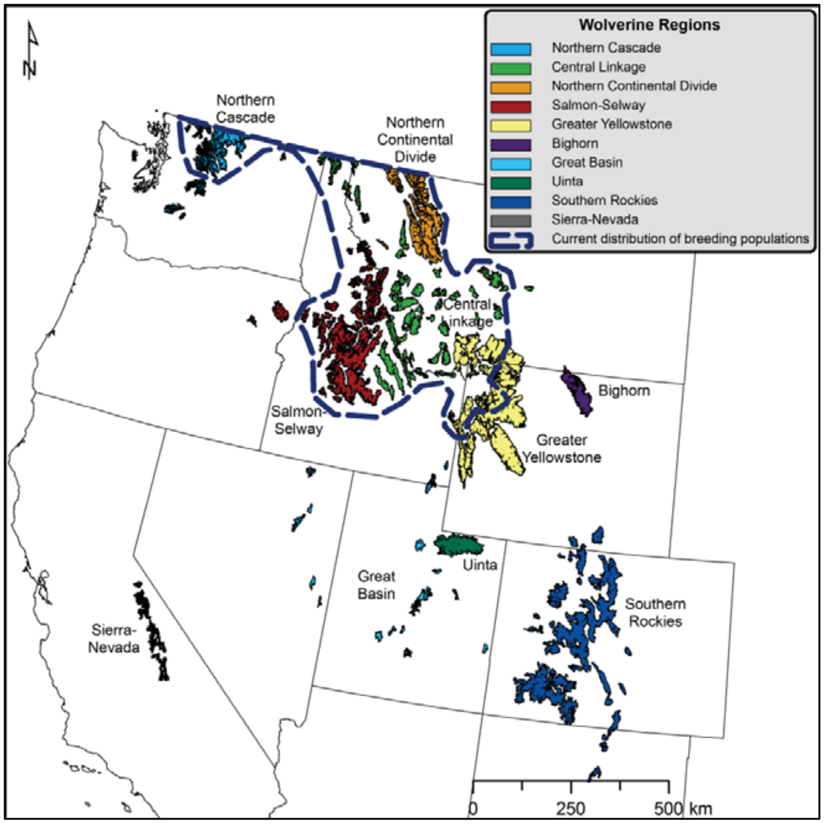


Figure 5. Major blocks (>100 km^2) of primary wolverine habitat (suitable for use by resident adults) in the western United States as predicted with a first order (species distribution) logistic regression and grouped into useful management regions. Current distribution of breeding populations based on contemporary records are also depicted with the dashed line.

influences of numerous jurisdictional authorities, therefore coordinated planning and management to achieve specific functions at the landscape-scale is warranted. For example, the Central Linkage Region (CLR; Fig. 5) consists of a large number of fairly small habitat patches that contain reproductive females and sit between the major ecosystems of the Northern U.S. Rockies. Maintaining high adult female survival and reproductive rates in the CLR would likely benefit metapopulation demographics and gene flow. Recent changes to wolverine trapping regulations in Montana were designed with this landscape-level goal in mind (Montana Fish, Wildlife and Parks 2008). However, successfully achieving dispersal/gene flow in the Northern U.S.

Table 3. *Estimates of wolverine population capacity and current population size by region (as in Fig. 5) in the western contiguous United States based on resource selection function habitat modeling of wolverine telemetry data.*

Region	Population Capacity Estimate (95% CI)[a]	Current Population Estimate (95% CI)[a]
Northern Cascade	35 (27–105)	31 (25–89)
Northern Continental Divide	51 (41–143)	51 (41–143)
Salmon-Selway	105 (84–310)	101 (81–295)
Central Linkage	75 (53–236)	75 (53–233)
Greater Yellowstone	135 (109–381)	52 (42–148)
Bighorn	15 (12–42)	0
Uinta	19 (15–52)	0
Great Basin	7 (4–39)	0
Sierra-Nevada	7 (5–29)	0
Southern Rockies	131 (104–387)	0
Western United States	580 (454–1724)	310 (242–908)

[a] Estimate of capacity within each primary habitat patch >100 km^2 was rounded down to the nearest integer and then summed by region. Estimates based on population size of 15.2 wolverines (95% CI = 12.3–42.0) in the Yellowstone study area where 11 individuals were known to be on the area and 20 was considered a reasonable upper limit (Paper I).

