Wolverine Ecology and Conservation in the Western United States

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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.

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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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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).

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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♀,
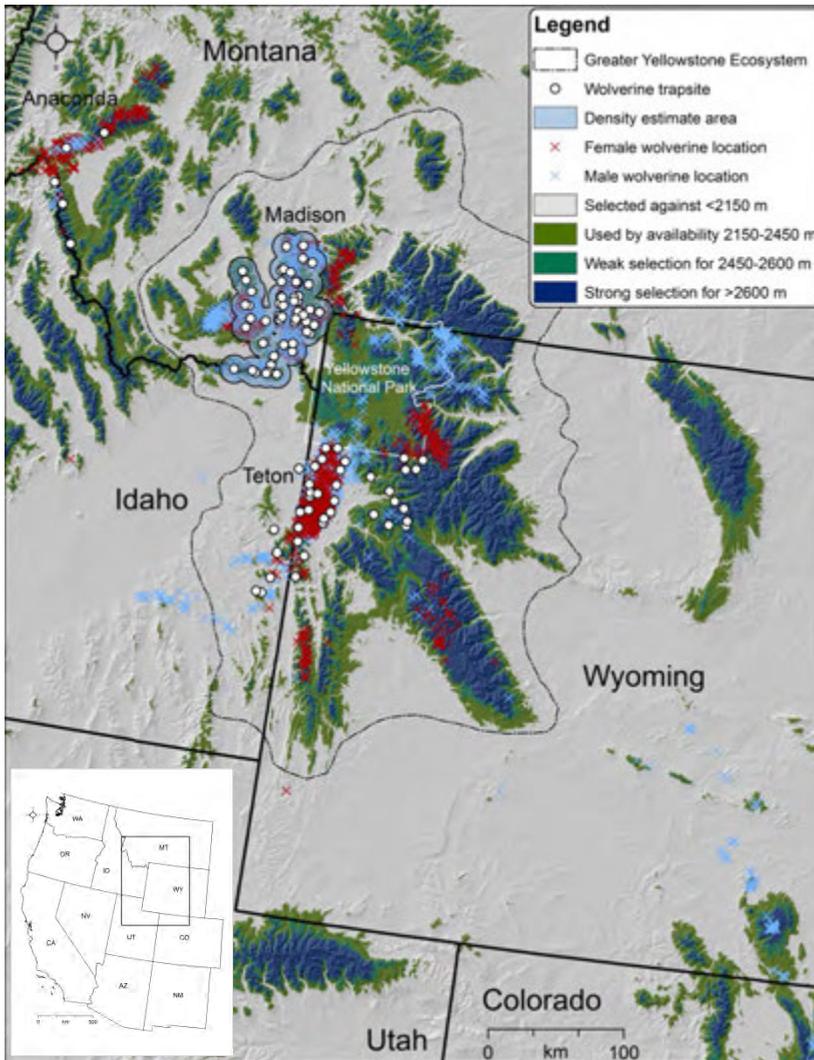
Figure 1. Map of the Greater Yellowstone Ecosystem and surrounding areas showing the three primary areas of wolverine capture and data collection (Madison, Teton, and Anaconda), 2001–2010. Trap locations, wolverine locations, and the density estimate area are displayed. Annual wolverine habitat selection 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.

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

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

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. 2007a)). 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.
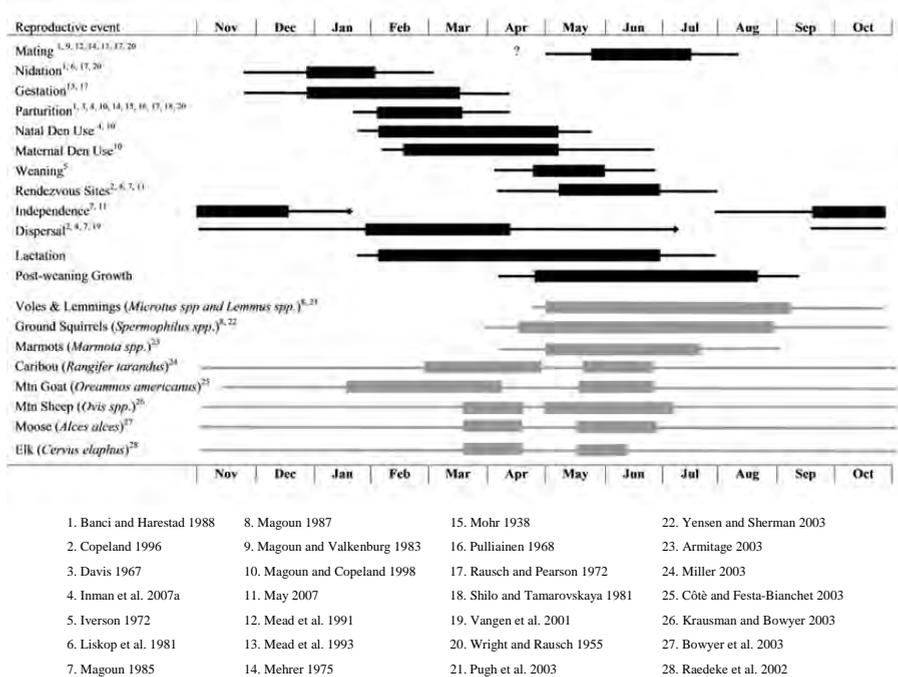

Reproductive event	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct

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
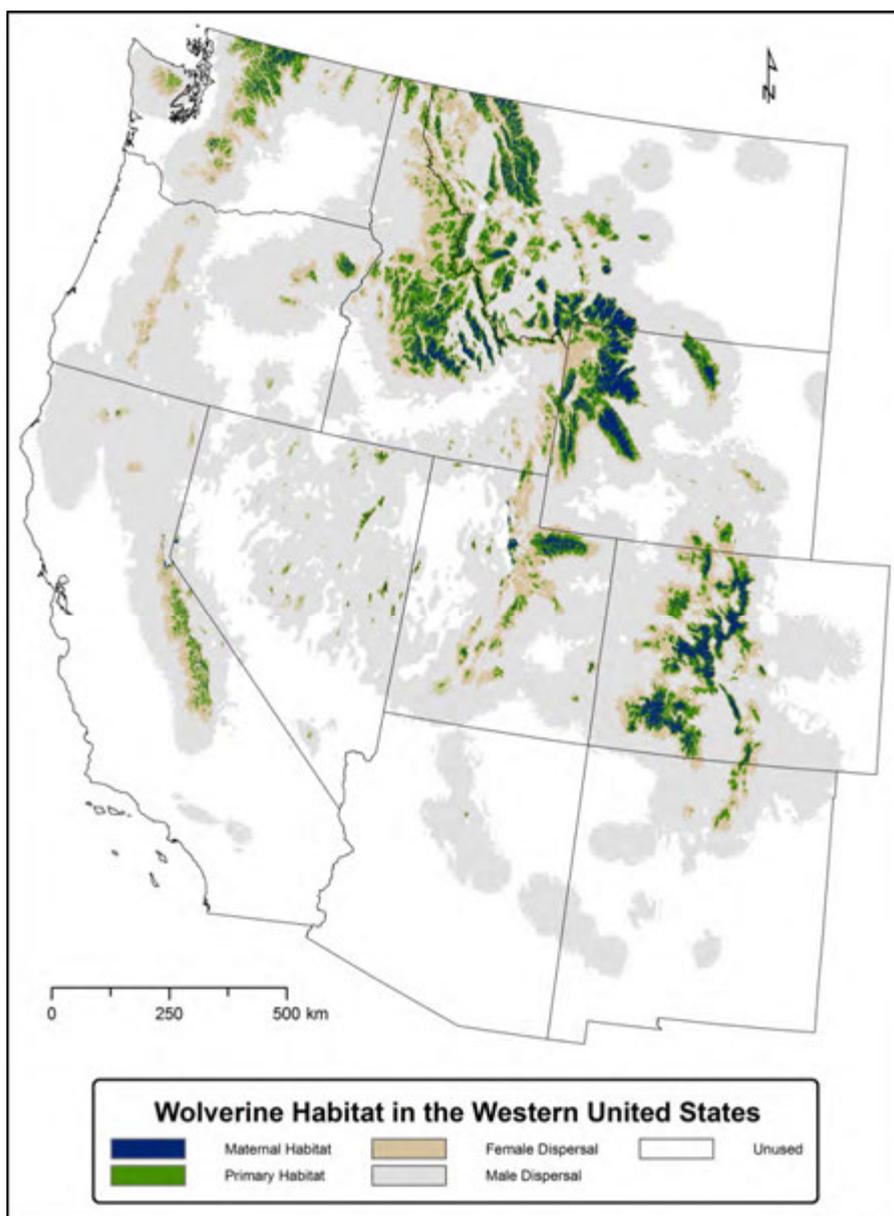
Figure 4. Areas of the western United States predicted to be maternal wolverine habitat (suitable for use by reproductive females), primary wolverine habitat (suitable for survival, i.e., use by resident adults), female dispersal habitat (suitable for relatively brief female dispersal movements), and 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.
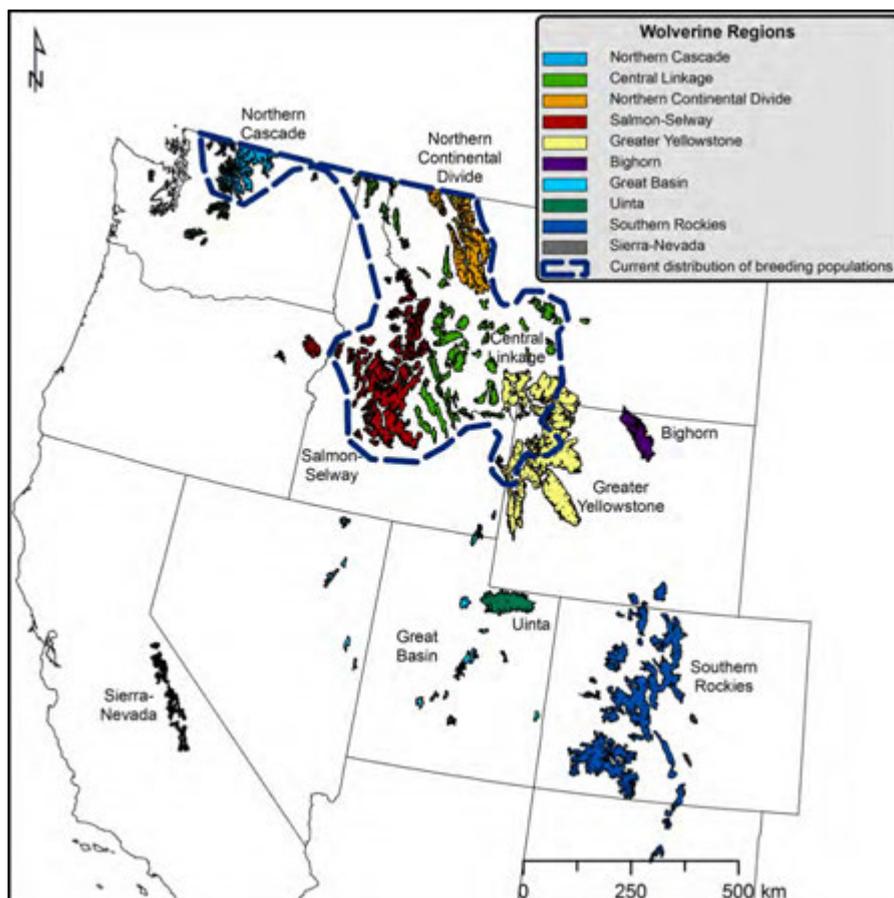
Figure 5. Major blocks (>100 km^2) of primary wolverine habitat (suitable for use by resident adults) in the western United States as predicted with a first order (species distribution) logistic regression and grouped into useful management regions. Current distribution of breeding populations based 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
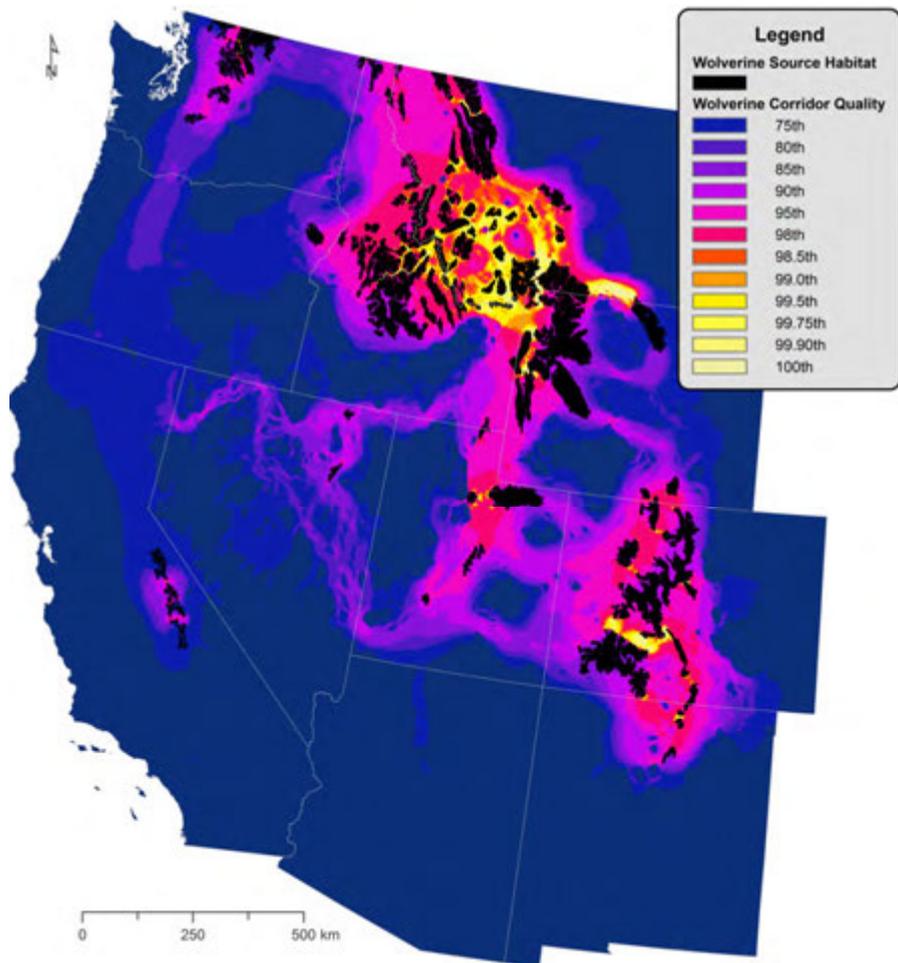
Figure 6. Relative value of lands across the western United States for wolverine dispersal and gene flow as determined by Circuitscape corridor analysis. Circuitscape is based on the theory of electrical current flow between "poles" across a "resistance surface." In this analysis, patches of wolverine 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 eluctidating 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.

References

Anderson, N.J. and K.E. Aune. 2008. Fecundity of female wolverine in Montana. *Intermountain Journal of Science* 14 (1–3):17–30.

Armitage, K.B. 2003. Marmots (*Marmota monax* and Allies). Pages 188–210 in G.A. Feldhamer, B.C. Thompson, and J.A. Chapman, editors. *Wild mammals of North America, biology, management, and conservation, Second edition*. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Association of Fish and Wildlife Agencies. 2011. *President's Task Force on Wildlife Diversity Funding. Final Report, September 1, 2011*. http://www.fishwildlife.org/files/President_s TaskForceonWildlifeDiversity_Funding_FINAL-REPORT.pdf >

Aubry, K.B., K.S. McKelvey, and J.P. Copeland. 2007. Distribution and broadscale habitat relations of the wolverine in the contiguous United States. *Journal of Wildlife Management* 71(7):2147–2158.

Bailey, V. 1930. *Animal life of Yellowstone National Park*. Charles C. Thomas, Springfield, Illinois, USA.

Banci, V. 1987. *Ecology and behavior of wolverines in Yukon*. MSc Thesis, Simon Fraser University, Burnaby, British Columbia, Canada.

Banci, V. 1994. Wolverine. Pages 99–127 in L.F. Ruggiero, K.B. Aubry, S.W. Buskirk, L.J. Lyon, and W.J. Zielinski, editors. *The scientific basis for conserving forest carnivores, American marten, fisher, lynx, and wolverine in the western United States*. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report RM–254, Fort Collins, Colorado.

Banci, V., and A. Harestad. 1988. Reproduction and natality of wolverine (*Gulo gulo*) in Yukon. *Annales Zoological Fennici*. 25:265–270.

Bean, M.J., and M.J. Rowland. 1997. *The Evolution of National Wildlife Law, Third Edition*. Praeger Publishers, Westport, Connecticut, USA.

Bergen, S., J. Beckman, and R.M. Inman. Unpublished manuscript. *Using circuit theory-based models to assess potential linkage zones for bears between Greater Yellowstone and the northern Rockies*.

Bowyer, R.T., V. Van Ballenberghe, and J.G. Kie. 2003. Moose (*Alces alces*). Pages 931–964 in G.A. Feldhamer, B.C. Thompson, and J.A. Chapman, editors. *Wild mammals of North*

America, biology, management, and conservation, Second edition. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Boyce, M.S., and L.L. McDonald. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution 14(7):268–272.

Boyce, M.S., P.R. Vernier, S.E. Nielsen, and F.K.A. Schmiegelow. 2002. Evaluating resource selection functions. *Ecological Modelling* 157:281–300.

Brown, D.G., K.M. Johnson, T.R. Loveland, and D.M. Theobald. 2005. Rural land-use trends in the conterminous United States, 1950–2000. *Ecological Applications*. 15(6):1851–1863.

Burnham, K.P. and D.R. Anderson. 2002. *Model Selection and Multimodel Inference: A Practical Information–theoretic Approach. Second edition*. Springer Science + Business Media, LLC, New York, New York, USA.

Copeland, J.P., E. Cesar, J.M. Peek, C.E. Harris, C.D. Long, and D.L. Hunter. 1995. A live trap for wolverine and other forest carnivores. *Wildlife Society Bulletin* 23:535–538.

Copeland, J.P. 1996. *Biology of the wolverine in central Idaho*. MSc Thesis, University of Idaho, Moscow, Idaho, USA.

Copeland, J.P., K.S. McKelvey, K.B. Aubry, A. Landa, J. Persson, R.M. Inman, J. Krebs, E. Lofroth, H. Golden, J.R. Squires, A. Magoun, M.K. Schwartz, J. Wilmot, C.L. Copeland, R.E. Yates, I. Kojola, R. May. 2010. The bioclimatic envelope of the wolverine (*Gulo gulo*): do climatic constraints limit its geographic distribution? *Canadian Journal of Zoology* 88(3): 233–246.

Côtè, S.D., and M. Festa-Bianchet. 2003. Mountain Goat (*Oreamnos americanus*). Pages 1061–1075 in G.A. Feldhamer, B.C. Thompson, and J.A. Chapman, editors. *Wild mammals of North America, biology, management, and conservation, Second edition*. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Davis, D.G. 1967. A brief note on the birth of wolverines *Gulo gulo* at Colorado Zoo. *International Zoo Yearbook* 7:127.

Despain, D.G. 1990, *Yellowstone vegetation: consequences of environment and history in a natural setting*. Roberts Rinehart, Boulder, Colorado, USA.

Gause, G.F. 1934. *The struggle for existence*. Williams and Wilkins, Baltimore, USA.

Golden, H.N., J.D. Henry, E.F. Becker, M.I. Goldstein, J.M. Morton, D. Frost, Sr., and A.J. Poe. 2007. Estimating wolverine (*Gulo gulo*) population size using quadrat sampling of tracks in snow. *Wildlife Biology* 13(Suppl. 2):52–61.

Gude, P., R. Rasker, and J. van den Noort. 2008. Potential for future development on fire-prone lands. *Journal of Forestry* June:198–205.

Gude, P.H., A.J. Hansen, and D.A. Jones. 2007. Biodiversity consequences of alternative future land use scenarios in Greater Yellowstone. *Ecological Applications* 17:1004–1018.

Haglund, B. 1966. De stora rovdjurens vintervanor I. *Viltrevy*. 3:81–310.