Rockies could also depend on other jurisdictions acting upon the same objective. For example, public land managers in the CLR could need to address winter recreation management (Krebs et al. 2007) such that reproductive rates are not encumbered, and a multitude of entities may need to secure the natural areas and highway crossings that would allow for successful dispersal through the CLR decades from now. Clearly, geographically coordinated goals will be key to successfully conserving this wolverine metapopulation.

Wolverines of the contiguous U.S. are dependent on successful dispersal among patches of habitat across a vast geographic scale. Given the accelerated development of private lands in valley bottoms across the western U.S. in recent decades (Johnson and Beale 1994, Brown et al. 2005, Gude et al. 2007, Gude et al. 2008), maintaining a network of natural areas among the patches of suitable reproductive habitat will be critical for long-term wolverine persistence. While there is no indication that dispersal is currently being limited by human development in a manner that has negative consequences for the wolverine metapopulation, it is reasonable to assume that willingness to disperse through developed areas and/or survival of dispersers moving through developed areas would be impacted by increasing road and housing densities at some point. Because housing developments and roads are relatively permanent and unregulated compared to human activities that might affect survival and reproductive rates (e.g., trapping and winter recreation), working to establish natural areas in locations most suitable for wolverine dispersal and movements of other wildlife species is important. The CLR appears to be a logical priority for wolverine connectivity efforts; the CLR and the 3 major core areas it sits between contain an estimated 90% of the current population and are connected to populations in Canada (Lofroth and Krebs 2007).

Our estimate of current population size was approximately half of capacity and was limited to portions of four states. Restoring wolverines to the Southern Rockies could substantially increase population size, genetic diversity, and resiliency and could function to establish a refugia for the species as climate change occurs. Recent records of wolverines in California during 2008 and Colorado during 2009 were both instances of individual males (Moriarty et al. 2009, Inman et al. 2009). While these dispersal events suggest the possibility of natural recolonization, it is important to consider that female wolverines have not been documented in either state for nearly a century, and our analysis suggests that female dispersal to either area is likely to be rare if possible at all (Fig. 4). As such, active restorations may be required to re-occupy these areas and could be viewed as proactive steps toward wolverine recovery in the contiguous U.S. Given the restricted number of haplotypes (low genetic variation) in the Northern U.S. Rockies (Schwartz et al. 2009), restorations could greatly improve genetic composition relative to natural recolonization. While climate change will not likely improve the suitability of wolverine habitat in the Southern Rockies or Sierra-Nevada, it is possible that by 2100 these areas may be some of the best remaining wolverine habitat within the contiguous U.S. (McKelvey et al. 2011, Peacock 2011). It is also possible that rugged, high elevation areas could retain the characteristics necessary for the wolverine's niche to a greater degree than the lower elevations and flatter topography of much of the species' northern distribution. If this were the case, mountainous areas even at the southern edge of distribution could act as continental-level refugia.

Despite the relatively vulnerable position that wolverines are in, our knowledge of fundamental population characteristics such as current distribution of reproductive females and population trajectory is lacking or based on sparse data. For instance, during the 11-yr period 1995–2005 only 15 verifiable records of wolverine occurrence that did not arise from opportunistic telemetry studies exist from within the states of Washington, Idaho, and Wyoming (Aubry et al. 2007). Because wolverines naturally exist at such low densities and inhabit rugged, remote terrain, even drastic changes in population size would likely go unnoticed for years if the current level of monitoring were to continue. Given the anticipated effects of climate change, there is clearly a need for an effective monitoring program that is designed at the metapopulation level to inform specific management actions. Because such a program would require a sampling effort distributed across several western states/provinces in extremely rugged and remote terrain that is accessed during winter, it must be well designed and highly coordinated. Our analysis provides an initial hypothesis for wolverine distribution and abundance that can be tested and refined by future surveys (see Table S3 in Paper III).