Hall, E.R. 1981. *The mammals of North America*. Second edition. John Wiley and Sons, New York, New York, USA.

Hash, H.S. 1987. Wolverine. Pages 575–585 in M. Novak, J.A. Baker, M.E. Obbard, and B. Malloch, editors. *Wild furbearer management and conservation in North America*. Ontario Ministry of Natural Resources, Toronto, Ontario, Canada.

Hebblewhite, M., D.G. Miquelle, A.A. Murzin, V.V. Aramilev, and D.G. Pikunov. 2011. Predicting potential habitat and population size for reintroduction of the Far Eastern leopards in the Russian Far East. *Biological Conservation* 144:2403–2413.

Hornocker, M.G., and H.S. Hash. 1981. Ecology of the wolverine in northwestern Montana. *Canadian Journal of Zoology* 59:1286–1301.

Hosmer, D.W., and S. Lemeshow. 2000. *Applied Logistic Regression, 2nd edition*. John Wiley & Sons, New York, New York, USA.

Huggins, R.M. 1989. On the statistical analysis of capture-recapture experiments. *Biometrika* 76:133–140.

Huggins, R.M. 1991. Some practical aspects of a conditional likelihood approach to capture experiments. *Biometrics* 47:725–732.

Hutchinson, G.E. 1957. Concluding remarks. *Cold Spring Harbor Symposium on Quantitative Biology*. 22: 415–427.

Inman, R.M., K.H. Inman, M.L. Packila, and A.J. McCue. 2007*a*. Wolverine reproductive rates and maternal habitat in Greater Yellowstone. Chapter 4, Pages 65–84 in *Greater Yellowstone Wolverine Study, Cumulative Report, May 2007*. Wildlife Conservation Society, North America Program, General Technical Report, Bozeman, Montana, USA.

Inman, R.M., M.L. Packila, K.H. Inman, B.C. Aber, R. Spence, and D. McCauley. 2009. *Greater Yellowstone Wolverine Program, Progress Report, December 2009*. Wildlife Conservation Society, North America Program, General Technical Report, Bozeman, Montana, USA.

IUCN. 2000. IUCN Red List categories. Gland, Switzerland.

Iversen, J.A. 1972. Basal metabolic rate of wolverines during growth. *Norwegian Journal of Zoology* 20:317–322.

Jacobson. C.A. 2008. *Wildlife conservation and management in the 21st century: Understanding challenges for institutional transformation*. PhD Dissertation, Cornell University, Ithaca, New York, USA.

Jacobson, C.A., J.F. Organ, D.J. Decker, G.R. Batcheller, and L. Carpenter. 2010. A conservation institution for the 21st century: Implications for state wildlife agencies. *Journal of Wildlife Management* 74(2):203–209.

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.

Johnson, K.M., and C.L. Beale. 1994. The recent revival of widespread population growth in nonmetropolitan areas of the United States. *Rural Sociology* 59(4):655– 667.

Krausman, P.R., and R.T. Bowyer. 2003. Mountain Sheep (*Ovis canadensis* and *O. dalli*). Pages 1095–1118 in G.A. Feldhamer, B.C. Thompson, and J.A. Chapman, editors. *Wild mammals of North America, biology, management, and conservation, Second edition.* The Johns Hopkins University Press, Baltimore, Maryland, USA.

Krebs, J., E. Lofroth, and I. Parfitt. 2007. Multiscale habitat use by wolverines in British Columbia, Canada. *Journal of Wildlife Management* 71(7):2180–2192.

Krott, P. 1960. Ways of the wolverine. Natural History 69:16–29.

Landa, A., O. Strand, J.E. Swenson, and T. Skogland. 1997. Wolverines and their prey in southern Norway. *Canadian Journal of Zoology* 75:1292–1299.

Landa, A., O. Strand, J.D.C. Linell, and T. Skogland. 1998. Home range sizes and altitude selection for arctic foxes and wolverines in an alpine environment. *Canadian Journal of Zoology* 76:448–457.

Liskop, K.S., R. Sadleir, and B.P. Saunders. 1981. Reproduction and harvest of wolverine in British Columbia. Pages 469–477 in J.A. Chapman, and D. Pursley, editors. *Proceedings of the Worldwide Furbearer Conference*, Worldwide Furbearer Conf., Inc., Frostburg, Maryland, USA.

Lofroth, E.C. and J.A. Krebs. 2007. The abundance and distribution of wolverines in British Columbia, Canada. *Journal of Wildlife Management* 71(7):2159–2169.

Lofroth, E.C., J.A. Krebs, W.L. Harrower, and D. Lewis. 2007. Food habits of wolverine, *Gulo gulo*, in montane ecosystems of British Columbia. *Wildlife Biology* 13(Suppl. 2):31–37.

Lofroth, E.C., R. Klafki, J.A. Krebs, and D. Lewis. 2008. Evaluation of live-capture techniques for free-ranging wolverines. *Journal of Wildlife Management* 72:1253–1261.

Loftus, A., R. Southwick, B. Byrne, and L. Bragg. 2011*a*. *Financial returns to Industry from the Federal Aid in Wildlife Restoration Program*. <http://www.southwickassociates.com/clients /client-project-links/ >

Loftus, A., R. Southwick, B. Byrne, and L. Bragg. 2011*b*. *Financial returns to Businesses from the Federal Aid in Sport Fish Restoration Program*. < http://www.southwickassociates.com /clients/client-project-links/ >

Loftus, A., R. Southwick, B. Byrne, and L. Bragg. 2011*c*. *The benefits to business from hunting and fishing excise taxes*. < http://www.southwickassociates.com/clients/client-project-links/ >

Magoun, A.J. 1985. *Population characteristics, ecology and management of wolverines in northwestern Alaska*. PhD Dissertation, University of Alaska, Fairbanks, Alaska, USA.

Magoun, A.J. 1987. Summer and winter diets of wolverines, *Gulo gulo*, in arctic Alaska. *Canadian Field Naturalist* 101:392–397.

Magoun, A.J., and J.P. Copeland. 1998. Characteristics of wolverine reproductive den sites. *Journal of Wildlife Management* 62:1313–1320.

Magoun, A.J., and P. Valkenburg. 1983. Breeding behavior of free-ranging wolverines (*Gulo gulo*). *Annales Zoological Fennici* 174:175–177.

Mattisson, J. 2011. *Interactions between Eurasian lynx and wolverines in the reindeer husbandry area*. PhD Dissertation, Swedish University of Agricultural Sciences, Uppsala, Sweden.

May, R. 2007. *Spatial ecology of wolverines in Scandinavia*. PhD Dissertation, Norwegian University of Science and Technology, Trondheim, Norway.

McKelvey, K.S., J.P. Copeland, M.K. Schwartz, J.S. Littell, K.B. Aubry, J.R. Squires, S.A. Parks, M.M. Elsner, and G.S. Mauger. 2011. Climate change predicted to shift wolverine distributions, connectivity, and dispersal corridors. *Ecological Applications* 21(8):2882–2897.

McRae, B.H. 2006. Isolation by resistance. *Evolution* 60(8):1551–1561.

McRae, B.H., B.G. Dickson, T.H. Keitt, and V.B. Shah. 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology* 89(10):2712–2724.

McRae, B.H., and V.B. Shah. 2009. *Circuitscape user's guide*. The University of California, Santa Barbara. Available at: http://www.circuitscape.org.

Mead, R.A., M. Rector, G. Starypan, S. Neirinckx, M. Jones, and M.N. DonCarlos. 1991. Reproductive biology of captive wolverines. *Journal of Mammalogy* 72: 807–814.

Mead, R.A., M. Bowles, G. Starypan, and M. Jones. 1993. Evidence of pseudopregnancy and induced ovulation in captive wolverines (*Gulo gulo*). *Zoo Biology* 12:353–358.

Mehrer, C.F. 1975. Gestation period in the wolverine (*Gulo gulo*). *Journal of Mammalogy* 57:570.

Miller, F.L. 2003. Caribou (*Rangifer tarandus*). Pages 965–997 in G.A. Feldhamer, B.C. Thompson, and J.A. Chapman, editors. *Wild mammals of North America, biology, management, and conservation, Second edition*. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Miller, K.V., L.I. Muller, and S. Demarais. 2003. White-tailed Deer (*Odocoileus virginianus*). Pages 906–930 in G.A. Feldhamer, B.C. Thompson, and J.A. Chapman, editors. *Wild mammals of North America, biology, management, and conservation. Second edition.* The Johns Hopkins University Press, Baltimore, Maryland, USA.

Mohr, C.O. 1947. Table of equivalent populations of North American small populations. *American Midland Naturalist* 37:223–249.

Mohr, E. 1938. Vom Jarv (*Gulo gulo* L.). *Zoologische Garten, Leipzig* 10:14–21.

Montana Fish, Wildlife and Parks. 2008. Furbearer Regulations. Helena, Montana, USA.

Moriarty, K.M., W.J. Zielinski, A.G. Gonzales, T.E. Dawson, K.M. Boatner, C.A. Wilson, F.V. Schlexer, K.L. Pilgrim, J.P. Copeland, M.K. Schwartz. 2009. Wolverine confirmation in California after nearly a century: native or long-distance immigrant? *Northwest Science* 83(2):154–162.

Murie, A. 1944. *The Wolves of Mount McKinley*. University of Washington Press, Seattle, Washington, USA.

Myhre, R. and S. Myrberget. 1975. Diet of wolverines in Norway. *Journal of Mammalogy* 56:752–757.

National Oceanic and Atmospheric Administration. 2007. *Western Regional Climate Center. Historic temperature and precipitation data for Ennis, Montana, 1948–2006.* <http://www.wrcc.dri.edu/index.html>

Natural Resources Conservation Service. 2007. *National Water and Climate Center, SNOTEL data and products. Historic temperature and precipitation data for Carrot Basin, Montana, 1983–2006.* < http://www.wcc.nrcs.usda.gov/snow/ >

Newby, F.E., and P.L. Wright. 1955. Distribution and status of the wolverine in Montana. *Journal of Mammalogy* 36(2):248–253.

Noss, R., C. Carroll, K. Vance-Borland, and G. Wuerthner. 2002. A multicriteria assessment of the irreplaceability and vulnerability of sites in the Greater Yellowstone Ecosystem. *Conservation Biology* 16:895–908.

Nowak, R.M. 1973. Return of the wolverine. National Parks and Conservation Magazine Feb:20–23.

Organ, J.F., S.P. Mahoney, and V. Geist. 2010. Born in the hands of hunters: The North American Model of Wildlife Conservation. *The Wildlife Professional* 4(3):22–27.

Packila, M.L., R.M. Inman, K.H. Inman, and A.J. McCue. 2007. Wolverine road crossings in western Greater Yellowstone. Chapter 7 in *Greater Yellowstone Wolverine Study, Cumulative Progress Report, May 2007*. Wildlife Conservation Society, North America Program, General Technical Report, Bozeman, Montana, USA.

Patten, D.T. 1991. Defining the Greater Yellowstone Ecosystem. Pages 19–25 in R.B. Keiter and M.S. Boyce, editors. T*he Greater Yellowstone Ecosystem: Redefining America's Wilderness Heritage*. Yale University Press, New Haven, Connecticut, USA.

Peacock, S. 2011. Projected 21st century climate change for wolverine habitats within the contiguous United States. *Environmental Research Letters* 6 (2011) 014007 (9pp).

Persson, J. 2003. *Population ecology of Scandinavian wolverines*. PhD Dissertation, Swedish University of Agricultural Sciences, Umeå, Sweden.

Persson, J. 2005. Female wolverine (*Gulo gulo*) reproduction: reproductive costs and winter food availability. *Canadian Journal of Zoology* 83:1453–1459.

Persson, J., A. Landa, R. Andersen, P. Segerström. 2006. Reproductive characteristics of female wolverines (*Gulo gulo*) in Scandinavia. *Journal of Mammalogy* 87(1):75–79.

Persson, J., P. Wedholm, and P. Segerström. 2010. Space use and territoriality of wolverines (*Gulo gulo*) in northern Scandinavia. *European Journal of Wildlife Research* 56:49–57.

Pugh, S.R., S. Johnson, and R.H. Tamarin. 2003. Voles (*Microtus species*). Pages 349–370 in G.A. Feldhamer, B.C. Thompson, and J.A. Chapman, editors. *Wild mammals of North America, biology, management, and conservation, Second edition*. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Pulliainen, E. 1968. Breeding biology of the wolverine (*Gulo gulo L.*) in Finland. Annales *Zoological Fennici* 5:338–344.

Raedeke, K.J., J.J. Millspaugh, and P.E. Clark. 2002. Population Characteristics. Pages 449–492 in D.E. Toweill and J.W. Thomas, editors. *North American Elk: Ecology and Management.* Smithsonian Institution Press, Washington, DC, USA.

Rausch, R.A., and A.M. Pearson. 1972. Notes on the wolverine in Alaska and the Yukon Territory. *Journal of Wildlife Management* 36(2):259–268.

Royle, J.A., A.J. Magoun, B. Gardner, P. Valkenburg, and R.E. Lowell. 2011. Density estimation in a wolverine population using spatial capture-recapture models. *Journal of Wildlife Management* 75(3):604–611.

Ruhl, J. B. 1998. The Endangered Species Act and Private Property: A Matter of Timing and Location. *Cornell Journal of Law and Public Policy* 8:37–53.

Samelius, G., R.T. Alisauskas, S. Lariviere, C. Bergman, C.J. Hendrickson, K. Phipps, and C. Wood. 2002. Foraging behaviours of wolverines at a large arctic goose colony. *Arctic* 55(2): 148–150.

Schwartz, C.C, M.A. Haroldson, G.C. White, R.B. Harris, S. Cherry, K.A. Keating, D. Moody, and C. Servheen. 2006. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. *Wildlife Monographs* 161.

Schwartz, C.C., M.A. Haroldson, and G.C. White. 2010. Hazards affecting grizzly bear survival in the Greater Yellowstone Ecosystem. *Journal of Wildlife Management* 74(4):654–667.

Schwartz, M.K., K.B. Aubry, K.S. McKelvey, K.L. Pilgrim, J.P. Copeland, J.R. Squires, R.M. Inman, S.M. Wisely, and L.F. Ruggiero. 2007. Inferring geographic isolation of wolverines in California using historical DNA. *Journal of Wildlife Management* 71(7):2170–2179.

Schwartz, M.K., J.P. Copeland, N.J. Anderson, J.R. Squires, R.M. Inman, K.S. McKelvey, K.L. Pilgrim, L.P. Waits, and S.A. Cushman. 2009. Wolverine gene flow across a narrow climatic niche. *Ecology* 90(11):3222–3232.

Seiler, A. 2003. *The toll of the automobile: Wildlife and roads in Sweden*. PhD Dissertation, Swedish University of Agricultural Sciences, Uppsala, Sweden.

Shilo, R.A., and M.A. Tamarovskaya. 1981. The growth and development of wolverines *Gulo gulo* at Novosibirsk Zoo. *International Zoo Yearbook* 21:146–147.

Silverman, B.W. 1986. *Density estimation for statistics and data analysis*. Chapman and Hall, London, United Kingdom.

Skinner, M.P. 1927. The predatory and furbearing animals of the Yellowstone National Park. Roosevelt Wildlife Bulletin 4(2):194–195.

Smith, D.W., E.E. Bangs, J.K. Oakleaf, C. Mack, J. Fontaine, D. Boyd, M. Jimenez, D.H. Pletscher, C.C. Niemeyer, T.J. Meier, D.R. Stahler, J. Holyan, V.J. Asher, and D.L. Murray. 2010. Survival of Colonizing Wolves in the Northern Rocky Mountains of the United States, 1982–2004. *Journal of Wildlife Management* 74(4):620–634.

Streubel, D. 1989. *Small mammals of the Yellowstone Ecosystem*. Roberts Rinehart, Boulder, Colorado, USA.

United States Fish and Wildlife Service. 1995. Endangered and Threatened Wildlife and Plants; 90-Day Finding for a Petition to List as Endangered or Threatened The Contiguous United States Population of the North American Wolverine. *Federal Register* Vol. 60, No. 75, Wednesday, April 19, 1995. 19567–19568.

United States Fish and Wildlife Service. 2010. Endangered and Threatened Wildlife and Plants; 12-Month Finding on a Petition to List the North American Wolverine as Endangered or Threatened. *Federal Register* Vol. 75, No. 239, Tuesday, December 14, 2010. 78030–78061.

United States Fish and Wildlife Service. 2012. 2011 *National Survey of Fishing, Hunting, and Wildlife-Associated Recreation, National Overview*, Issued August 2012. http://library.fws.gov/Pubs/nat_survey2011-national-overview-prelim-findings.pdf>

Vangen, K. M., J. Persson, A. Landa, R. Andersen, and P. Segerström. 2001. Characteristics of dispersal in wolverines. *Canadian Journal Zoology* 79:1641–1649.

White, G.C., and K.P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study 46* Supplement:120–138.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home range studies. *Ecology* 70:164–168.

Wright, P.L., and R. Rausch. 1955. Reproduction in the Wolverine, *Gulo gulo*. *Journal of Mammalogy* 36(2):346–355.

Yensen, E., and P.W. Sherman. 2003. Ground Squirrels (*Spermophilus* and *Ammospermophilus* species). Pages 211–231 in G.A. Feldhamer, B.C. Thompson, and J.A. Chapman, editors. *Wild mammals of North America, biology, management, and conservation, Second edition*. The Johns Hopkins University Press, Baltimore, Maryland, USA.

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I

Habitat Relations

Spatial Ecology of Wolverines at the Southern Periphery of Distribution

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ABSTRACT Wolverines (*Gulo gulo*) in the conterminous United States have experienced range contraction, are uncommon, and have been designated as warranted for protection under the United States Endangered Species Act. Data from the southern edge of the wolverine's circumpolar distribution is sparse, and development of effective conservation strategies would benefit from a more complete understanding of the species' ecology. We captured and radio-monitored 30 wolverines in the Greater Yellowstone Ecosystem (GYE), tested for seasonal habitat selection by elevation band, and examined a suite of spatial characteristics to clarify our understanding of the wolverine's niche. Wolverines in GYE selected for areas >2,600 m latitude-adjusted elevation (LAE; $n = 2,257$ wolverine locations [12 F, 6 M]). Wolverines avoided areas <2,150 m LAE, including during winter when the vast majority of ungulates were pushed to these elevations by deep snow. Wolverine home ranges were large relative to body size, averaging 303 km² for adult females and 797 km² for adult males ($n = 13$ [8 F, 5 M] and 33 wolverine-years). Resident adults fit with Global Positioning System (GPS) collars used an area >75% the size of their multi-year home range in an average of 32 days ($n = 7$ [5 F, 2 M]). Average movement rates of 1.3 km/2-hr indicated that both sexes move distances equivalent to the diameter of their home range every 2 days or the circumference of their home range in <1 week ($n = 1,329$ 2-hr movements, $n = 12$ individuals [7 F, 5 M]). This capability for movement, the short time-frame over which home ranges were developed, and a lack of home range overlap by same sex adults ($\bar{x} = 2.1\%$ overlap, 90% CI = 0.0–4.8%, $n = 22$ pairs) suggested territoriality. We estimated wolverine density to be 3.5/1,000 km² of area >2,150 m LAE (95% CI = 2.8–9.6). Dispersal movements extended to at least 170 km for both sexes ($n = 5$ F, 2 M). At the southern edge of distribution, where suitable and unsuitable conditions exist in close proximity, wolverines selected high-elevation areas near alpine tree-line where a mix of forest, meadow, and boulder fields were present, deep snow-cover existed during winter, and low temperatures near freezing can occur throughout the year. Persistence in these areas where the growing season is brief requires large home ranges that are regularly patrolled, a social system that provides exclusive access to resources, and low densities. These characteristics, along with low reproductive rates, are prevalent throughout the species range, indicating that wolverines are specialists at exploiting a cold, unproductive niche where interspecific competition is limited. The vulnerability inherent in occupying this unproductive niche was likely influential in previous declines within the conterminous United States and will remain a factor as wolverines encounter modern human influences. Conserving wolverines in the conterminous United States will require collaborative management over a large geographic scale. © 2011 The Wildlife Society.