3.4 Wildlife as Public Domain: Endangered Status, Connectivity, and Critical Habitat of the Wolverine (Paper IV)

The greatest potential for wolverine dispersal was concentrated in western Montana and along Montana's borders with Idaho and Wyoming proximate to this area (Fig.6). We refer to this general area as the Central Linkage Region (CLR) because it sits between 3 large blocks of publically owned lands in the Northern U.S. Rockies: the Northern Continental Divide, Salmon-Selway, and Greater Yellowstone Ecosystems (Fig. 5). Our result was scalable and can identify highest priority areas at the multi-state level or within a local geography. Total area ranked ≥98.5th percentile (top 1.5%) of the western U.S. was 46,069 km^2. Fifty-six percent of this top 1.5% of non-source, connectivity habitat was in public ownership, whereas 44%, or 20,306 km^2 (approximately 5 million acres) was in private ownership.

3.4.1 Metapopulation connectivity

Our connectivity analysis further highlights the importance of maintaining connectivity in the CLR to ensure wolverine persistence in the contiguous U.S. The CLR contains reproductive female wolverines (Anderson and Aune 2008), and sits between 3 of the largest areas of source wolverine habitat in the contiguous U.S. (Paper III). Together with the large ecosystems it connects, this area also represents the vast majority of suitable habitat presently occupied by reproductive females (Aubry et al. 2007, Paper III). While both the Southern Rockies and Sierra-Nevada may play an important role for wolverines if populations returned or were restored, our analysis suggests that the Sierra-Nevada would provide a greater degree of population redundancy (separation beneficial in case of disease etc.) whereas the Southern Rockies would provide more resiliency via genetic interchange.

3.4.2 Wolverines, connectivity, and critical habitat.

We estimated that nearly half of the highest-quality wolverine connectivity habitat is privately owned. Significant blocks of private land sit between

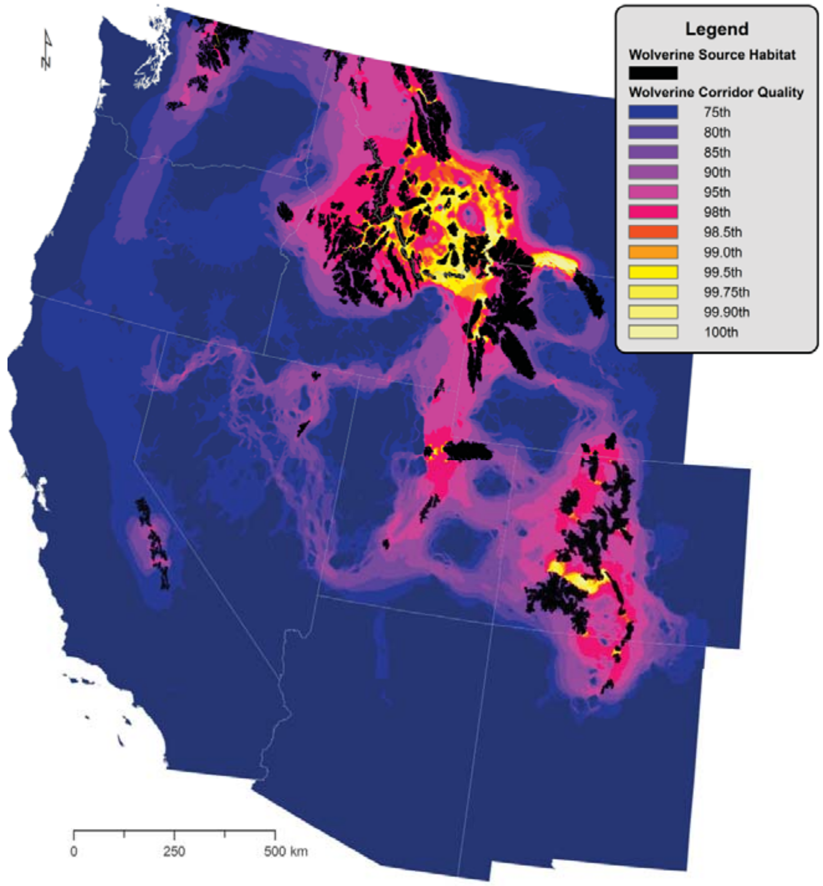


Figure 6. Relative value of lands across the western United States for wolverine dispersal and gene flow as determined by Circuitscape corridor analysis. Circuitscape is based on the theory of electrical current flow between "poles" across a "resistance surface." In this analysis, patches of wolverine habitat of high enough quality for use by resident adults are "sources" that represent an electrical pole (black patches). Relative corridor quality across the metapopulation, i.e., "conductance" or dispersal/gene flow potential, is displayed based on percentiles of total area where lighter colored areas (yellow) represent the greatest potential for dispersal and darker areas (blue) represent the least potential for dispersal.

publically owned wolverine habitats and are subject to potential development. We therefore argue that loss of connectivity is as significant of a threat to wolverine persistence as climate change. The Fish and Wildlife Service (FWS; 2010) considered climate to be a significant threat based on: 1) forecasts of weather scenarios that have a degree of uncertainty; 2) an unknown specific threshold at which climate will reduce survival, recruitment, or gene flow; and 3) a 50–100 year time-frame over which changing conditions will threaten population viability. We suggest that 1) it is possible to forecast housing development with a similar degree of certainty as can be achieved for climate change (e.g., Gude et al. 2007); 2) that although the threshold of housing development required to reduce survival and gene flow is also undefined, the exact mechanisms by which wolverines would be impacted (road-kill and reduced permeability) are better established within the wildlife literature (e.g., Seiler 2003, Schwartz et al. 2010) than the specific mechanisms regarding wolverines and climate change (Copeland et al. 2010, Paper II); and 3) there is no less certainty regarding the time frame over which loss of connectivity will begin impacting individuals and populations. In addition, because climate change is borderless, the impact could continue even if greenhouse gas emissions were regulated. Therefore if similar logic were applied to connectivity, FWS could designate dispersal corridors as critical habitat.

However, private property rights are a highly provocative issue, so establishing dispersal corridors as critical habitat and attempting to regulate development of private lands would be a poor choice for conservation because of the backlash this would likely cause. Regulating would also be profoundly unfair to rural landowners and could eventually erode support for endangered species conservation (Ruhl 1998). In order to achieve wolverine persistence, distribute the financial burden for doing so equitably, and reward (rather than punish) those who have maintained lands in a state that continues to function for wildlife, new financial incentives that can benefit rural counties and non-affluent landowners must be developed. This action and others of significance for wolverine persistence in the contiguous U.S. (Paper III) will require substantial increases in funding available for non-game wildlife. This wolverine-specific situation represents a larger and fundamental problem for conservation: How do we equip the Institution of the state wildlife agency with the means necessary for successfully conserving habitat and non-game species through the 21st century?

3.4.3 Wolverines and the conservation Institution for the 21st century

The wolverine, with its susceptibility to climate change and the nature of its small metapopulation occurring over a vast geographic area, is emblematic of several of the major conservation challenges that lie ahead in the 21st century. The very foundation of conservation is foremost among them – our system for financing the scientific research and conservation actions that translate our laws/desires into reality on the ground (Jacobson et al. 2010).