KEY WORDS density, dispersal, *Gulo gulo*, home range, movement, niche, territory, wolverine, Yellowstone.

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Wolverines (*Gulo gulo*) appear to have been extirpated, or very nearly so, from the conterminous United States by about 1930 (Aubry et al. 2007). Although some recovery has occurred (Newby and McDougal 1964, Aubry et al. 2007, Inman et al. 2009, Moriarty et al. 2009) the species is uncommon and has been designated as warranted for protection under the United States Endangered Species Act (U.S. Fish and Wildlife Service 2010). Climate change was considered the primary threat during the listing process (U.S. Fish and Wildlife Service 2010). Other issues of concern include absence from portions of historical distribution (Aubry et al. 2007), potential impacts from increasing levels of backcountry recreational use during winter (Copeland 1996, Greater Yellowstone Coordinating Committee 1999, Krebs et al. 2007), appropriate regulation of human-caused mortality (Krebs et al. 2004), and increasing human infrastructure (Gude et al. 2007). A paucity of data on wolverine ecology in the conterminous United States inhibits the development and implementation of an effective conservation strategy (Ruggiero et al. 2007).

Wolverine ecology has been studied at northern latitudes in taiga, tundra, or boreal montane forests where the predominant ungulate species 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; Whitman et al. 1986; Persson et al. 2006, 2010). However, the conterminous United States sits at the southern periphery of the wolverine's holarctic distribution, and fundamental differences in vegetation, predator, and prey composition, including the possibility of relatively abundant carrion, could result in different spatial use and demographic characteristics.

Wolverine data from the conterminous United States are sparse. According to Ruggiero et al. (2007), the only peer-reviewed journal article reporting wolverine habitat relations, home range size, or behavior through 2007 was a single study in northwest Montana (Hornocker and Hash 1981). Two natal den sites had also been described (Magoun and Copeland 1998), along with dispersal movements of a single male (Inman et al. 2004) and genetic diversity and population structure of wolverines in Montana (Cegelski et al. 2006). More recent publications include works on historical genetics in California (Schwartz et al. 2007), distribution and broadscale habitat relations (Aubry et al. 2007; Schwartz et al. 2007, 2009; Copeland et al. 2010), seasonal habitat associations (Copeland et al. 2007), and fecundity (Anderson and Aune 2008). However, published accounts of even primary metrics such as home range size for adult females remain limited to a single estimate that is somewhat confounded by combining subadult and adult females into 1 average (Hornocker and Hash 1981). Thus, fundamental information on home range size, movement rates, social organization, density, and dispersal is absent or minimal. In addition, telemetry data from within the conterminous United States was obtained in areas that did not contain the full suite of native large carnivores during the period when wolverines were studied, that is, either grizzly bears (*Ursus*

arctos) and/or wolves (*Canis lupus*) were absent (Hornocker and Hash 1981, Copeland 1996). Populations of these large carnivores have continued to expand in recent years (Schwartz et al. 2006, Smith et al. 2010) and may influence wolverine ecology via competition for resources, provisioning of resources (scavenging opportunities), or direct mortality. Our goal was to document and assimilate information on fundamental ecological metrics at the southern edge of distribution to gain a better understanding of the adaptive strategies that enable occupation of the wolverine's niche.

STUDY AREA

Our research occurred at 2 focal areas in the Madison and Teton mountain ranges within the Greater Yellowstone Ecosystem (GYE; Fig. 1). The GYE is 108,000 km^2 of primarily public lands that include the Yellowstone Plateau and 14 surrounding mountain ranges in Idaho, Montana, and Wyoming (Patten 1991, Noss et al. 2002). Elevations ranged from approximately 1,400–4,200 m. Precipitation increased with elevation and varied from 32 cm to 126 cm of rainfall per year (National Oceanic and Atmospheric Administration 2007, Natural Resources Conservation Service 2007). Snow usually fell as dry powder and depths at higher elevations were often in excess of 350 cm. A variety of vegetative communities were present (Despain 1990). Low-elevation valleys contained short-grass prairie or sagebrush communities. Lower elevation forests included lodgepole pine (*Pinus contorta*) or Douglas-fir (*Pseudotsuga menziesii*), with Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and whitebark pine (*Pinus albicaulis*) becoming more common with increasing elevation. Alpine tree-line typically occurred within approximately 150 m of 2,750-m elevation. The highest elevations were alpine tundra or talus fields where snow was typically present for at least 9 months of the year (Natural Resources Conservation Service 2007). Mixed forest types were common throughout the ecosystem and all forest types were interspersed with grass, forb, or shrub meadows. A diverse fauna was present (Bailey 1930, Streubel 1989) and included a variety of ungulates and large carnivores that are not found across much of the wolverine's circumpolar distribution, including elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), bison (*Bison bison*), pronghorn (*Antilocapra americana*), cougar (*Puma concolor*), bobcat (*Lynx rufus*), badger (*Taxidea taxus*), raccoon (*Procyon lotor*), and coyote (*Canis latrans*). Other species present in GYE and common within wolverine distribution included grizzly bear, black bear (*Ursus americanus*), gray wolf, red fox (*Vulpes vulpes*), lynx (*Lynx canadensis*), American marten (*Martes americana*), moose, bighorn sheep (*Ovis canadensis*), and mountain goat (*Oreamnos americanus*). Public lands and wildlife populations in GYE were managed by 3 State Wildlife Departments (Idaho, Montana, Wyoming), 2 National Parks (Grand Teton, Yellowstone), 6 National Forests (Gallatin, Beaverhead-Deerlodge, Caribou-Targhee, Bridger Teton, Shoshone, Custer), 3 state-level Bureau of Land Management (BLM) offices (Idaho, Montana, Wyoming), 2 National Wildlife Refuges (Red Rocks
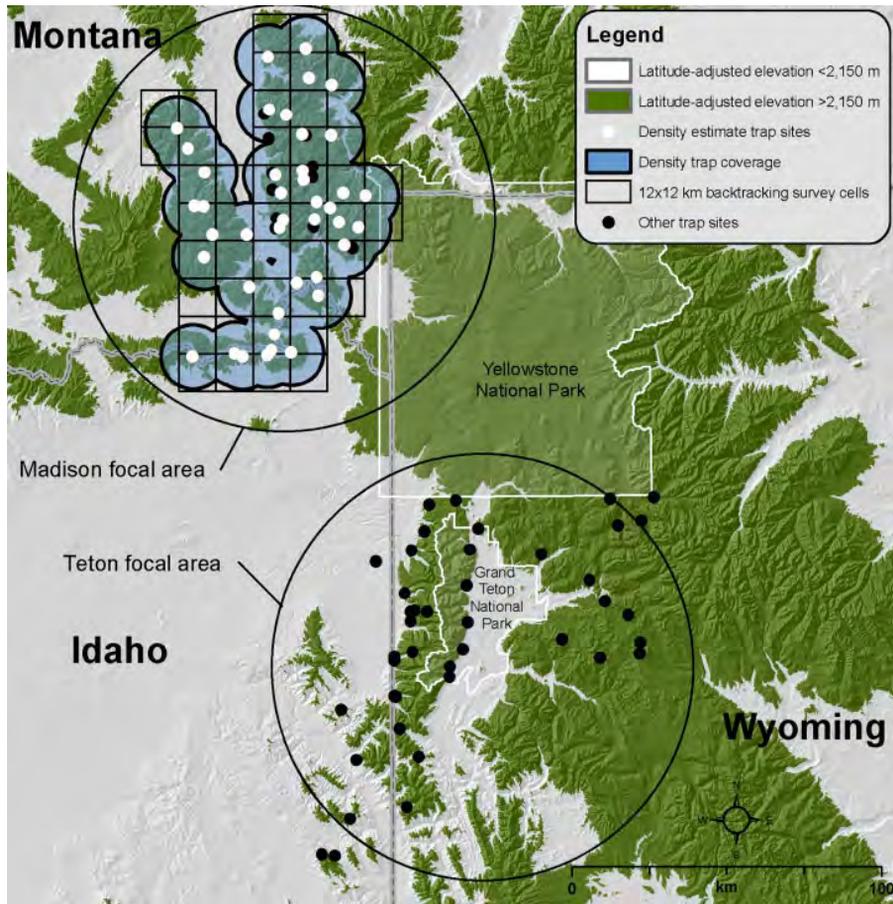
Figure 1. Wolverine study site in the Madison and Teton focal areas, Greater Yellowstone Ecosystem of Idaho, Montana, and Wyoming, USA, 2001–2008.

Lakes, National Elk Refuge), and additional state and federal entities.

METHODS

Capture, Monitoring, Age-Classification, and Genetic Analysis

We captured wolverines during winters of 2000–2008 using box traps (Copeland et al. 1995, Lofroth et al. 2008) equipped with trap-transmitters (Telonics, TBT-500, Mesa, AZ). We also captured juvenile wolverines by hand at den or rendezvous sites (Persson et al. 2006). We used a variable-powered CO_2 pistol (CO_2 PI, Dan-Inject, Fort Collins, CO) or a hand syringe (juveniles) to deliver an initial dose of approximately 7.5 mg/kg ketamine + 0.25 mg/kg medetomidine (Arnemo and Fahlman 2007). We surgically implanted all wolverines with an intra-peritoneal very high frequency (VHF) radio-transmit-

ter (Advanced Telemetry Systems M1245, M1250, M1255, Isanti, MN; Telonics Imp400L, Imp300L). We administered oxygen at a rate of 0.5 L/min to compensate for the effect of elevation on partial pressure of arterial oxygen (Fahlman et al. 2008, Inman et al. 2009). We followed handling procedures approved by the Animal Care and Use Committees of the Hornocker Wildlife Institute/ Wildlife Conservation Society (2000-RMW-504, 2000–2006) and Montana Department of Fish, Wildlife and Parks (IACUC 1–2006, 2006–2007). We attempted to collect aerial VHF telemetry locations at an approximate 10-day interval. We estimated telemetry error by comparing aerial locations with actual ground locations of mortalities, dropped collars, and transmitters placed on the ground. We also fit 12 wolverines with Global Positioning System (GPS) collars programmed to collect locations at various intervals (Televilt POSREC 300, Telemetry Solutions, Concord, CA; Lotek Wireless Inc. 3300SL, Newmarket,

Ontario, Canada). Global Positioning System collars weighed approximately 300 g and we typically programmed the drop-off mechanism to fire after a period of approximately 3 months. We obtained the vast majority of GPS collar data during February and March. We estimated ages based on earliest known alive date, toothwear, cementum annuli, and the lack of descended testes (taken to indicate approximately 12 months of age at winter capture). Based on age of reproductive maturity for female wolverines (Persson et al. 2006), we classified animals ≥3 years old as adults and <3 years as subadults. Subadults referred to as yearlings were 1 to 2 years old, and those referred to as juveniles or cubs were <1 year old. We collected a small tissue sample from the incision site of each captured wolverine and scat or hair samples from snow-tracked wolverines and dried them in desiccant. All samples were delivered to the United States Forest Service, Rocky Mountain Research Station Genetics Lab, Missoula, Montana for DNA extraction, genotyping, and relatedness analysis as outlined in Inman et al. (2004) and Schwartz et al. (2007).

Habitat Selection, Home Range Size, and Spatial Organization

We conducted a simple first-order habitat analysis (Johnson 1980) using design II (Manly et al. 2002) where we categorized areas into 150-m latitude-adjusted elevation (LAE) bands (Brock and Inman 2006). We developed the LAE layer by using 30-m vegetation data from the National Landcover Dataset (Homer et al. 2001) to regress alpine tree-line within each degree of latitude. We used 2,257 VHF wolverine locations collected from 18 individuals (12 F, 6 M) and the selection ratio function in the R statistical package (Manly et al., 2002, R Core Development Team 2011) to determine which elevation bands were selected for or against by wolverines ($\alpha = 0.05$). We considered November to April to be winter and May to October to be summer.

We used the animal movements extension (Hooge et al. 1999) in Arcview 3.2® (Environmental Systems Research Institute, Inc. [ESRI], Redlands, CA) to calculate annual home range size with 2 techniques: 100% minimum convex polygon (MCP; Mohr 1947) and 95% fixed kernel with least squares cross validation (Silverman 1986, Worton 1989). Our annual period for analysis was 1 March to 28 February based on wolverine birth date (Magoun and Copeland 1998). We analyzed data from only those wolverine-years that included >20 VHF locations over a period of >225 days. We did not use GPS data to estimate annual home range sizes because of the limited number of individuals fit with GPS collars and short length of time that GPS collars typically collected locations (≤3 months). To identify the number and type of political jurisdictions used by each wolverine, we used a Geographic Information System (GIS; ArcGIS 9.2, ESRI) and spatial data delineating the boundaries of federal, state, native American, and private lands (Wyoming Spatial Data Center 1994; Montana Natural Heritage Program 2005; U.S. Bureau of Land Management 2005; U.S. Geological Survey 2005a, b).

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 calculated movement distances over independent (separate and exclusive) 2-hr and 24-hr sampling periods with GPS collar data. We related these movement distances to home range size as a means of evaluating whether wolverine home ranges are too large to be defended as a territory (cf. Koehler et al. 1980). We also used GPS locations to assess whether wolverines develop their home range with movements throughout a large proportion of the home range within a few weeks as opposed to seasonal shifts into new areas of the annual range. We accomplished this by calculating the average number of weeks over which resident adult wolverines used an area >75% of their multi-year home range size. The first step was construction of multi-year 95% MCP home ranges using all VHF locations of each of 7 resident adults who had been fit with a GPS collar. Then we constructed weekly 100% MCPs using GPS locations, and finally we calculated the proportion of the multi-year home range that was used each week(s). Weeks were cumulative, that is, week 4 included all locations from weeks 1 to 4. To estimate the degree of spatial overlap between individuals, we used data from all pairs of wolverines that had been radio-marked within an individual focal area. Individuals were capable of moving to any point within a focal area, thus each pair had the opportunity to overlap. We did not calculate overlap of a female and her offspring during the offspring's first year. For each pair of wolverines, we calculated a pair of percent area overlaps (PAOs) with annual 100% MCP home ranges constructed with VHF locations. We did this by dividing the total area shared by the individuals during a year by the annual home range of animal A (first PAO) and also by the annual home range of animal B (second PAO; Kernohan et al. 2001). We estimated mean PAO between pairs of wolverines classified by sex (same-sex or opposite-sex) and age-class (adults, adult–subadult, subadults), and tested for differences in PAO between same-sex and opposite-sex pairs within each age-class category using the Wilcoxon rank sum test.

Population Estimation, Density, and Dispersal

We obtained mark-resight data on the Madison focal area during 6 encounter efforts. The Madison focal area was approximately 10,000 km², however we based our estimate of density on a 4,381-km² area as described below. Our first encounter effort (marking) occurred over 3 annual capture periods during winters (Dec–Apr) of 2001–2004. For analysis, we considered only those animals radio-marked and known to be alive on 1 December 2004 to have been captured during the first encounter effort. Our second through fifth encounter efforts consisted of 4 log box capture sessions during winter 2004–2005 (1 Dec–22 Dec, 28 Dec–22 Jan, 23 Jan–17 Feb, 18 Feb–13 Mar). We based trap distribution on the area where wolverines were most likely to occur and the average winter home range size of female wolverines: First, we used 2,150 m LAE as a lower boundary for the area to be effectively covered by our traps. Second, we defined the

area sampled by a trap as a circle, centered on the trap, with an area equivalent to the mean winter home range size for female wolverines (335 km^2 or 10.33-km radius). We distributed traps so that the aggregate of traps covered >95% of the study area above 2,150 m LAE (Fig. 1). Based on habitat characteristics of successful versus unsuccessful traps during previous years, we placed new traps at or near alpine tree-line as often as possible. Our sixth encounter effort (resight) consisted of a technique that was independent of attracting wolverines to a site. We used snow-tracking to obtain wolverine hair and scat for DNA immediately following the conclusion of the log box capture efforts (Ulizio et al. 2006). We placed a 12 km × 12 km grid over the study area, resulting in 44 cells to be surveyed (Fig. 1). We located the beginning point for a transect above 2,150 m LAE in each cell. Between 21 March and 24 April 2005 we surveyed a 10-km route through wolverine habitat where snow, wind, and terrain conditions were most favorable for encountering tracks and obtaining samples (e.g., wind-blown ridges were avoided). When we encountered a presumed wolverine track, we followed it until obtaining 6 hair samples (a cluster of hair was 1 sample) or 2 scats along each track (Ulizio et al. 2006). We surveyed 10 km within each cell, which did not include distances traveled while following a wolverine track.

We used Program MARK (White and Burnham 1999) to estimate population size using the Huggins (1989, 1991) closed captures model and data from both log box captures and snow-tracking transects. We fit the models M_0 (null), M_t (time), and M_b (behavioral response; Otis et al. 1978), and M_{h2} (2-mixture model for individual heterogeneity; Pledger 2000) to the data, plus an M_t model with occasions constrained equal for the same type of encounter, M_0 with encounter probabilities gender-specific, and M_0 with genotype misidentification errors (Lukacs and Burnham 2005, White 2008). We performed model weighting with second-order Akaike's Information Criterion (AIC$_c$) weights (Burnham and Anderson 2002) to provide model-averaged estimates. We computed asymmetric confidence intervals based on the log-transformation of the number of animals never encountered added to the number of animals encountered. We used this estimate of population size to derive an estimate of density. As described above, we considered the area sampled for the population estimate to be all areas >2,150 m LAE and within a 10.33-km radius of the traps; thus we sampled a 4,381 km^2 area (Fig. 1).

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. We classified individuals as an offspring when we captured them at a den or rendezvous site with the mother or we established a maternal relationship with a combination of both field observations and genetic data. We considered a dispersal-related movement to have initiated when the offspring was located >2 home range radii from the arithmetic center of their mother's most recent annual 95% fixed kernel home range (Vangen et al. 2001). We considered locations made on separate excursions, that is, to distinct mountain ranges or with a documented return to within 2 home range radii of the center of their

mother's home range, to be independent and indicative of the distances wolverines are capable of dispersing. We measured only the most distant movement for each dispersal-related movement. We estimated age at initiation of dispersal by determining the age of the offspring at the time when they first moved >2 home range radii from the center of their mother's home range.

RESULTS

Between January 2001–February 2008, we captured 30 wolverines (19 F, 11 M). We constructed 92 box traps and captured 29 individuals 107 times during 8,174 trap-nights for an overall trap success rate of 1 wolverine/76 trap-nights. We radio-marked 4 juvenile wolverines at den sites during April–August, and 3 of these were subsequently captured in box traps. We obtained 5,807 relocations (2,359 VHF and 3,448 GPS), and monitored 24 individuals for periods >1 year, 12 individuals for >3 years, and 6 individuals for >5 years through February 2008. We estimated VHF telemetry location error to be 239 m ($n = 17$, SE $= 58$ m).

Habitat Selection, Home Range Size, and Spatial Organization

We found strong evidence that wolverines were selective in their use of elevation bands annually, during summer, and during winter ($P < 0.001$). On an annual basis, wolverines selected for areas >2,600 m LAE and against areas <2,150 m LAE. During summer, wolverines selected for areas >2,600 m LAE, and during winter selection shifted lower to areas between 2,450 m and 3,050 m LAE (Figs. 2 and 3).

We estimated size of 56 annual home ranges with 2,078 VHF locations of 24 wolverines (15 F, 9 M; Table 1). Minimum convex polygon home ranges of adult females averaged 303 km^2 whereas adult male home ranges averaged 797 km^2. Minimum annual home range size for a parturient female was approximately 100–150 km^2 (smallest during year raising cubs). We located individual wolverines within an average of 4.0 major management units, for example, a National Forest, a National Park, or a BLM district ($n = 25$ wolverines, range $= 1$–14 management units). We located 80% of these individuals within ≥3 major management units and 52% within ≥4. Eighty-six percent of wolverine locations occurred on lands administered by the United States Forest Service, 12% on National Park Service lands, and 2% occurred on all other ownerships. Thirty-six percent of all wolverine locations occurred in designated wilderness.

We estimated movement rates with GPS collar data for 1,329 independent, straight-line, 2-hr movement distances, and 269 independent, straight-line, 24-hr movement distances. We recorded the vast majority of these movements during winter. Males moved approximately 2–3 times farther than females on average (Table 2). Movement rates of dispersers were similar to resident adults with the exception that dispersers moved a greater maximum distance during a 24-hr period. Based on average 2-hr movement rates, adult wolverines traveled a distance equivalent to the diameter of the
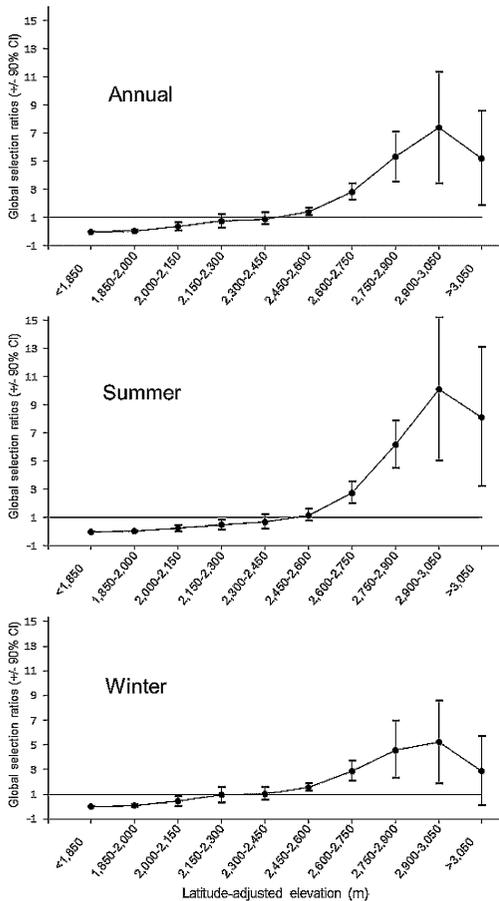
Figure 2. Selection indices (90% CI) for annual and seasonal wolverine use by 150 m latitude-adjusted elevation band, Greater Yellowstone Ecosystem of Idaho, Montana, and Wyoming, USA, 2001–2008.

average home range in <2 days or around the circumference in <1 week. Travel at maximum observed 2-hr rates would require <6 hr and <24 hr to travel a home range radius or circumference, respectively. Actual minimum distance traveled during a 24-hr interval (multiple GPS locations) averaged 15.5 km for 4 males (range = 0.5–56.6 km, $n = 84$, SE = 1.3 km) and averaged 7.5 km for 6 females (range = 0.0–27.9 km, $n = 185$, SE = 0.39 km).

We estimated temporal development of annual home ranges for 7 resident adult wolverines that were monitored for 2–6 years with VHF transmitters and also fit with a GPS collar (5 F, 2 M, $\bar{x}$ years monitored with VHF = 4, $\bar{x}$ GPS locations = 390). These wolverines used an area ≥75% of their multi-year MCP home range size in an average of 4.6 weeks (32 days; range = 1–7 weeks; Fig. 4). A recently parturient female required the maximum number of weeks to use an area ≥75% of her multi-year

home range. When we omitted this individual, the wolverines used 87% of their multi-year home ranges in an average of 29 days. Thus, extensive movements throughout the annual home range occurred over brief time intervals for both sexes. The above movements occurred during winter; however, VHF data indicated that similar movements likely occur during other seasons.

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 1 case (Table 3). In 2 cases, extensive GPS data did not reveal any significant forays into an adjacent same-sex territory, rather it confirmed the lack thereof (Fig. 5). Degree of overlap was greater for opposite-sex pairs than for same-sex pairs of adults ($Z = 4.04$, $P < 0.001$) and subadults ($Z = 2.09$, $P = 0.04$). Overlap did not differ between same-sex or opposite-sex adult-subadult pairs ($Z = -1.57$, $P = 0.12$). On each of the 4 occasions when a resident adult wolverine died, same-sex adults that we had not previously located within the dead individual's home range began using portions of the unoccupied home range, or same-sex subadults expanded into the dead individual's former home range and occupied most or all of it (Fig. 6). Movements into these dead adults' former home ranges occurred within a maximum of 3–7 weeks. We also captured a same-sex yearling in the former home range of a dead subadult on 3 occasions. These captures occurred late in our capture effort (after 63–90 days of multiple traps operating in the areas the wolverines subsequently used) and captured individuals were 11.5–12.5 months of age, suggesting that they may have recently dispersed into the vacated areas.

Population Estimation, Density, and Dispersal

Five radio-marked wolverines were alive and in the study area at the initiation of our recapture efforts during December 2004. We monitored 15–24 log box traps between 5 December 2004 and 13 March 2005 (1,980 trap-nights), and we captured 10 wolverines 19 times (second through fifth encounter efforts). During the sixth encounter effort (snow-tracking) we sampled each of the 44 12 km × 12 km grid cells with a 10-km transect. We were not able to accomplish a second round of 10-km transects because of unusually high avalanche danger and poor tracking conditions that spring. Three of 6 tracks confirmed as wolverine via DNA provided DNA of high enough quality to obtain an individual identification; 2 were marked wolverines, and 1 was unmarked. Overall, we recaptured 4 of 5 wolverines marked during the first encounter effort (those marked during previous winters and alive at initiation of the density estimate) and identified 7 new individuals. The model weighted average population estimate was 15.2 wolverines (95% CI = 12.3–42.0) with individual model estimates ranging from 13.9 to 18.2 wolverines (Table 4). We based our estimate of density on 4,381 km^2 of area >2,150 m LAE that was sampled by our trap distribution. 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). This estimate did not include any cubs of the year (born Feb–Mar 2005).
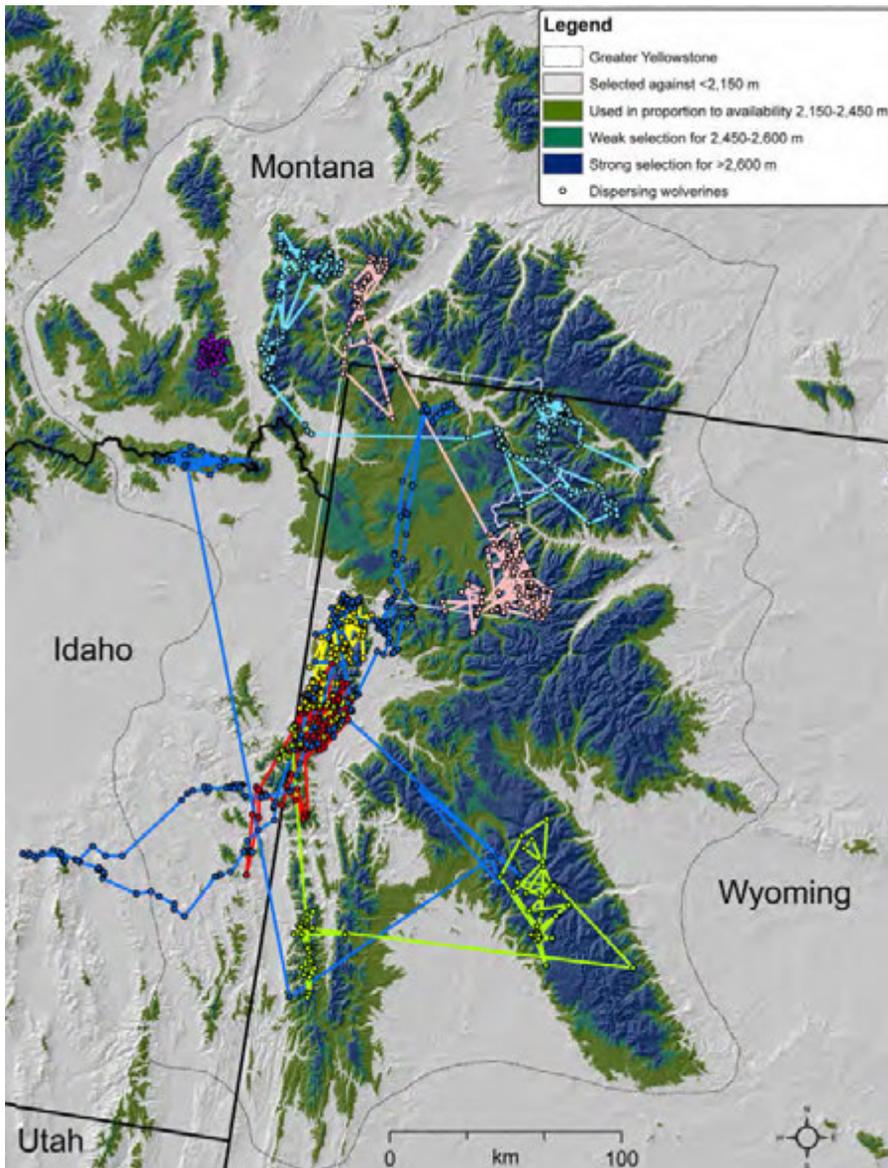
Figure 3. Annual wolverine habitat selection by 150 m latitude-adjusted elevation band, and wolverine dispersal movements, Greater Yellowstone Ecosystem of Idaho, Montana, and Wyoming, USA, 2001–2008. Each color represents a different individual and consecutive locations are connected with a straight line. Males are blues and all other colors are females.

We documented 25 dispersal-related movements made by 7 offspring (5 F, 2 M; Fig. 3). Maximum distance from the mother's home range center was 170 km for males and 173 km for females. 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). First documented dispersal-related movements occurred at 11.4 months of age on average (range = 8.4–14.1 months, $n = 6$). Pulses of dispersal-related movements occurred near the time when litters are born and snow conditions may facilitate travel (Fig. 7).

Table 1. Mean annual (1 Mar–28 Feb) home range size (km²) of radio-marked wolverines using 95% fixed kernel (FK) and 100% minimum convex polygon (MCP) estimators, Greater Yellowstone Ecosystem of Idaho, Montana and Wyoming, USA, 2001–2007[a].

Sex	Age-class	w[b]	n[c]	l[d]	Days[e]	95% FK Mean	95% FK SE	100% MCP Mean	100% MCP SE
Female	Adult	8	20	41	357	400	92	303	54
	Subadult	10	17	35	343	1,175	383	884	297
Male	Adult	5	13	36	346	1,160	155	797	87
	Subadult	6	6	32	341	3,292	1,527	2,689	1,565

[a] Very high frequency (VHF) locations only; all individuals were located >20 times over a minimum 225 day period.
[b] Number of individual wolverines; annual home ranges of 3 females and 2 males were measured as both subadults and adults.
[c] Number of annual home ranges.
[d] Mean number of locations per annual home range.
[e] Mean number of days monitored during annual home range.

Table 2. Wolverine movement distances (km) during 2-hr and 24-hr periods as determined with Global Positioning System (GPS) collars, Greater Yellowstone Ecosystem of Idaho, Montana and Wyoming, USA, 2002–2007.

Sex	2-hr w[a]	2-hr n[b]	2-hr Mean	2-hr Range	2-hr SE	24-hr w[a]	24-hr n[b]	24-hr Mean	24-hr Range	24-hr SE
Female	7	785	0.90	0.00–7.67	0.05	6	185	4.59	0.00–17.45	0.30
Male	5	544	1.90	0.00–13.82	0.10	4	84	12.04	0.02–54.01	1.13

[a] Number of individual wolverines.
[b] Number of independent (non-overlapping), straight-line movements.

DISCUSSION

Wolverines in GYE selected elevations at and above tree-line during summer and shifted to slightly lower areas centered at tree-line during winter. This pattern was similar to wolverines in northwest Montana and Idaho (Hornocker and Hash 1981, Copeland et al. 2007). Although wolverines shifted lower during winter, they still avoided the low-elevation winter ranges where there were thousands of elk, scavenging opportunities, and virtually no human activity. The nearly complete lack of tree or talus escape cover at low elevations along with the presence of potential predators (wolves and cougars) and competitors (coyotes, bobcats, wolves, and cougars) may have discouraged wolverine use of these areas. Habitat in the areas wolverines selected was characterized by steep terrain with a mix of tree cover, alpine meadow, boulders, and avalanche chutes. Deep snow exists during winter, and the wolverine's large feet allow it to travel relatively easily in these environments. Temperatures in these areas are generally cool and can fall below freezing during any month. Snow persists in patches well into summer. As a result, the growing season in the areas wolverines inhabit in GYE are brief and relatively unproductive. The correlation between wolverine presence and persistent spring snow cover (Copeland et al. 2010) suggests that occupying cold, snow-covered, and relatively unproductive environments is a common pattern throughout the global distribution of the species. For wolverines, an apparent tradeoff exists between resource acquisition on one hand and avoidance of predation and competition on the other. Wolverines balance these competing interests by exploiting an unproductive niche where predation and interspecific competition are reduced.

Home range size of GYE wolverines was large relative to body size. Comparison of minimum reported home range size of female carnivores typically weighing 6–12 kg in North America indicates that wolverine home ranges are 21–104 times larger than those of the coyote, badger, and bobcat, 8 times that of lynx, and over 500 times that of the raccoon (Anderson and Lovallo 2003, Bekoff and Gese 2003, Copeland and Whitman 2003, Gehrt 2003, Lindzey 2003). Despite differences in habitat, competitor, predator, and prey composition, the wolverine home range sizes we measured were similar to those reported elsewhere in the conterminous United States and British Columbia (Hornocker and Hash 1981, Copeland 1996, Krebs et al. 2007). Home range size of mammals is related to body mass, and within a trophic class a species living in less productive habitat will have a larger home range than that predicted by the generalized relationship between home range and body mass (Harestad and Bunnell 1979). The home range size of wolverines indicates that their niche is based upon exploitation of relatively unproductive habitats. The smaller home ranges reported from wolverine studies at more northern latitudes (Magoun 1985, Persson et al. 2010) suggest either that resources are more limited in GYE or that competition for resources is more intense.

Spatial distribution patterns of the Mustelidae are typically described as intra-sexual territoriality, where only home ranges of opposite sexes overlap (Powell 1979). Wolverine-specific reports exist for both intra-sexual territoriality (Magoun 1985, Copeland 1996, Hedmark et al.
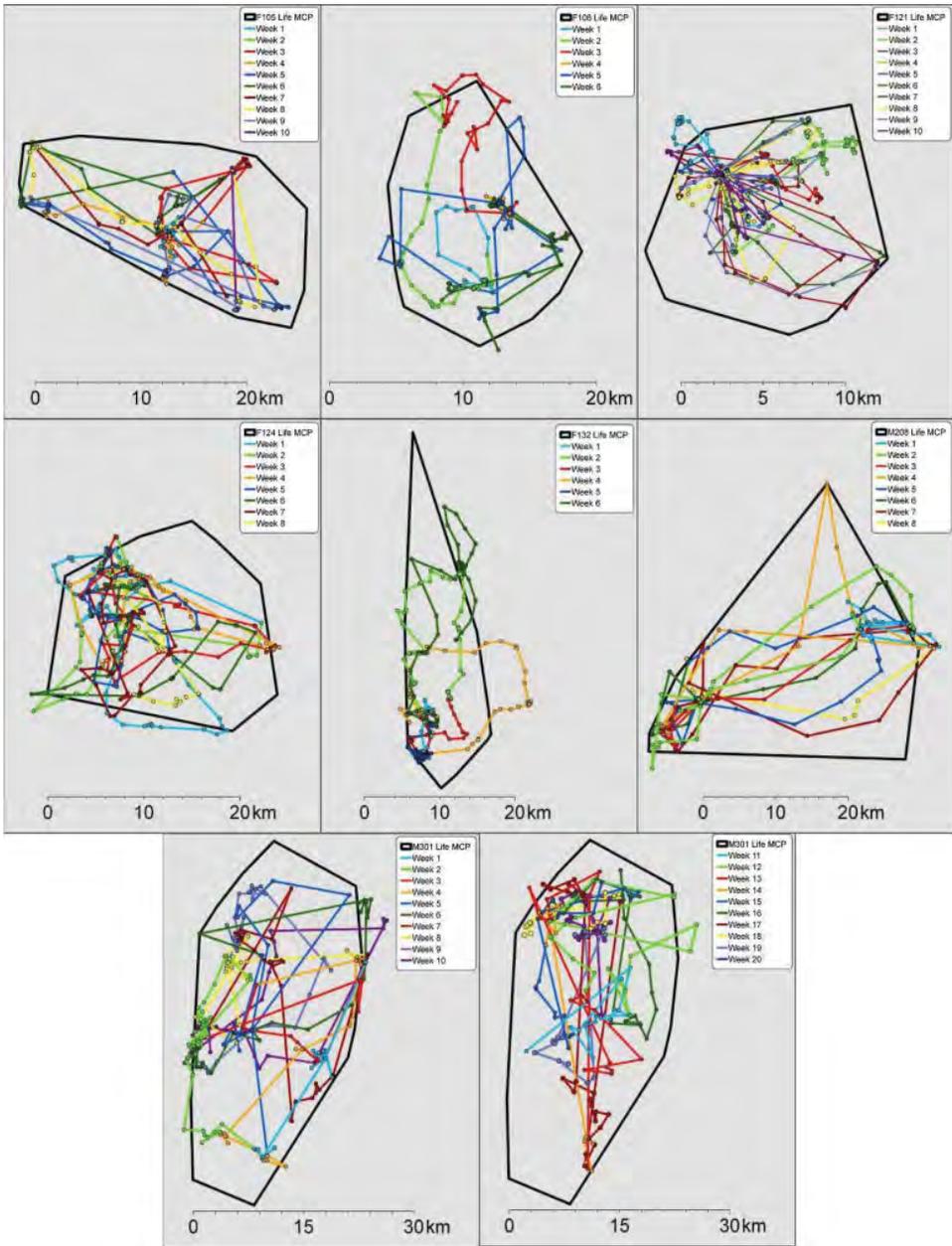
Figure 4. Weekly movements of resident adult wolverines (5 F, 2 M) recorded with Global Positioning System collars, Greater Yellowstone Ecosystem of Idaho, Montana and Wyoming, USA, 2004–2007. Black polygons are multi-year 95% minimum convex polygon (MCP) home ranges and each color represents movements during a 1-week period.

Table 3. Mean percent area overlap of annual 100% minimum convex polygon home ranges by same-sex and opposite-sex pairs of adult, adult–subadult, and subadult wolverines, Greater Yellowstone Ecosystem of Idaho, Montana and Wyoming, USA, 2001–2006[a].

Sex-age class category	*n* (pairs)	Percent area overlap				*P*-value
		Mean	SE	95% CI		
Adult pairs						
Same-sex	22	2.1	1.6	0.0–5.3		<0.001
Opposite-sex	17	25.9	6.1	13.8–37.9		
Adult–subadult pairs						
Same-sex	34	12.7	2.7	7.4–18.0		0.12
Opposite-sex	34	24.1	4.3	15.8–32.5		
Subadult pairs						
Same-sex	11	5.4	3.4	0.0–12.1		0.04
Opposite-sex	10	21.4	7.7	6.3–36.4		

[a] Very high frequency (VHF) radio-locations only; annual home range is 1 March–28 February.

2007, Persson et al. 2010) and for a high degree of spatial overlap but with temporal separation (Hornocker et al. 1983). Arguments against territoriality by wolverines include the lack of ability to defend such a large home range (Koehler et al. 1980). Our data on movement rates in relation to home range size, temporal development of the home range, minimal overlap of same-sex adults, and relatively immediate shifts upon a death suggest that wolverines are capable of patrolling a large territory and provide further support for intra-sexual territoriality. Reproductive success is closely correlated to the amount of energy that a female wolverine can obtain (Persson 2005), and for predators that are capable of individually acquiring prey, the presence of conspecifics reduces foraging efficiency (Sandell 1989). Since wolverines feed on individually obtainable prey and occupy relatively unproductive habitats, it follows that behaviors for maintaining exclusive access to resources would likely have selective advantage. Frequent marking behavior (Pulliainen and Ovaskainen 1975, Koehler et al. 1980) is likely part of an adaptive strategy that involves maintenance of exclusive territories within sexes so that feeding and breeding opportunities are monopolized by dominant individuals and their immediate offspring.