When the North American Model of Conservation (Organ et al. 2010) was developing at the beginning of the 20th century, unregulated, intentional mortality *was* the major conservation issue. But this issue has largely been addressed with nearly 100 years of effort founded on a legal system and dedicated funding from sportsmen. However, wolverines are now threatened by indirect, habitat-related factors such as climate change and connectivity at the landscape scale. Importantly, these 21st century issues are the result of impacts from all of society, not just those who harvest game. Today, everyone who drives a car or consumes goods and services impacts wildlife, both game and non-game, and the concept of the "non-consumptive user" is outdated and unrealistic. While society's interest in conserving non-game species has increased, the current sportsman-based funding system simply cannot meet the needs of wolverines and hundreds of other non-game species over the coming century in addition to those for which the state agencies are already responsible. "More than 1,000 species are listed under the federal Endangered Species Act and State Wildlife Action Plans identified over 12,000 species that are at-risk and likely headed to federal listing unless proactive action is taken" (Association of Fish and Wildlife Agencies 2011).

Jacobson (2008) and Jacobson et al. (2010) provide a thoughtful assessment of this situation. While we generally agree with their 4 ideal components of a "reformed" Institution of the state wildlife agency (broad-based funding, trustee-based governance, multidisciplinary science, and diverse stakeholder involvement), we offer here some suggestions and nuances.

Solving this problem requires all wildlife enthusiasts recognize that we in our entirety are a minority special interest group, and that continued support for the Public Trust Doctrine upon which conservation is founded can erode. We must therefore build out from our current and somewhat fractured base into a larger constituency. Step one is securing the commitment of traditional wildlife supporters (sportsmen). Key elements therein are a) a dialog that recognizes and respects the culture and achievements of sportsmen (e.g., "expanding the historically successful model" as opposed to "reforming to remain legitimate"), and b) assuring that their activities will remain a priority component of an expanded Institution. Step two is expanding Institutional mission to include wildlife biodiversity and outdoor enthusiasts. The Missouri Department of Conservation provides a good example of successfully working with the public to broaden their scope in ways that their public was willing to finance (see

Jacobson 2008, Ch. 4). We suggest focusing initially on expanding user-based funding with a public land recreational license and an excise tax on a broader range of outdoor gear. Jacobson et al. (2010) recommend against this due to the potential for the number of supporters to wane (e.g., hunter numbers). In reality though, all revenue sources (sales tax, portion of gambling revenues, etc.) are subject to wane if public support diminishes for any reason. Sportsmen along with biodiversity and outdoor enthusiasts are the people most interested in conservation and therefore probably most reliable over the long term. By building a core of support among these users, any ebb of support from the non-interested public could be buffered. As evidenced in Missouri, a thoughtful process of public outreach can result in a cycle of facilities development, new constituents, and improved support (Jacobson 2008). Step three is expanding Institutional mission to the non-wildlife-oriented public. This is key to a durable solution because this segment includes the majority of the public. This could be accomplished by linking biodiversity monitoring to water quality programs as applied components of public school science and math curricula. By using biodiversity to monitor factors that influence local human health, more of the non-wildlife-oriented public will find value in biodiversity and be willing to support the mission of state wildlife agencies. Integrating students into the process could provide many secondary benefits. For instance, students could gain direct experience recognizing local environmental problems, creating solutions, and governing factors that influence them.

Over the last century, sportsmen and the hunting/fishing industry have developed an investment feedback loop where their dollars have funded maintenance of a natural resource (game species) whose increase has led to 37 million annual users driving a $75 billion annual economy that invests $2.5 billion in dedicated, wildlife-specific funds to conservation each year (Loftus et al. 2011*a*, 2011*b*, 2011*c*; U.S. Fish and Wildlife Service 2012). The opportunity exists to broaden this proactive feedback loop and its conservation impact with investments in infrastructure that facilitates outdoor recreation (e.g., hut-to-hut cross country ski system), non-game related activities (e.g., birding facilities and events), and public education (e.g., student water quality monitoring). Taking advantage of this opportunity will increase the number of constituents for the Public Trust Doctrine that is the foundation of wildlife conservation. It could also provide significant benefits to public health, education, and quality of life. The continued viability of the wolverine in the contiguous United States, a candidate endangered species threatened by climate change and other modern impacts derived from all of society, depends on a fundamental shift in the way conservation of non-game wildlife and habitat are financed.