Although comparisons of density among wolverine studies must be made with caution because of the variety of methods used and wide confidence intervals (Table 5), our estimate of 3.5 wolverines/1,000 km[2] is at the low end of reported values for North America and low relative to other carnivores in GYE. For example, pre-1990 density estimates for the threatened Yellowstone grizzly bear (near low point) were in the range of 9–12 bears/1,000 km[2] (Schwartz et al. 2006), approximately triple that of our estimate for wolverines. Applying our wolverine density estimate across the entire 52,375 km[2] area of the GYE that lies above 2,150 m LAE (Fig. 3) suggests the potential for 182 wolverines. However, the current population size is likely much smaller since much of this area is not proximate to landscapes at elevations that were strongly selected (e.g., the interior of Yellowstone National Park; Fig. 3), and every wolverine we monitored used elevations that were strongly selected. Furthermore, large areas of GYE recently surveyed for wolverines did not result in detections (Murphy et al. 2011), and presence/density in other large areas of GYE such as the Wind River Range is unknown. In any case, wolverine density at present, and likely historically, is low and therefore the population is small and relatively vulnerable. This vulnerability likely contributed to historic wolverine population declines in the conterminous United States that occurred earlier than declines of other carnivores that were specifically persecuted (Paquet and Carbyn 2003, Schwartz et al. 2003, Aubry et al. 2007).

The dispersal distances we measured in GYE indicate that wolverine populations occur over a vast geographic area where management decisions are made by a diversity of jurisdictional authorities. Vangen et al. (2001) reported maximum dispersal distances of 101 km for 11 male and 178 km for 11 female wolverines in Scandinavia. However, they

Figure 5. Global Positioning System (GPS) locations of 2 adult female wolverines with adjacent home ranges, Greater Yellowstone Ecosystem of Idaho, Montana, and Wyoming, USA, February–April 2007.
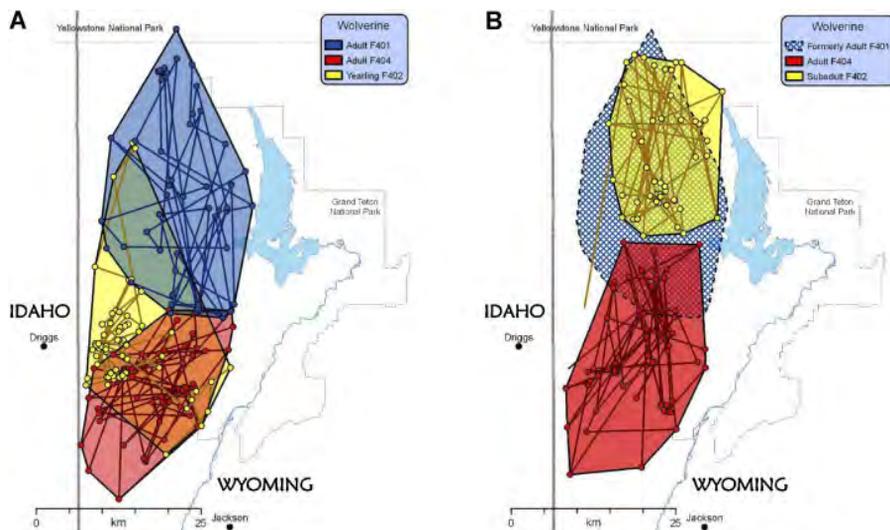
Figure 6. Female wolverine locations, movements, and annual 100% minimum convex polygon (MCP) home ranges (A) before and (B) after the death of adult female F401, Teton Range, Greater Yellowstone Ecosystem of Idaho, Montana, and Wyoming, USA, 2002–2004.

cautioned that this might be an underestimation. Our data indicate that both males and females are capable of dispersing to areas at least 170 km from their mother's home range; however, this may also underestimate the distances wolverines disperse. For example, using a GPS collar, we documented an exploratory movement by a male that extended 112 km from its mother's center of activity and covered over 200 km in less than 6 days. Therefore, single instances when wolverines are unable to be located during weekly telemetry flights may be the result of a long-distance movement. Despite regular aerial searches including extensions over large portions of GYE, M304 was missing for periods of 334, 189, and 136 days, and F421 for 82 days (Fig. 7). We believe it likely that these individuals moved beyond the GYE. Duration of monitoring may also be a factor in under-

estimating dispersal distances. Of the 4 offspring we documented dispersing long distances (>150 km), all initiated significant movements at 11–13 months of age, and 2 of these 4 individuals made additional long distance movements (>145 km) at 23–24 months of age (Fig. 7). One individual moved >225 km between 36 months and 40 months of age. Wolverines estimated to be 2 to 3 years old made several movements of approximately 200 km in Idaho (Copeland 1996). Therefore, wolverine dispersal can occur over multiple years and monitoring individuals for several years might be required to fully understand dispersal patterns. Wolverines have traveled as far as 300 km and 378 km in Alaska (Magoun 1985, Gardner et al. 1986), and genetic sampling suggests the potential for wolverines to disperse as much as 500 km (Flagstad et al. 2004).

Table 4. Estimated population size and density of wolverines in the Madison, Gravelly, and Centennial Mountain Ranges of the Greater Yellowstone Ecosystem of Idaho, Montana, and Wyoming, USA, December 2004–April 2005.

Model[a]	Model weight	Population estimate	SE	95% CI	Density (95% CI) (wolverines/1,000 km^2)[b]
M_0	0.32	14.1	2.04	10.1–18.1	3.2 (2.3–4.1)
M_0 + gender	0.32	15.6	3.87	8.0–23.1	3.6 (1.8–5.3)
M_b	0.16	18.2	10.78	0.0–39.3	4.2 (0.0–9.0)
M_0 + genotype	0.11	14.1	2.04	10.1–18.1	3.2 (2.3–4.1)
M_t with occasions equal	0.05	14.1	2.03	10.1–18.0	3.2 (2.3–4.1)
M_{h2}	0.04	14.1	2.04	10.1–18.1	3.2 (2.3–4.1)
M_t	0.01	13.9	1.92	10.1–17.7	3.2 (2.3–4.0)
Weighted average		15.2	5.24[c]	12.3–42.0[d]	3.5 (2.8–9.6)

[a] M_0 = null model; M_0 + gender = encounter probabilities gender specific; M_b = behavioral response; M_0 + genotype = genotype misidentification errors; M_t with occasions equal = occasions constrained equal for encounter type; M_{h2} = 2-mixture model for individual heterogeneity; M_t = time.
[b] Area sampled was 4,381 km^2 above 2,150 m latitude-adjusted elevation.
[c] Unconditional SE.
[d] Based on calculation of asymmetric confidence interval using unconditional SE.
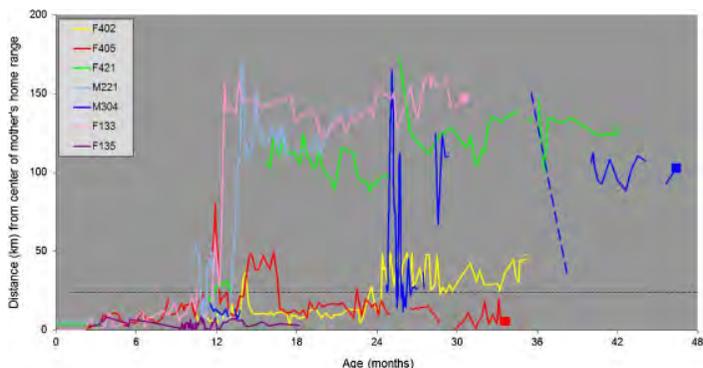
Figure 7. Distance, age at initiation, and duration of dispersal related movements of 7 wolverines (5 F, 2 M), Greater Yellowstone Ecosystem of Idaho, Montana, and Wyoming, USA, 2001–2007. The black dashed line represents the diameter of the average adult female home range. Gaps in lines representing wolverines indicate periods where the individual was searched for but could not be located. Filled circles represent individuals that were still being monitored as of 28 February 2008; open circles represent individuals that were missing or whose transmitter has failed; a square represents a dead individual. The blue dashed line indicates an undocumented but likely move by M304 through or near the mother's home range between known locations in distant mountain ranges.

Table 5. Wolverine density estimates (wolverines/1,000 km^2) from North America.

Density	95% CI	Location	Refs.	Method
15.4		Montana	Hornocker and Hash (1981)	Census, home range
14.1[a]		Alaska	Magoun (1985)	Census, home range
9.7	8.5–10.9	Yukon	Golden et al. (2007)	Quadrat sampling
9.7	5.9–14.9	Alaska	Royle et al. (2011)	Camera-trapping
6.5	2.8–10.2	N British Columbia	Lofroth and Krebs (2007)	Mark-recapture-resight
5.8	3.6–7.9	S British Columbia	Lofroth and Krebs (2007)	Mark-recapture-resight
5.6		Yukon	Banci and Harestad (1990)	Census, home range
5.2	3.1–7.2	Alaska	Becker (1991)	Transect intercept probability
4.5		Idaho	Copeland (1996)	Census, home range, reproduction
3.5	2.8–9.6	Yellowstone	This study	Mark-recapture-resight
3.0	2.2–3.8	Alaska	Golden et al. (2007)	Quadrat sampling

[a] Estimate occurred during autumn so included cubs of the year.

By synthesizing information on spatial ecology at the edge of distribution, where both suitable and unsuitable conditions exist 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 deep snow exists during winter, the growing season is brief, and food resources are relatively limited. Although 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, using 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; Landa et al. 1998; Persson et al. 2006, 2010; Golden et al. 2007). When viewed together, these characteristics indicate that wolverines are specifically adapted to exploit a cold, unpro-

ductive niche where resources are scarce and interspecific competition is limited. Success within this niche likely requires behavioral adaptations that make efficient use of the limited food resources, including strategies for outcompeting other scavenging organisms such as insects and bacteria. Research on the specific mechanisms wolverines use to occupy their cold, snowy niche could improve conservation strategies, including those related to climate change.

MANAGEMENT IMPLICATIONS

The once-extirpated wolverine population of the conterminous United States 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, Copeland et al. 2010). Clearly, the wolverine population of GYE is cumulatively influenced by a complexity of land

ownerships and management authorities. Therefore, similar to grizzly bear management (Interagency Conservation Strategy Team 2007), implementation of a conservation strategy that addresses wolverine needs in a coordinated fashion is more likely to ensure persistence. However, in the case of the wolverine, this GYE scale is likely too small for a viable population. A viable population may require an area as broad as the western United States and, as such, wolverine management in GYE and other areas would be most effectively designed by considering each area's role within the context of the larger metapopulation. Designing effective metapopulation conservation strategies would be greatly facilitated by development of an empirical prediction of wolverine habitat across the western United States, particularly one distinguishing among areas suitable for use by resident animals, reproductive females, and dispersal movements. With this tool it would be possible for multiple management entities to conceptualize and collaboratively implement practices facilitating survival, reproduction, and gene-flow at the most effective locations from the metapopulation perspective.

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LITERATURE CITED

Anderson, E. M., and M. J. Lovallo. 2003. Bobcat and lynx. Pages 758–786 in G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Wild mammals of North America, biology, management, and conservation. Second edition. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Anderson, N. J., and K. E. Aune. 2008. Fecundity of female wolverine in Montana. Intermountain Journal of Science 14:17–30.

Arnemo, J., and Å. Fahlman. 2007. Biomedical protocols for free-ranging brown bears, gray wolves, wolverines and lynx. Norwegian School of Veterinary Science, General Technical Report, Tromsø, Norway.

Aubry, K. B., K. S. McKelvey, and J. P. Copeland. 2007. Geographic distribution and broad-scale habitat associations of the wolverine in the United States: an historical analysis. Journal of Wildlife Management 71:2147–2158.

Bailey, V. 1930. Animal life of Yellowstone National Park. Charles C. Thomas, Springfield, Illinois, USA.

Banci, V. 1987. Ecology and behavior of wolverines in Yukon. Thesis, Simon Fraser University, Burnaby, British Columbia, Canada.

Banci, V., and A. Harestad. 1990. Home range and habitat use of wolverines Gulo gulo in Yukon, Canada. Holarctic Ecology 13:195–200.

Becker, E. F. 1991. A terrestrial furbearer estimator based on probability sampling. Journal of Wildlife Management 55:730–737.

Bekoff, M., and E. M. Gese. 2003. Coyote. Pages 467–481 in G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Wild mammals of North America, biology, management, and conservation. Second edition. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Brock, B. L., and R. M. Inman. 2006. Use of latitude-adjusted elevation in broad-scale species distribution models. Intermountain Journal of Sciences 12:12–17.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information–theoretic approach. Second edition. Springer Science + Business Media, LLC, New York, New York, USA.

Cegelski, C. C., L. P. Waits, N. J. Anderson, O. Flagstad, C. Strobeck, and C. J. Kyle. 2006. Genetic diversity and populations structure of wolverine (Gulo gulo) populations at the southern edge of their current distribution in North America with implications for genetic viability. Conservation Genetics 7:197–211.

Copeland, J. P., E. Cesar, J. M. Peek, C. E. Harris, C. D. Long, and D. L. Hunter. 1995. A live trap for wolverine and other forest carnivores. Wildlife Society Bulletin 23:535–538.

Copeland, J. 1996. Biology of the wolverine in central Idaho. Thesis, University of Idaho, Moscow, USA.

Copeland, J. P., and J. S. Whitman. 2003. Wolverine. Pages 672–682 in G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Wild mammals of North America, biology, management, and conservation. Second edition. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Copeland, J. P., J. M. Peek, C. R. Groves, W. E. Melquist, K. S. McKelvey, G. M. McDaniel, C. D. Long, and C. E. Harris. 2007. Seasonal habitat associations of the wolverine in central Idaho. Journal of Wildlife Management 71:2201–2212.

Copeland, J. P., K. S. McKelvey, K. B. Aubry, A. Landa, J. Persson, R. M. Inman, J. Krebs, E. Lofroth, H. Golden, J. R. Squires, A. Magoun, M. K. Schwartz, J. Wilmot, C. L. Copeland, R. E. Yates, I. Kojola, and R. May. 2010. The bioclimatic envelope of the wolverine (Gulo gulo spp.): do climatic constraints limit its geographic distribution? Canadian Journal of Zoology 88(3):233–246.

Despain, D. G. 1990, Yellowstone vegetation: consequences of environment and history in a natural setting. Roberts Rinehart, Boulder, Colorado, USA.

Fahlman, Å., J. M. Arnemo, J. Persson, P. Segerström, and G. Nyman. 2008. Capture and Medetomidine-Ketamine anesthesia of free-ranging wolverines (Gulo gulo). Journal of Wildlife Diseases 44(1):133–142.

Flagstad, Å., E. Hedmark, A. Landa, H. Brøseth, J. Persson, R. Andersen, P. Segerström, and H. Ellegren. 2004. Colonization history and noninvasive monitoring of a reestablished wolverine population. Conservation Biology 18:676–688.

Gardner, C. L., W. B. Ballard, and R. H. Jessup. 1986. Long distance movement by an adult wolverine. Journal of Mammalogy 67:603.

Gehrt, S. D. 2003. Raccoon. Pages 611–634 in G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Wild mammals of North America, biology, management, and conservation. Second edition. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Golden, H. N., J. D. Henry, E. F. Becker, M. I. Goldstein, J. M. Morton, D. Frost, Sr., and A. J. Poe. 2007. Estimating wolverine (Gulo gulo) population size using quadrat sampling of tracks in snow. Wildlife Biology 13 (Suppl 2): 52–61.

Greater Yellowstone Coordinating Committee. 1999. Winter visitor use management: a multi-agency assessment, final report of Information for Coordinating Winter Recreation in the Greater Yellowstone Area. Montana State University, Bozeman, USA.

Gude, P. H., A. J. Hansen, and D. A. Jones. 2007. Biodiversity consequences of alternative future land use scenarios in Greater Yellowstone. Ecological Applications 17:1004–1018.

Harestad, A. S., and F. L. Bunnell. 1979. Home range and body weight—a reevaluation. Ecology 60:389–402.

Hedmark, E., J. Persson, P. Segerström, A. Landa, and H. Ellegren. 2007. Paternity and mating system in wolverines *Gulo gulo*. Wildlife Biology 13 (Suppl 2): 13–30.

Homer, C., C. Huang, L. Yang, B. Wylie, and M. Coan. 2001. Development of a 2001 National Land-cover Database for the United States. Photogrammetric Engineering and Remote Sensing 70:829–840.

Hooge, P. N., W. Eichenlaub, and E. Solomon. 1999. The animal movement program extension to Arcview. Version 2.0. Alaska Biological Science Center, U.S. Geological Survey, Anchorage, Alaska, USA.

Hornocker, M. G., and H. S. Hash. 1981. Ecology of the wolverine in Northwestern Montana. Canadian Journal of Zoology 59:1286–1301.

Hornocker, M. G., J. P. Messick, and W. E. Melquist. 1983. Spatial strategies in three species of Mustelidae. Acta Zoologica Fennica 174:185–188.

Huggins, R. M. 1989. On the statistical analysis of capture-recapture experiments. Biometrika 76:133–140.

Huggins, R. M. 1991. Some practical aspects of a conditional likelihood approach to capture experiments. Biometrics 47:725–732.

Inman, R. M., R. R. Wigglesworth, K. H. Inman, M. K. Schwartz, B. L. Brock, and J. D. Rieck. 2004. Wolverine makes extensive movements in the Greater Yellowstone Ecosystem. Northwest Science 78:261–266.

Inman, R. M., M. L. Packila, K. H. Inman, B. C. Aber, R. Spence, and D. McCauley. 2009. Greater Yellowstone Wolverine Program, Progress Report, December 2009. Wildlife Conservation Society, North America Program, General Technical Report, Bozeman, Montana, USA.

Interagency Conservation Strategy Team. 2007. Final Conservation Strategy for the Grizzly Bear in the Greater Yellowstone Area. <http://www.fws.gov/mountain-prairie/species/mammals/grizzly/Final_Conservation_Strategy.pdf>. Accessed 16 Sep 2010.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use. Pages 125–166 *in* J. J. Millspaugh and J. M. Marzluff, editors. Radio tracking and animal populations. Academic Press, London, United Kingdom.

Koehler, G. M., M. G. Hornocker, and H. S. Hash. 1980. Wolverine marking behavior. Canadian Field-Naturalist 94:339–341.

Krebs, J., E. Lofroth, J. Copeland, V. Banci, C. Dooley, H. Golden, A. Magoun, R. Mulders, and B. Schultz. 2004. Synthesis of survival rates and causes of mortality in North American wolverines. Journal of Wildlife Management 68:493–502.

Krebs, J., E. C. Lofroth, and I. Parfitt. 2007. Multiscale habitat use by wolverines in British Columbia, Canada. Journal of Wildlife Management 71:2180–2192.

Landa, A., O. Strand, J. D. C. Linell, and T. Skogland. 1998. Home range sizes and altitude selection for arctic foxes and wolverines in an alpine environment. Canadian Journal of Zoology 76:448–457.

Lindzey, F. G. 2003. Badger. Pages 683–691 *in* G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Wild mammals of North America, biology, management, and conservation. Second edition. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Lofroth, E. C., and J. Krebs. 2007. The abundance and distribution of wolverines in British Columbia, Canada. Journal of Wildlife Management 71:2159–2169.

Lofroth, E. C., R. Klafki, J. A. Krebs, and D. Lewis. 2008. Evaluation of live-capture techniques for free-ranging wolverines. Journal of Wildlife Management 72:1253–1261.

Lukacs, P. M., and K. P. Burnham. 2005. Estimating population size from DNA-based closed capture-recapture data incorporating genotyping error. Journal of Wildlife Management 69:396–403.

Magoun, A. J. 1985. Population characteristics, ecology and management of wolverines in northwestern Alaska. Dissertation, University of Alaska, Fairbanks, USA.

Magoun, A. J., and J. P. Copeland. 1998. Characteristics of wolverine reproductive den sites. Journal of Wildlife Management 62:1313–1320.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals, statistical design and analysis for field studies. Second edition. Kluwer Academic Publishers, Dordrecht, The Netherlands.

May, R. 2007. Spatial ecology of wolverines in Scandinavia. Dissertation, Norwegian University of Science and Technology, Trondheim, Norway.

Mohr, C. O. 1947. Table of equivalent populations of North American small populations. American Midland Naturalist 37:223–249.

Montana Natural Heritage Program. 2005. Land ownership and management areas in Montana. Montana Natural Heritage Program. Montana State Library, Helena, Montana, USA.

Moriarty, K. M., W. J. Zielinski, A. G. Gonzales, T. E. Dawson, K. M. Boatner, C. A. Wilson, F. V. Schlexer, K. L. Pilgrim, J. P. Copeland, and M. K. Schwartz. 2009. Wolverine confirmation in California after nearly a century: native or long-distance immigrant? Northwest Science 83(2): 154–162.

Murphy, K., J. Wilmot, J. Copeland, D. Tyers, J. Squires. with contributions from R. M. Inman, M. L. Packila, D. McWhirter, 2011. Wolverine Conservation in Yellowstone National Park Final Report. YCR-2011-02. National Park Service, Yellowstone National Park Yellowstone Center for Resources, Yellowstone, National Park, Mammoth, Wyoming, USA.

National Oceanic and Atmospheric Administration [NOAA]. 2007. Western Regional Climate Center. Historic temperature and precipitation data for Ennis, Montana, 1948–2006. <http://www.wrcc.dri.edu/index.html>. Accessed 5 Jan 2007.

Natural Resources Conservation Service [NRCS]. 2007. National Water and Climate Center, SNOTEL data and products. Historic temperature and precipitation data for Carrot Basin, Montana, 1983–2006. <http://www.wcc.nrcs.usda.gov/snow/>. Accessed 5 Jan 2007.

Newby, F. E., and J. J. McDougal. 1964. Range extension of the wolverine in Montana. Journal of Mammalogy 45:485–486.

Noss, R., C. Carroll, K. Vance-Borland, and G. Wuerthner. 2002. A multicriteria assessment of the irreplaceability and vulnerability of sites in the Greater Yellowstone Ecosystem. Conservation Biology 16:895–908.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs 62:1–135.

Packila, M. L., R. M. Inman, K. H. Inman, and A. J. McCue. 2007. Wolverine road crossings in western Greater Yellowstone. Chapter 7 *in* Greater Yellowstone Wolverine Study, Cumulative Progress Report, May 2007. Wildlife Conservation Society, North America Program, General Technical Report, Bozeman, Montana, USA.

Paquet, P. C., and L. N. Carbyn. 2003. Gray wolf. Pages 482–510 *in* G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Wild mammals of North America, biology, management, and conservation. Second edition. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Patten, D. T. 1991. Defining the Greater Yellowstone Ecosystem. Pages 19–25 *in* R. B. Keiter and M. S. Boyce, editors. The Greater Yellowstone Ecosystem: redefining America's wilderness heritage. Yale University Press, New Haven, Connecticut, USA.

Persson, J. 2003. Population ecology of Scandinavian wolverines. Dissertation, Swedish University of Agricultural Sciences, Umeå, Sweden.

Persson, J. 2005. Female wolverine (*Gulo gulo*) reproduction: reproductive costs and winter food availability. Canadian Journal of Zoology 83:1453–1459.

Persson, J., A. Landa, R. Andersen, and P. Segerström. 2006. Reproductive characteristics of female wolverines (*Gulo gulo*) in Scandinavia. Journal of Mammalogy 87:75–79.

Persson, J., P. Wedholm, and P. Segerström. 2010. Space use and territoriality of wolverines (*Gulo gulo*) in northern Scandinavia. European Journal of Wildlife Research 56:49–57.

Pledger, S. 2000. Unified maximum likelihood estimates for closed capture-recapture models using mixtures. Biometrics 56:434–442.

Powell, R. A. 1979. Mustelid spacing patterns: variations on a theme by *Mustela*. Zhurnal Tierpsychologie 50:153–165.

Pulliainen, E., and P. Ovaskainen. 1975. Territory marking by a wolverine (*Gulo gulo*) in northeastern Lapland. Annales Zoologica Fennici 12:268–270.

R Core Development Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Royle, J. A., A. J. Magoun, B. Gardner, P. Valkenburg, and R. E. Lowell. 2011. Density estimation in a wolverine population using spatial capture-recapture models. Journal of Wildlife Management 75(3):604–611.

Ruggiero, L. F., K. S. McKelvey, K. B. Aubry, J. P. Copeland, D. H. Pletscher, and M. G. Hornocker. 2007. Wolverine conservation and management. Journal of Wildlife Management 71:2145–2146.

Sandell, M. 1989. The mating tactics and spacing patterns of solitary carnivores. Pages 164–182 *in* J. L. Gittleman, editor. Carnivore behavior, ecology, and evolution. Volume 1. Cornell University Press, Ithaca, New York, USA.

Schwartz, C. C., S. D. Miller, and M. A. Haroldson. 2003. Grizzly bear (*Ursus arctos*). Pages 556–586 *in* G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Wild mammals of North America, biology, management, and conservation. Second edition. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Schwartz, C. C., M. A. Haroldson, G. C. White, R. B. Harris, S. Cherry, K. A. Keating, D. Moody, and C. Servheen. 2006. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. Wildlife Monographs 161.

Schwartz, M. K., K. B. Aubry, K. S. McKelvey, K. L. Pilgrim, J. P. Copeland, J. R. Squires, R. M. Inman, S. M. Wisely, and L. F. Ruggiero. 2007. Inferring geographic isolation of wolverines in California using historical DNA. Journal of Wildlife Management 71:2170–2179.

Schwartz, M. K., J. P. Copeland, N. J. Anderson, J. R. Squires, R. M. Inman, K. S. McKelvey, K. L. Pilgrim, L. P. Waits, and S. A. Cushman. 2009. Wolverine gene flow across a narrow climatic niche. Ecology 90(11):3222–3232.

Silverman, B. W. 1986. Density estimation for statistics and data analysis. Chapman and Hall, London, United Kingdom.

Smith, D. W., E. E. Bangs, J. K. Oakleaf, C. Mack, J. Fontaine, D. Boyd, M. Jimenez, D. H. Pletscher, C. C. Niemeyer, T. J. Meier, D. R. Stahler, J. Holyan, V. J. Asher, and D. L. Murray. 2010. Survival of colonizing wolves in the Northern Rocky Mountains of the United States, 1982–2004. Journal of Wildlife Management 74:620–634.

Streubel, D. 1989. Small mammals of the Yellowstone Ecosystem. Roberts Rinehart, Boulder, Colorado, USA.

Ulizio, T. J., J. R. Squires, D. H. Pletscher, M. K. Schwartz, J. J. Claar, and L. F. Ruggiero. 2006. The efficacy of using snow track to provide genetic data from wolverine. Wildlife Society Bulletin 34:1326–1332.

U.S. Bureau of Land Management. 2005. Land status of Idaho. United States Department of Interior, Bureau of Land Management, Idaho State, Office, Branch of Engineering and Geographic Sciences, Boise, Idaho, USA.

U.S. Fish and Wildlife Service. 2010. Endangered and threatened wildlife and plants; 12-month finding on a petition to list the North American wolverine as endangered or threatened. Federal Register Vol. 75, No. 239, Tuesday, December 14, 2010. 78030–78061. <http://www.fws.gov/mountain-prairie/species/mammals/wolverine/75FR78030.pdf>. Accessed 14 Dec 2010.

U.S. Geological Survey. 2005a. Federal lands of the United States. National Atlas of the United States, United States Department of Interior, Geological Survey, Reston, Virginia, USA.

U.S. Geological Survey. 2005b. Indian lands of the United States, National Atlas of the United States. United States Department of Interior, Geological Survey, Reston, Virginia, USA.

Vangen, K. M., J. Persson, A. Landa, R. Andersen, and P. Segerström. 2001. Characteristics of dispersal in wolverines. Canadian Journal Zoology 79:1641–1649.

Whitman, J. S., W. B. Ballard, and C. L. Gardner. 1986. Home range and habitat use by wolverines in southcentral Alaska. Journal of Wildlife Management 50:460–463.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 (Suppl): 120–138.

White, G. C. 2008. Closed population estimation models and their extensions in Program MARK. Environmental and Ecological Statistics 15:89–99.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home range studies. Ecology 70:164–168.

Wyoming Spatial Data Center. 1994. Wyoming GAP analysis. University of Wyoming Spatial Data and Visualization Center, Laramie, Wyoming, USA.

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The wolverine's niche: linking reproductive chronology, caching, competition, and climate

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Wolverines are demographically vulnerable and susceptible to impacts from climate change. Their distribution is correlated with persistent spring snow cover, but food-based explanations for this relationship have not been explored. We synthesize information on the timing of both wolverine reproductive events and food availability to improve our understanding of the behaviors, habitat features, and foods that influence reproductive success. Wolverine births are constrained to a brief period of the year and occur at an earlier date than other nonhibernating, northern carnivores. Our examination suggests that this timing is adaptive because it allows wolverines to take advantage of a cold, low-productivity niche by appending the scarce resources available during winter to the brief period of summer abundance. The wolverine's bet-hedging reproductive strategy appears to require success in 2 stages. First, they must fuel lactation (February–April) with caches amassed over winter or acquisition of a sudden food bonanza (e.g., winter-killed ungulates); otherwise, early litter loss occurs. Next, they must fuel the majority of postweaning growth during the brief but relatively reliable summer period of resource abundance. The 1st stage is likely dependent on scavenged ungulate resources over most of the wolverine's range, whereas the 2nd stage varies by region. In some regions the 2nd stage may continue to be focused on scavenging ungulate remains that have been provided by larger predators. In other regions the 2nd stage may be focused on predation by wolverines on small prey or neonatal ungulates. During all seasons and regions, caching in cold, structured microsites 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. This ''refrigeration-zone'' hypothesis represents a food-based explanation for the correlation between wolverine distribution and persistent spring snow cover. Understanding regional differences in foods that fuel reproduction and underlying causes to the limits of distribution could be important for maintaining wolverine populations in the future.

Key words: cache, climate change, competition, distribution, delayed implantation, food, *Gulo gulo*, niche, reproduction, wolverine

Wolverines (*Gulo gulo*) are demographically vulnerable, have experienced historical declines in some regions, and are susceptible to impacts from climate change (Aubry et al. 2007; Copeland et al. 2010; Persson et al. 2006). The wolverine is a species of conservation concern in some parts of its distribution. In Scandinavia, the species is considered vulnerable in Sweden and endangered in Norway (National Red List— Gärdenfors 2010; Kålås et al. 2010). In the lower 48 United States, the wolverine was recently designated as warranted for protection under the United States Endangered Species Act (ESA—United States Fish and Wildlife Service 2010). Climate change was the primary threat leading to ESA designation in the United States. To develop conservation strategies capable of ensuring wolverine persistence through the

21st century, we must fully understand the factors that influence distribution and enable them to reproduce successfully.

Reproduction is a key component of fitness that is ultimately limited by the amount of energy that can be channeled toward offspring (Bronson 1989; Stearns 1992). In seasonal environments, timing the most energetically demanding periods of reproduction to occur when food resources are abundant can be a critical factor for individual fitness. For example, ungulate births typically occur within a narrow annual window related to a flush of nutrition (Geist 2002; Miller 2003), and even small differences in birth dates within this window can influence overwinter survival (Singer et al. 1997). On the other hand, species whose food resources are relatively constant are less constrained to specific time periods for reproduction, e.g., mountain lions (*Puma concolor*) and bobcats (*Lynx rufus*— Anderson and Lovallo 2003; Pierce and Bleich 2003). The energy required for carnivores to reproduce (conception through weaning) can be >100 times the daily metabolic requirement (Oftedal and Gittleman 1989), and lactation is often the most demanding phase of the female's reproductive cycle. However, postweaning growth of offspring also requires higher levels of energy and may represent the constraint that determines the timing of reproduction (Bronson 1989; Lack 1968). Clearly, natural selection will favor individuals that time these critical and energetically demanding periods of reproduction to occur during the season of food abundance.

The timing of reproductive events in relation to food availability may be particularly critical for the wolverine. The wolverine's large feet are a morphological adaptation that allows it to travel easily over deep snow, and the species is distributed in circumpolar fashion across the tundra, boreal, and montane biomes (Copeland and Whitman 2003). Throughout its distribution, the wolverine displays extremely large home ranges, territoriality, low densities, and low reproductive rates (Copeland 1996; Inman et al. 2012; Krebs et al. 2007; Lofroth and Krebs 2007; Magoun 1985; Mattisson et al. 2011a; Persson et al. 2006, 2010). These adaptations are necessary for exploiting a cold, low-productivity niche where growing seasons are brief and food resources are limited (Inman et al. 2012). Starvation is a significant natural cause of wolverine mortality in some populations (Krebs et al. 2004). In addition, Persson (2005) experimentally demonstrated that wolverine reproduction in Scandinavia was limited by winter food availability. Taken together, these factors suggest that wolverines need to be exceptionally efficient in channeling available food resources into reproduction to persist within their niche.

The wolverine's reproductive chronology is unique in that birth occurs earlier than for other northern carnivores that do not hibernate (Fig. 1). However, our knowledge of the specific mechanisms that wolverines utilize to reproduce within their relatively unproductive niche is incomplete. For instance, although it is clear that wolverines are opportunistic and utilize a wide variety of foods (Banci 1994; Hash 1987; Lofroth et al. 2007; Magoun 1987), no attempt has been made to discern which foods specifically fuel the most energetically demanding periods of reproduction. Caching is a common
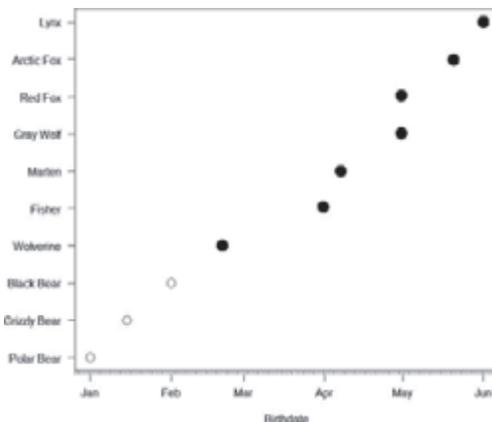
FIG. 1.—Median reported birthdates of northern carnivores (Amstrup 2003; Anderson and Lovallo 2003; Cypher 2003; Paquet and Carbyn 2003; Pelton 2003; Powell et al. 2003; Schwartz et al. 2003). Hollow circles indicate species that hibernate.

behavior (Haglund 1966; Landa et al. 1997; Magoun 1987; Mattisson 2011; May 2007; Samelius et al. 2002), yet there has been no effort to determine how or why it could be a key in the reproductive process. At present, distributional limits of the wolverine are suggested to depend on where they can give birth and/or avoid physiologically prohibitive summer temperatures (Copeland et al. 2010) rather than where and how they can successfully compete for food. Clarifying our understanding of these fundamental aspects of the wolverine's ecology can help develop more effective conservation strategies for the species.

Given the adaptive significance of acquiring food resources for reproduction most efficiently, the wolverine's reproductive chronology can provide key insights for how the species exploits its niche. Although many authors have reported anecdotally on the timing of events associated with wolverine reproduction, no comprehensive, easily interpreted, chronological sequence has been published. Herein we consolidate the available information regarding the timing of events related to wolverine reproduction. We then attempt to identify specific mechanisms by which this chronology is adaptive for wolverines; we discuss behavioral adaptations necessary to occupy the species' niche, habitat features that may influence their distribution, and the potential influence of various food sources on reproductive success.

MATERIALS AND METHODS

Because this review was intended to summarize information available from numerous sources, virtually all of which are based on small sample sizes obtained using different methodologies, we present the data used to define the extent and peak of each reproductive event along with our synopsis in the ''Results'' section. We estimated the extent and peak periods

of reproductive events on the basis of similarities among studies and by weighting each study's contribution on the basis of sample size, technique, and whether observations were based on wild or captive wolverines. We also used personal knowledge related to the timing of reproductive events obtained during wolverine field studies that we conducted (Inman et al. 2012; Magoun 1985; Mattisson 2011; Persson 2003; Persson et al. 2006; Royle et al. 2011). We also reviewed the literature to determine time periods during the year when the species wolverines use as food are likely to be more 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 these chronologies 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.

RESULTS

Mating season.—Mead et al. (1991) obtained blood samples and vaginal smears from 8 captive female wolverines throughout the year and reported 3 waves of ovarian activity related to sexual receptivity occurring during May to early June, mid-June to July, and August; vaginal cornification began increasing in May and maximal cornification and vulva enlargement occurred during June and July. Mead et al. (1991) reported that females were anestrus from September to April. Rausch and Pearson (1972) examined the carcasses of 417 female wolverines but were not able to define the proestrus period. The vast majority of the wolverines were killed between November and April; thus only 3 contained strong evidence of imminent (follicle) or recent (corpora lutea) estrous, all of which occurred from 16 to 28 June. Wright and Rausch (1955) found no evidence of ovarian activity in 2 lactating females killed 9 and 10 April. However, in northern Sweden 1 captured female had a swollen vulva as early as 2 April, another on 26 April, and several in early May (J. Persson, pers. obs.).

Wright and Rausch (1955) examined 8 adult male wolverines killed November–April for spermatogenesis; 0 of 5 killed in November–January contained sperm, whereas 1 of 2 in February and 1 of 1 in April did; in addition, sperm were present in 2 young males killed 31 March and 4 April. Danilov and Tumanov (1972) examined 2 males in mid-March that were both fertile. Liskop et al. (1981) detected spermatogenesis in 1 of 2 males killed in January, 2 of 5 in February, and 1 of 2 in March. Rausch and Pearson (1972) examined 43 pairs of male testes for weight, spermatogenesis, and the presence of epididymal sperm. Although they concluded that peak mating condition of males occurred during late May and June, they thought that mating may occur over a longer period. Given their statement that ''testes collected in late winter clearly showed an increase in weight, spermatogenesis, and the presence of epididymal sperm,'' their report suggests males were prepared to mate by at least March and April. Mead et al. (1991) measured changes in plasma testosterone levels

and testes size in 7 captive males and suggested that males reach near-maximal testes size by early April and peak in June. Rausch and Pearson (1972), Mead et al. (1991), and Banci and Harestad (1988) all found evidence of testes beginning to increase in size by March. Results from both Rausch and Pearson (1972) and Mead et al. (1991) indicate that testicular regression begins in July and is likely completed by early August.

Observations of assumed mating by wild wolverines are limited to 7 cases occurring mid-April, 27 April, 15 May, 5, 9, 11 June, and 6 August (Krott and Gardner 1985; Magoun and Valkenburg 1983; J. Persson, pers. obs.). Seven matings occurred 7 June–14 July at a captive facility in Washington State (D. Pedersen, pers. comm.). Five of the matings occurred from 7 to 27 June. Four of the matings were by the same female in 4 different years. In Europe, observations of 69 matings in captivity took place from 17 May to 25 July, and 45% occurred during the first 2 weeks of June (Blomqvist 2001). Captive wolverines were observed to mate on 10 April and at the end of May in Sweden (Krott 1959). Other matings by captive wolverines were observed on 31 May (Mehrer 1975) and from 17 to 22 July (Mohr 1938). Mating pairs were not monitored continuously, so mating could have occurred on other days as well.

In summary, June appears to be the peak of a wolverine mating season that extends from at least May through early August (Fig. 2). Males appear to be prepared to mate by March, possibly as early as January, but the evidence for females being prepared before May is limited and somewhat contradictory.

Nidation.—Almost all information on nidation (and therefore, on gestation) is derived from trapper-caught wolverines and many dates of capture are likely approximate. Wolverines exhibit delayed implantation (Rausch and Pearson 1972; Wright and Rausch 1955). Wright and Rausch (1955) examined 7 adult female reproductive tracts and suggested that nidation occurs during January. Banci and Harestad (1988) sampled 56 individuals and found evidence of active pregnancy beginning as early as November. Rausch and Pearson (1972) found evidence of blastocysts, fetuses, or postpartum condition in 122 female wolverines and only 4% of carcasses obtained by the end of December contained a macroscopic fetus. Rausch and Pearson (1972) found that the number of reproductive tracts containing unimplanted blastocysts declined dramatically after January, suggesting that most nidation had occurred by the end of January. Unimplanted blastocysts were found by Rausch and Pearson (1972) and Liskop et al. (1981) as late as March. Given a 45-day gestation period (see below), implantation that occurred 1 March would result in a mid-April birth, but data on parturition suggest that such late births occur very rarely (see below). Wolverines may resorb fetuses (Banci and Harestad 1988) and it is possible that blastocysts could be present in March but remain unimplanted for the same physiological reasons that could lead to resorption.