4 Wolverine Conservation in the Western United States

4.1 The Niche: Different Centuries, Similar Vulnerability

Wolverines are morphologically, demographically, and behaviourally adapted to exploit cold, low productivity environments where snow is present much of the year (Copeland et al. 2010, Papers I and II). This niche results in inherently vulnerable populations due to their low densities and limited capacity for growth. The once-extirpated wolverine population of the contiguous U.S. has responded positively to the regulation of intentional human-caused mortality that was the major thrust of wildlife conservation during the 20th century. However, because of the unproductive niche wolverines have evolved to occupy, this species will be vulnerable again, this time to the conservation challenges of the 21st century such as roads, rural sprawl, recreation, and climate change (Gude et al. 2007, Krebs et al. 2007, Packila et al. 2007, McKelvey et al. 2011).

4.2 Conservation Priorities at Scale

The wolverine metapopulation of the contiguous U.S. is cumulatively influenced by a complexity of land ownerships and management authorities. Clearly, implementation of conservation strategies that address wolverine needs in a coordinated fashion across this vast geography is needed to ensure persistence (Papers I and III). Through identification of suitable habitats, population capacities, and areas where dispersal potential is greatest for the metapopulation (Papers III and IV), we were able to identify priority conservation actions. These include:

1. Securing connectivity in the Central Linkage Region,
2. Restoring populations to the Southern Rockies, and
3. Establishing a coordinated metapopulation-wide monitoring program.

By elucidating metapopulation-level functions for specific geographies, organizations with varied goals can better focus their resources on specific actions that would benefit wolverines in a coordinated fashion. Securing connectivity in the Central Linkage Region is likely critical for achieving sufficient dispersal and gene flow throughout the core population of the Northern U.S. Rockies. Our connectivity analysis (Paper IV) can aid this process by identifying areas where the probability of wolverine dispersal is greatest at a variety of operational scales. Additional efforts to ensure adequate survival and reproductive rates may be necessary for the Central Linkage Region to function successfully (e.g., harvest and winter recreation). Restoration to the Southern Rockies could increase population size by >30% and establish a genetically diverse population in an area that may be robust to climate change (McKelvey et al. 2011, Peacock 2011). If restorations were to take place, Paper III can aid in determining release locations and initial population targets. In the absence of an established monitoring program, drastic changes in wolverine population numbers would likely go undetected for years. Given their small population size and the assumption that climate will negatively influence wolverines (U.S. Fish and Wildlife Service 2010), a monitoring program that defines distribution and identifies factors influencing vital rates is warranted. Paper III provides an initial hypothesis for wolverine distribution and abundance that can be tested and refined (see Table S3 in Paper III). Because wolverine populations in British Columbia and Alberta are proximate to core wolverine areas of contiguous U.S., provincial participation is likely important.

4.3 Looking Back from Century 22: Wolverines and the Necessity of Broadening the North American Model

Accomplishing the actions outlined above will require funding in excess of that available for wolverines at present. Wolverine conservation in the contiguous U.S. provides a specific example of the present mismatch between society's articulated desire to conserve the native fauna and its willingness to fund the actions necessary to do so. The continued viability of the wolverine in the contiguous United States, a candidate endangered species threatened by climate change and other modern impacts derived from all of society, depends on a fundamental shift in the way conservation of wildlife and habitat are financed. Many great conservation successes were made during the 20th century. Fulfilling the Public Trust Doctrine and passing the conservation legacy on to those of the 22nd century requires us to act now to broaden the mission, constituency, and funding base of state wildlife agencies.

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