Although mating occurs during spring/summer, active gestation may begin as early as November and as late as

Reproductive event	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
Mating [1, 9, 12, 14, 15, 17, 20]						?						
Nidation [1, 6, 17, 20]												
Gestation [13, 17]												
Parturition [1, 3, 4, 10, 14, 15, 16, 17, 18, 20]												
Reproductive Den Use [4, 10, 11]												
Weaning [5]												
Rendezvous Sites [2, 4, 7, 11]												
Independence [7, 11]												
Dispersal [2, 4, 7, 19]												
Lactation [1, 3, 4, 10, 14, 15, 16, 17, 18, 20]												
Post-weaning Growth [5, 11]												
Voles & Lemmings (*Microtus spp* and *Lemmus spp.*) [8, 21]												
Ground Squirrels (*Spermophilus spp.*) [8, 22]												
Marmots (*Marmota spp.*) [23]												
Caribou (*Rangifer tarandus*) [24]												
Mtn Goat (*Oreamnos americanus*) [25]												
Mtn Sheep (*Ovis spp.*) [26]												
Moose (*Alces alces*) [27]												
Elk (*Cervus elaphus*) [28]												
	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct

1. Banci and Harestad 1988
2. Copeland 1996
3. Davis 1967
4. Inman et al. 2007
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
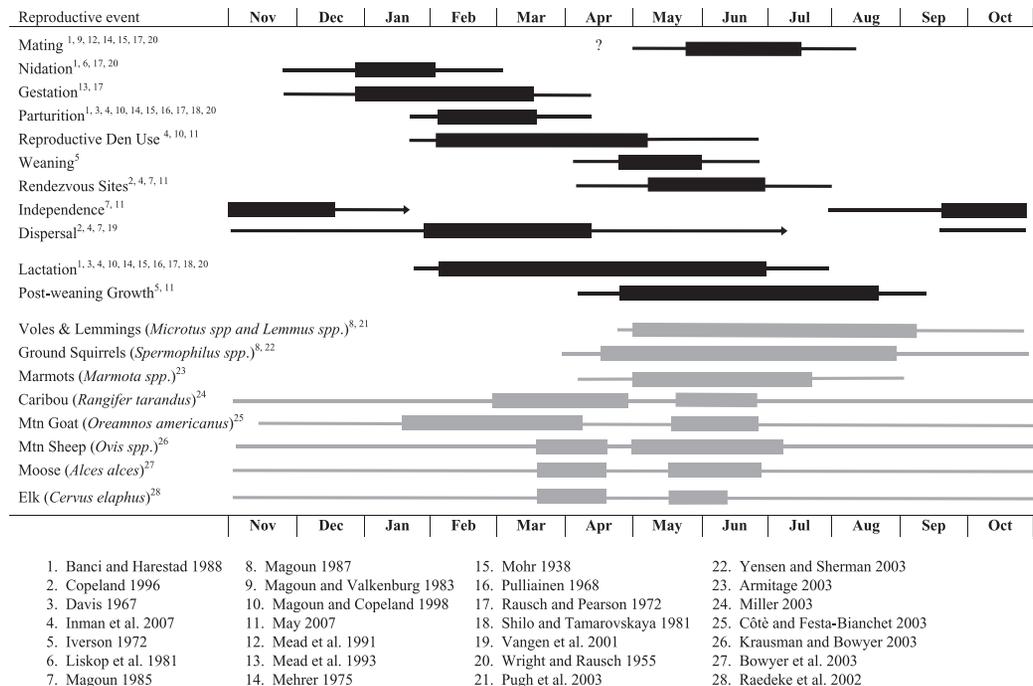27. Bowyer et al. 2003
28. Raedeke et al. 2002

FIG. 2.—Range (thin line) and peak (thick line) time periods associated with wolverine (*Gulo gulo*) reproductive biology and availability of food items.

March, with the peak of implantation occurring during late December to early February (Fig. 2). Data on nidation are not available from the southern portion of wolverine range. If there are latitudinal differences in birth date, nidation date likely also differs.

Gestation.—Rausch and Pearson (1972) suggested an active gestation period of 30–40 days on the basis of 50% of females killed in February having implanted embryos and 64% of those killed in March being postpartum. Mead et al. (1993) suggested that active gestation occurs for approximately 50 days on the basis of elevated progesterone profiles of captive females. We used a 45-day gestation period to aid interpolation of other reproductive events (Fig. 2).

Parturition.—Wright and Rausch (1955) reported that parturition appears to occur in late March or early April on the basis of 7 adult female reproductive tracts. After examining 122 female reproductive tracts with evidence of blastocysts, fetuses, or postpartum condition, Rausch and Pearson (1972) reported that parturition occurred from January to March, and in 1 case (0.8%) as late as mid-April; peak parturition was February, but the authors did not specify whether this was late February or earlier. Banci and Harestad (1988) found evidence of postpartum condition in 6 females; 1 had given birth in January and 5 in February. Both Rausch and Pearson (1972) and Banci and Harestad (1988) reported that the percentage of females that had active pregnancies increased from December to February and decreased thereafter.

Pulliainen (1968) obtained information on parturition from 2 reproductive tracts and from wolverine bounty hunters who dug out 31 wolverine dens. Pulliainen (1968) reported 4 litters as ''blind,'' which are <5 weeks old (D. Pedersen, pers. comm.), during January and on 6 February, 20 March, and 25 March. Pulliainen (1968) also found embryos in reproductive tracts in late March and suggested that parturition occurs primarily during February and March. Magoun and Copeland (1998) estimated date of parturition by comparing tooth eruption, body size, or pelage coloration of the cubs with that of known-age, captive wolverine cubs; they reported dates of 16, 18, and 23 February in Idaho and 24 February, 1, 4, and 6 March in Alaska. Inman et al. (2007) used repeated very-high-frequency (VHF) radiotelemetry locations during the denning season combined with subsequent observations of cubs to estimate parturition dates (more specifically the beginning date for use of natal den site) in the Yellowstone region of Idaho, Montana, and Wyoming on 29 January and 5, 18 (*n* = 2), and 23 February; 1 additional female wearing a global positioning system (GPS) collar began using a natal den on 16 February. On the basis of GPS collar locations, parturition dates (initial natal den use) for females in northern Sweden were estimated to be 1, 8, 11, 12, 16 (*n* = 2), 18 (*n* = 2), 19, and 21 February (J. Persson, pers. obs.). In addition, females immobilized there on 2 February (*n* = 3), 9 February (*n* = 1), and 15 February

($n = 2$) were pregnant (on the basis of palpation). Two females immobilized 23 February had given birth (were lactating).

The birth of 19 litters by 7 captive females occurred from 30 January to 18 March (D. Pedersen, pers. comm.). The peak in births occurred from 23 February to 6 March (11 of 19), with 4 before this period and 4 after. In February, 1 birth occurred in the 1st week, 2 in the 3rd week, and 6 in the last week. In March, 5 births occurred in the 1st week, 3 in the 2nd week, and 1 in the 3rd week. One female gave birth to 9 litters over a 10-year period; 8 of these births occurred from 23 February to 10 March and 1 birth occurred on 30 January. Sixty percent of 30 births at European zoos took place during the last 2 weeks of February; all occurred during the months of February (81%) and March (19%—Blomqvist 2001). Other captive females have given birth on 16 February (Davis 1967), 17 February (Mohr 1938), 26 February (Myhre and Myrberget 1975), and in March (Shilo and Tamarovskaya 1981).

In summary, the peak period for parturition appears to be February through mid-March. This period corresponds well with peak periods of nidation occurring from late December through early February and an approximate 45-day active gestation period. Births outside this period occur (late January and mid-March to mid-April), but appear to be rare (Fig. 2).

Reproductive den use.—The sites where female wolverines keep cubs before weaning have been distinguished as natal dens (birth location) and maternal dens (site used subsequent to natal den but before weaning—Magoun 1985; Magoun and Copeland 1998). Use of natal dens obviously begins no later than parturition; however, it is unknown whether females investigate or prepare the natal den before giving birth. Dates for abandonment of natal dens and initiation of maternal dens were difficult to establish. Natal dens have commonly been assumed to be used until cubs are old enough to be weaned; thus the 1st move away from the natal den would be to a rendezvous site. However, this has mainly been based on VHF radiotracking, which may not be accurate enough to detect short moves ($\sim$200 m) from a natal to a maternal den. Cubs in Idaho were moved between den sites at approximately 15–30 days of age (Magoun and Copeland 1998), and monitoring of females with GPS collars has shown that some females move to and between multiple den sites in March–April (J. Persson, R. Inman, pers. obs.). Magoun and Copeland (1998) reported that natal dens were abandoned in Alaska and Idaho when ''maximum daily temperatures rose above freezing for a number of days for the 1st time since denning commenced.'' These dates obviously differ by latitude, elevation, and year. Other factors such as parasites, defending against intraspecific predation, or disturbance could also influence den shifts. Overall, it appears that the timing of a shift from a natal den to a maternal den varies widely and that further research is needed to establish the prevalence, timing, causes, and function of these shifts. For the purposes of this paper we do not distinguish between these two types of dens but use the inclusive term ''reproductive dens'' to refer to dens used before weaning (Magoun and Copeland 1998). Movements

away from these reproductive denning areas typically occurred during late April and early May in Sweden (J. Persson, pers. obs.), mid-May in Norway (May 2007), 18 April–5 May in northwest Alaska (Magoun and Copeland 1998), and 16 April–2 May in the Yellowstone region (Inman et al. 2007). Thus the reproductive den(s) are commonly used from early February through mid-May (Fig. 2).

Weaning.—Myhre and Myrberget (1975) estimated that cubs are weaned (beginning to eat solid foods) at 7–8 weeks on the basis of stomach contents, but ages of cubs were assigned by comparison with weight curves of captive cubs, which may gain weight more quickly than wild cubs. Iversen (1972) speculated that weaning occurs at 10 weeks of age on the basis of the timing of a metabolic break he measured in 3 captive wolverine cubs, the relationship of this metabolic break and weaning in other species, and age at weaning in other carnivores. Captive cubs also become interested in solid foods at about 10 weeks (D. Pedersen, pers. comm. and A. Magoun, pers. obs.). On the basis of an age of weaning of 10 weeks and our estimated parturition dates, most cubs would be weaned during late April and May. The age at which cubs no longer nurse is unknown, but nursing can occur until about 3.5 months (D. Pedersen, pers. comm.; A. Magoun, pers. obs.). Photographs of the abdomen of a wild wolverine indicated that lactation was still occurring on 13 May but regression of teat size for this female had occurred by the time she was photographed with motion-detection cameras again on 18 June (A. Magoun, pers. obs.), although the survival of the cubs was unknown. The following year, noticeable regression in teat size for this same female had occurred by the end of June and 2 cubs were photographed with the female on July 31. Thus, nursing appears to end during late May and June.

Rendezvous sites.—Rendezvous sites are locations used after weaning where the female leaves cubs and from which they will not depart without her; the female either brings food back to the cubs or returns to lead them to a food source (Magoun 1985). Differentiation of reproductive dens and rendezvous sites at the time of weaning is based on behavioral differences associated with weaning (Magoun and Copeland 1998). Once the cubs are weaned, their need for meat increases and the female probably needs to be away from the cubs more frequently than when she is nursing them. The need to hunt, along with the cubs' ability to travel short distances, allows the female to move cubs closer to foraging sites and cached food rather than bringing food back to a den. On the basis of parturition dates, time to weaning, and observed den abandonment, rendezvous site use begins to peak in early May (Fig. 2). Magoun (1985) observed female offspring groups and suggested that the cubs began traveling regularly with their mother, rather than remaining at rendezvous sites, by late June or early July.

Independence.—Magoun (1985) showed that cubs spend a considerable amount of time foraging on their own within their mother's home range during August. However, she was not able to observe mother–offspring interactions in the latter part of July so cubs may begin foraging independently as early

as late July. Observations of 2 captive-reared cubs taken to a remote field area for behavioral observations indicated that excursions away from the mother may begin in late July but cubs are not accomplished hunters by then (A. Magoun, pers. obs.). May (2007) radiotracked family groups (mothers and cubs) from the beginning of May to 1 March and suggested that cubs were nearly full-grown and nutritionally independent from the mother by September. The period in which cubs begin to forage on their own probably varies with birth date and growth rate.

Dispersal.—Vangen et al. (2001) studied timing of exploratory movements and dispersal of 24 known-age juvenile wolverines and found that wolverines were 11 months old on average when they made their 1st exploratory movement outside their mother's home range. The range of age at dispersal was 7–18 months for males and 7–26 months for females; median ages were 10 months for males and 11 months for females (Vangen et al. 2001). Magoun (1985) reported 2 dispersal events occurring at 8–12 months and at 12 months of age; circumstantial evidence suggested that dispersal occurred as early as January and as late as May (10–14 months of age). Copeland (1996) reported that 2 males estimated to be 2 years of age made long-distance movements outside of their own home ranges; both disappeared from radio contact in February. Inman et al. (2012) reported that exploratory movements began at 11 months of age on average (range = 8–14 months, $n = 6$) and continued through at least 36 months of age for some individuals. Inman et al. (2012) reported that pulses of dispersal-related movements appeared to occur near the time of parturition. 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 (Fig. 2).

Food availability.—Wolverines are opportunistic foragers and food items include caribou/reindeer (*Rangifer tarandus*), moose (*Alces alces*), mountain goats (*Oreamnos americanus*), sheep (*Ovis* spp.), elk (*Cervus elaphus*), beavers (*Castor* spp.), marmots (*Marmota* spp.), ground squirrels (*Spermophilus* spp.), voles (*Microtus* spp.), lemmings (*Lemmus* spp.), hares (*Lepus* spp.), porcupine (*Erethizon dorsatum*), birds, bird eggs, insect larva, amphibians, and berries (Copeland and Whitman 2003; Dalerum et al. 2009; Lofroth et al. 2007; Magoun 1987; Mattisson et al. 2011b; Packila et al. 2007; Samelius et al. 2002; van Dijk et al. 2008).

Adult ungulates are generally thought to be taken in the form of carrion. However, wolverine predation on semidomestic reindeer (Bjärvall et al. 1990; Haglund 1966; Landa et al. 1997; Mattisson et al. 2011b), caribou (Gustine et al. 2006; Wittmer et al. 2005), and domestic sheep (Landa et al. 1999) can occur with some regularity. Wolverine predation on other adult ungulates, such as moose, occurs at least occasionally under specific conditions (Haglund 1974; Wittmer et al. 2005). In areas where most ungulates and larger predators move to winter range that is outside of the areas used by wolverines (Inman et al. 2012; Magoun 1985), scavengeable resources may be scarce during winter. In areas where larger predators and ungulates do not move to winter

ranges outside of wolverine habitat, scavengeable ungulate resources are likely available at some roughly base rate throughout the year (Mattisson et al. 2011b). In all areas, late winter (March–April) probably represents higher than usual levels of adult ungulate mortality for reasons including ease of predation with deep snow conditions or weakened animals, avalanches, starvation, and return of migrant ungulate herds (Bowyer et al. 2003; Côtè and Festa-Bianchet 2003; Krausman and Bowyer 2003; Miller 2003; Raedeke et al. 2002). Haglund (1966) suggested that March and April were the part of winter when availability of reindeer as both carcasses and prey for wolverines peaked in Scandinavia. In tundra ecosystems, movements of large numbers of migratory caribou in the same period may provide a temporary increase in available carcasses (Dalerum et al. 2009; Magoun 1985).

Wittmer et al. (2005) found that caribou in British Columbia were more likely to die from predation during spring calving and in summer than during other seasons. Neonatal ungulates are vulnerable to predation by wolverines. For example, the wolverine was the main predator on caribou calves in British Columbia (Gustine et al. 2006). Caribou (reindeer), moose, mountain goats, elk, and mountain sheep give birth in May to early June (Bowyer et al. 2003; Côtè and Festa-Bianchet 2003; Krausman and Bowyer 2003; Miller 2003; Raedeke et al. 2002). In summary, ungulate biomass accessible to wolverines probably peaks during late winter to early summer because of overwinter mortality, migration, and the birthing period. Although ungulate resources are likely to be lower during winter within all regions, this difference is far more pronounced in regions where the vast majority of ungulates and their predators migrate out of wolverine habitat during winter.

Those species of ground squirrels that overlap with wolverine distribution in North America are obligate hibernators with an active season of approximately May–September (Yensen and Sherman 2003). Dates of emergence and immergence vary annually due to weather and snow cover and squirrels can emerge as early as March and immerge as late as November (Magoun 1987; Yensen and Sherman 2003). Ground squirrels rear 1 litter per year, and young become active above ground during June. Marmots are also obligate hibernators, and the general period of emergence is April and immergence is September (Armitage 2003). Burrows are critical resources for marmots that are used by many generations (Armitage 2003), possibly providing a reliable point source of food for wolverines. Young marmots are active above ground by June (Armitage 2003). Voles are active throughout the year but become more vulnerable to predation by wolverines after snow melting exposes them, typically in May (Magoun 1987; Pugh et al. 2003). Smaller prey are also available at a low but base rate throughout the year but likely have a significant peak during May through August when snowmelt exposes microtines, hibernating rodents emerge, and the nesting season of many birds peaks.

Wolverines cache foods frequently during both winter and summer and this behavior likely extends availability beyond the peak periods of mortality and wolverine predation. The

behavior appears to be innate given that a captive cub demonstrated caching behavior at less than 3 months of age (A. Magoun, pers. obs.). Adult females cached ground squirrels and ptarmigan (*Lagopus* spp.) during summer in Alaska, and wolverines fed on cached ground squirrels during winter (Magoun 1987). Wolverines killed and cached geese and their eggs during June and July in Nunavut; however, some of these carcasses had rotted several days later (Samelius et al. 2002). May (2007) documented that wolverines partitioned and cached reindeer carcasses within a few nights during late winter/early spring, and that portions of up to 7 individual reindeer were located at a reproductive female's den site. Mattisson (2011) used GPS collar locations to investigate kill sites and found that wolverines of both sexes and during all seasons moved back and forth between carcasses and cache sites, removing large amounts of the carcass in a short time. At present it appears that caching occurs year-round and is utilized by both sexes; however, the degree to which specific time periods, sexes, or reproductive classes may differ is unknown.

Overall, calories available to wolverines probably reach a maximum from March to August (Fig. 2). Because weather factors that cause mortality of ungulates during winter vary greatly from year to year, annual consistency of accessible food is probably greatest during summer (May–August). The diversity of food sources is also likely greatest during summer (May–June). Major differences may occur by region during winter on the basis of whether one or more ungulate species and their predator(s) remain within wolverine habitat or migrate to areas of winter range where wolverines do not occur.

DISCUSSION

Our examination suggests that caching is likely an important behavioral adaptation that complements the morphology and demography of the wolverine and allows it to occupy its niche. Even though the vast majority (>90%) of mature female wolverines are pregnant in a given year (Banci and Harestad 1988; Rausch and Pearson 1972), mean annual proportion of females reproducing appears to be about 50% or less (Copeland 1996; Inman et al. 2007; Magoun 1985; Persson et al. 2006). This suggests that resorption or early litter loss is common. Early litter loss may be more adaptive for wolverines because the cost of gestation is low and, unlike a hibernating bear, it is possible for a female wolverine to suddenly acquire a major energetic source for lactation such as an ungulate carcass. This is consistent with the bet-hedging strategy of mustelids (Ferguson et al. 1996). Winter can be a period of unpredictable and low food availability for wolverines (Magoun 1985; Persson 2005), and caching behavior is common, including by reproductive females (Magoun 1987; May 2007). Early litter loss may occur unless caches accumulated over the winter allow sufficient female condition for lactation. Thus caches likely fuel much of the period of early lactation and may be critical for neonate survival. Accordingly, habitat features that facilitate caching may be critical for wolverine reproduction, i.e., structure that

prevents access by avian and large mammalian competitors along with cold temperatures that inhibit consumption by insects and bacteria.

Caches increase the predictability of food resources, reduce the energy spent searching for food during the demanding period of lactation, and decrease the time away from vulnerable newborns. Food caching can be considered functionally analogous to storage of body fat (McNamara et al. 1990), but without added body weight, which could be important for a species like the wolverine that is forced to move over large areas in search of food (Inman et al. 2012; Mattisson 2011). Bevanger (1992:9) first noted the relevance of ''nature's own natural fridges—swamps, snowdrifts, and rocky screes,'' as important places for wolverines to store food. Magoun and Copeland (1998) also suggested that den location could be related to areas where rearing young would be improved by better food storage during summer. We expect that the limits to wolverine distribution are ultimately related to the species' ability to avoid competition by existing in cold, low-productivity environments and accumulating (caching) the limited food resources present therein. As such, we propose a ''refrigeration-zone'' hypothesis as a food/competition-based explanation for the observed correlation between wolverine distribution and the area encompassed by 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 (Inman et al. 2012; Persson et al. 2010), low densities (Golden et al. 2007; Inman et al. 2012; Lofroth and Krebs 2007; Royle et al. 2011), low fecundity (Copeland 1996; Inman et al. 2007; Magoun 1985; Persson et al. 2006), and bioclimatic envelope (Copeland et al. 2010).

Although ungulate carrion as described above may be critical due to its use during lactation and beyond, the wolverine's reproductive chronology makes it difficult to dismiss summer foods, including nonungulate prey, as insignificant or even less significant. Juvenile wolverines gain most of their adult body size within 7 months of birth, and absolute weight gain during the postweaning period is greater than that from nidation to weaning (J. Persson, A. Magoun, pers. obs.). Thus, although lactation may be the most energetically demanding period for a reproductive female, the period of postweaning growth represents a significantly greater energetic demand from the environment by the family group. For wolverines, this period of growth occurs during summer (May–August). In addition, the longer the female continues to invest in the litter, the more she borrows significant physiological resources from the next potential litter to achieve success with the current litter (Persson 2005). Therefore, litter loss that occurs during summer results in both reproductive failure in the current year and reduced potential to reproduce the next year. Early litter loss is common, but starvation as the ultimate cause of juvenile mortality during summer is rare (Persson et al. 2009). This suggests that food availability is generally higher and more predictable and/or that juveniles are less sensitive to food shortage in summertime. Summer foods, whatever they may be, are also likely to be key to wolverine reproductive success.

TABLE 1.—Percentage of wolverine (*Gulo gulo*) food habit observations made during summer (May-October) and winter (November–April).

Reference	Summer			Winter				Method
	n	No. ungulate items	No. nonungulate items	*n*	No. ungulate items	No. nonungulate items	Empty	
Rausch and Pearson 1972[a]	.	.	.	193	44	41	99	Gastrointestinal tracts
Newell 1978[b]	15	1	16	30	9	26	.	Scats
Hornocker and Hash 1981	.	.	.	56	40	36	.	Scats
Gardner 1985[b]	9	3	6	35	16	17	.	Summer observations, winter gastrointestinal tracts
Magoun 1987	33	6	27	82	30	67	.	Summer observations, winter scats
Banci 1987	.	.	.	411	186	360	126	Gastrointestinal tracts
Poole 1992[b]	.	.	.	173	149	83	.	Stomachs
Copeland 1996	33	24	24	84	69	73	.	Scats and foraging events
Landa et al. 1997[a]	.	.	.	347	335	210	.	Scats from dens
Lofroth et al 2007	12	5	11	475	305	269	.	Scats and stomachs
Lofroth et al 2007	19	6	13	128	106	22	.	Foraging events
Packila et al. 2007	13	6	8	48	36	10	.	Scats and foraging events
Total observations	134	51	105	2,062	1,325	1,214		
% of total observations	6%			94%				

[a] Primarily winter observations, but a small number may have occurred during May.
[b] As reported by Banci (1994).

Few studies of summer food habits exist for wolverines, largely because snow-tracking is not usually possible during this period. In fact, approximately 94% of food habit samples have been obtained during winter (Table 1). Therefore it is not surprising that the items that dominate winter foraging are often thought to be of greater significance (Banci 1994; Banci and Harestad 1988; Dalerum et al. 2009; Lofroth et al. 2007; Rausch and Pearson 1972). Persson's (2005) supplemental feeding experiment suggests that winter is usually a period of low food availability for wolverines. It is possible that winter foods may typically allow wolverines to survive this season and fuel lactation in years when availability is great enough. On the basis

of the timing of reproductive events, summer foods appear to have an equally important role, and the limited information specific to summer diet indicates that predation on small prey occurs frequently in most areas (Gardner 1985; Lofroth et al. 2007; Magoun 1987; Packila et al. 2007). Total biomass obtained from small prey can be significant; 1 female was observed to eat 2 small mammals or ptarmigan chicks, an adult ptarmigan, a ground squirrel, and 2 eggs during a 2½-h period in June (Magoun 1987). In addition, wolverines have been documented as the main predator of woodland caribou calves during the calving season (Gustine et al. 2006), and predation on reindeer and other ungulate neonates occurs (Bjärvall et al.

FIG. 3.—This elk calf was killed by a female wolverine (*Gulo gulo*) on 16 June 2004 in southwestern Montana. She had moved parts of the carcass to a rendezvous site where she had a cub. She dragged the remainder of the carcass to another cache site under large boulders (right photo) where there was ice that was likely to be present until autumn. Structure and cold temperatures may be critical habitat features for cache longevity because they inhibit competition from avian, mammalian (e.g., bears), insect, and bacterial competitors.

1990; Landa et al. 1997; Mattisson et al. 2011b; Fig. 3). Given these factors, it is difficult to rule out predation during summer, including nonungulate prey, as a major factor in reproductive success and population dynamics of wolverines. Therefore, cached ungulate carrion and summer foods both appear to play critical roles in reproductive success for wolverines.

Despite the wolverine's flexibility in utilizing a wide variety of food resources and obtaining them through both scavenging and predation, it may be important to consider regionally and seasonally specific food resources that influence reproduction. If managers assume that wolverines scavenge ungulate carrion provided by larger predators and only occasionally utilize small prey, they could logically conclude that ensuring adequate food supplies simply consists of maintaining significant ungulate herds along with large predators. Although this might hold true in some areas, failure to ensure adequate populations of small prey could lead to deficient energetic supplies for reproduction in other areas. Better information on summer food habits of wolverines is needed within each of the biomes where the species occurs. Information on female body condition throughout the year would also be valuable in understanding key resources and limiting factors.

Wolverines were recently listed as warranted for protection under the ESA based in large part on the threat of climate change reducing distribution and connectivity (McKelvey et al. 2011; United States Fish and Wildlife Service 2010). To develop conservation actions for the species, we must understand the direct cause or causes by which climate limits distribution. For instance, is there an average ambient temperature above which wolverines are physiologically compromised? Will females be unable to find a denning area with sufficient thermal cover for cubs if snowpack changes during spring? Will competition for food increase if snow conditions allow prolonged presence of terrestrial competitors and higher temperatures compromise the wolverine's ability to cache food away from insects and bacteria? Although these hypotheses are not mutually exclusive, our examination of the wolverine's reproductive chronology suggests that 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.

ACKNOWLEDGMENTS

LITERATURE CITED

AMSTRUP, S. C. 2003. Polar bear (*Ursus maritimus*). Pp. 587–610 in Wild mammals of North America, biology, management, and conservation (G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, eds.). 2nd ed. The Johns Hopkins University Press, Baltimore, Maryland.

ANDERSON, E. M., AND M. J. LOVALLO. 2003. Bobcat and lynx (*Lynx rufus* and *Lynx canadensis*). Pp. 758–786 in Wild mammals of North America, biology, management, and conservation (G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, eds.). 2nd ed. The Johns Hopkins University Press, Baltimore, Maryland.

ARMITAGE, K. B. 2003. Marmots (*Marmota monax* and allies). Pp. 188–210 in Wild mammals of North America, biology, management, and conservation (G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, eds.). 2nd ed. The Johns Hopkins University Press, Baltimore, Maryland.

AUBRY, K. B., K. S. McKELVEY, AND J. P. COPELAND. 2007. Distribution and broadscale habitat relations of the wolverine in the contiguous United States. Journal of Wildlife Management 71:2147–2158.

BANCI, V. 1987. Ecology and behavior of wolverine in Yukon. M.S. thesis, University of British Columbia, Vancouver, Canada.

BANCI, V. 1994. Wolverine. Pp. 99–127 in The scientific basis for conserving forest carnivores, American marten, fisher, lynx, and wolverine in the western United States (L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, L. J. Lyon, and W. J. Zielinski, eds.). USDA Forest Service, Rocky Mountain Forest, and Range Experiment Station, General Technical Report RM-254.

BANCI, V., AND A. HARESTAD. 1988. Reproduction and natality of wolverine (*Gulo gulo*) in Yukon. Annales Zoological Fennici 25:265–270.

BEVANGER, K. 1992. Report on the Norwegian wolverine (*Gulo gulo* L.). Small Carnivore Conservation 6:8–10.

BJÄRVALL, A., R. FRANZÉN, M. NORDKVIST, AND G. ÅHMAN. 1990. Renar och rovdjur. Rovdjurens effekter på rennäringen. Naturvårdsverkets förlag. Solna, Sweden.

BLOMQVIST, L. 2001. Management of captive wolverines *Gulo gulo* in Europe; studbook and guidelines to husbandry. Vol. 2. European Association of Zoos and Aquaria. VTT-Grafiska, Vimmerby, Sweden.

BOWYER, R. T., V. VAN BALLENBERGHE, AND J. G. KIE. 2003. Moose (*Alces alces*). Pp. 931–964 in Wild mammals of North America, biology, management, and conservation (G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, eds.). 2nd ed. The Johns Hopkins University Press, Baltimore, Maryland.

BRONSON, F. H. 1989. Mammalian reproductive biology. University of Chicago Press, Chicago, Illinois.

COPELAND, J. P. 1996. Biology of the wolverine in central Idaho. M.S. thesis. University of Idaho, Moscow.

COPELAND, J. P., AND J. S. WHITMAN. 2003. Wolverine. Pp. 672–682 in Wild mammals of North America, biology, management, and conservation (G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, eds.). 2nd ed. The Johns Hopkins University Press, Baltimore, Maryland.

COPELAND, J. P., ET AL. 2010. The bioclimatic envelope of the wolverine (*Gulo gulo*): do climatic constraints limit its geographic distribution? Canadian Journal of Zoology 88:233–246.

CÔTÉ, S. D., AND M. FESTA-BIANCHET. 2003. Mountain goat (*Oreamnos americanus*). Pp. 1061–1075 in Wild mammals of North America, biology, management, and conservation (G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, eds.). 2nd ed. The Johns Hopkins University Press, Baltimore, Maryland.

CYPHER, B. L. 2003. Foxes (*Vulpes* species, *Urocyon* species, and *Alopex lagopus*). Pp. 511–546 in Wild mammals of North America, biology, management, and conservation (G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, eds.). 2nd ed. The Johns Hopkins University Press, Baltimore, Maryland.

Dalerum, F., K. Kunkel, A. Angerbjörn, and B. S. Shultz. 2009. Diet of wolverines (*Gulo gulo*) in the western Brooks Range, Alaska. Polar Research 28:246–253.

Danilov, P. I. and I. L. Tumanov. 1972. Male reproductive cycles in the Mustelidae. Zoologicheskii Zhurnal 51:871–881. [In Russian]

Davis, D. G. 1967. A brief note on the birth of wolverines *Gulo gulo* at Colorado Zoo. International Zoo Yearbook 7:127.

Ferguson, S. H., J. A. Virgl, and S. Larivière. 1996. Evolution of delayed implantation and associated grade shifts in life history traits of North American carnivores. Ecoscience 3:7–17.

Gärdenfors, U. 2010. The 2010 red list of Swedish species. Swedish Species Information Centre, Swedish University of Agricultural Sciences.

Gardner, C. L. 1985. The ecology of wolverines in southcentral Alaska. M.S. thesis, University of Alaska, Fairbanks.

Geist, V. 2002. Adaptive behavioral strategies. Pp. 389–433 in North American elk: ecology and management (D. E. Toweill and J. W. Thomas, eds.). Smithsonian Institution Press, Washington, D.C.

Golden, H. N., et al. 2007. Estimating wolverine (*Gulo gulo*) population size using quadrat sampling of tracks in snow. Wildlife Biology 13 (Suppl. 2):52–61.

Gustine, D. D., K. L. Parker, R. J. Lay, M. P. Gillingham, and D. C. Heard. 2006. Calf survival of woodland caribou in a multipredator ecosystem. Wildlife Monographs 165:1–32.

Haglund, B. 1966. De stora rovdjurens vintervanor I. Viltrevy 3:81–310.

Haglund, B. 1974. Moose relations with predators in Sweden, with special reference to bear and wolverine. Le Naturaliste Canadien 101:457–466.

Hash, H. S. 1987. Wolverine. Pp. 575–585 in Wild furbearer management and conservation in North America (M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, eds.). Ontario Ministry of Natural Resources, Toronto, Ontario, Canada.

Hornocker, M. G., and H. S. Hash. 1981. Ecology of the wolverine in northwestern Montana. Canadian Journal of Zoology 59:1286–1301.

Inman, R. M., K. H. Inman, M. L. Packila, and A. J. McCue. 2007. Wolverine reproductive rates and maternal habitat in Greater Yellowstone. Chapter 4 in Greater Yellowstone Wolverine Study, Cumulative Report, May 2007. Wildlife Conservation Society, North America Program, General Technical Report.

Inman, R. M., et al. 2012. Spatial ecology of wolverines at the southern periphery of distribution. Journal of Wildlife Management 76(4):778–792.

Iversen, J. A. 1972. Basal metabolic rate of wolverines during growth. Norwegian Journal of Zoology 20:317–322.

Kålås, J. A., Å. Viken, S. Henriksen, and S. Skjelseth. 2010. The 2010 Norwegian red list for species. Norwegian Biodiversity Information Centre, Norway.

Krausman, P. R., and R. T. Bowyer. 2003. Mountain sheep (*Ovis canadensis* and *O. dalli*). Pp. 1095–1118 in Wild mammals of North America, biology, management, and conservation (G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, eds.). 2nd ed. The Johns Hopkins University Press, Baltimore, Maryland.

Krebs, J., et al. 2004. Synthesis of survival rates and causes of mortality in North American wolverines. Journal of Wildlife Management 68:493–502.

Krebs, J., E. Lofroth, and I. Parfitt. 2007. Multiscale habitat use by wolverines in British Columbia, Canada. Journal of Wildlife Management 71:2180–2192.

Krott, P. 1959. Der Vielfrass (*Gulo gulo* L. 1758). Monograph Wildsäuget. 13:1–159. (Cited in Haglund, B. 1966.)

Krott, P., and C. Gardner. 1985. Wolverine breeding behavior in Alaska. Saugietierkundliche Mitteilungen 32:87.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen & Co., London.

Landa, A., K. Gudvangen, J. E. Swenson, and E. Røskaft, 1999. Factors associated with wolverine *Gulo gulo* predation on domestic sheep. Journal of Applied Ecology 36:963–973.

Landa, A., O. Strand, J. E. Swenson, and T. Skogland. 1997. Wolverines and their prey in southern Norway. Canadian Journal of Zoology 75:1292–1299.

Liskop, K. S., R. Sadleir, and B. P. Saunders. 1981. Reproduction and harvest of wolverine in British Columbia. Pages 469–477 in Proceedings of the Worldwide Furbearer Conference (J. A. Chapman, and D. Pursley, eds.). Worldwide Furbearer Conf., Inc., Frostburg, Maryland.

Lofroth, E. C., and J. A. Krebs. 2007. The abundance and distribution of wolverines in British Columbia, Canada. Journal of Wildlife Management 71:2159–2169.

Lofroth, E. C., J. A. Krebs, W. L. Harrower, and D. Lewis. 2007. Food habits of wolverine, *Gulo gulo*, in montane ecosystems of British Columbia. Wildlife Biology 13(Suppl. 2):31–37.

Magoun, A. J. 1985. Population characteristics, ecology, and management of wolverines in Northwestern Alaska. Ph.D. dissertation, University of Alaska, Fairbanks.

Magoun, A. J. 1987. Summer and winter diets of wolverines, *Gulo gulo*, in arctic Alaska. Canadian Field Naturalist 101:392–397.

Magoun, A. J., and J. P. Copeland. 1998. Characteristics of wolverine reproductive den sites. Journal of Wildlife Management 62:1313–1320.

Magoun, A. J., and P. Valkenburg. 1983. Breeding behavior of free-ranging wolverines (*Gulo gulo*). Acta Zoologica Fennica 174:175–177.

Mattisson, J. 2011. Interactions between Eurasian lynx and wolverines in the reindeer husbandry area. Ph.D. dissertation, no. 2011:10, Swedish University of Agricultural Sciences, Uppsala, Sweden.

Mattisson, J., H. Andrén, J. Persson, and P. Segerström. 2011b. The influence of intraguild interactions on resource use by wolverines and Eurasian lynx. Journal of Mammalogy 92:1321–1330.

Mattisson, J., J. Persson, H. Andrén, and P. Segerström. 2011a. Temporal and spatial interactions between an obligate predator, the Eurasian lynx (*Lynx lynx*), and a facultative scavenger, the wolverine (*Gulo gulo*). Canadian Journal of Zoology 89:79–89.

May, R. 2007. Spatial ecology of wolverines in Scandinavia. Ph.D. dissertation, Norwegian University of Science and Technology, Trondheim, Norway.

McKelvey, K. S., et al. 2011. Climate change predicted to shift wolverine distributions, connectivity, and dispersal corridors. Ecological Applications 21:2882–2897.

McNamara, J. M., A. I. Houston, and J. R. Krebs. 1990. Why hoard? The economics of food storing tits *Parus* spp. Behavioral Ecology 1:12–23.

Mead, R. A., M. Bowles, G. Starypan, and M. Jones. 1993. Evidence of pseudopregnancy and induced ovulation in captive wolverines (*Gulo gulo*). Zoo Biology 12:353–358.

Mead, R. A., M. Rector, G. Starypan, S. Neirinckx, M. Jones, and M. N. DonCarlos. 1991. Reproductive biology of captive wolverines. Journal of Mammalogy 72:807–814.

Mehrer, C. F. 1975. Gestation period in the wolverine (*Gulo gulo*). Journal of Mammalogy 57:570.

Miller, F. L. 2003. Caribou (*Rangifer tarandus*). Pp. 965–997 in Wild mammals of North America, biology, management, and conservation (G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, eds.). 2nd ed. The Johns Hopkins University Press, Baltimore, Maryland.

MOHR, E. 1938. Vom Jarv (*Gulo gulo* L.). Zoologische Garten, Leipzig 10:14–21.

MYHRE, R., AND S. MYRBERGET. 1975. Diet of wolverines in Norway. Journal of Mammalogy 56:752–757.

NEWELL, D. S. 1978. A wolf, wolverine, fox and bear scat study from northern British Columbia. British Columbia Fish and Wildlife Branch Report:1–53.

OFTEDAL, O. T., AND J. L. GITTLEMAN. 1989. Patterns of energy output during reproduction in carnivores. Pp. 355–378 in Carnivore behavior, ecology, and evolution (J. L. Gittleman, ed.). Cornell University Press, Ithaca, New York.

PACKILA, M. L., A. J. MCCUE, R. M. INMAN, AND K. H. INMAN. 2007. Wolverine food habits in Greater Yellowstone. Chapter 8 in Greater Yellowstone Wolverine Study, Cumulative Report, May 2007. Wildlife Conservation Society, North America Program, General Technical Report.

PAQUET, P. C., AND L. N. CARBYN. 2003. Gray wolf (*Canis lupus* and allies). Pp. 482–510 in Wild mammals of North America, biology, management, and conservation (G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, eds.). 2nd ed. The Johns Hopkins University Press, Baltimore, Maryland.

PELTON, M. R. 2003. Black bear (*Ursus americanus*). Pp. 547–555 in Wild mammals of North America, biology, management, and conservation (G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, eds.). 2nd ed. The Johns Hopkins University Press, Baltimore, Maryland.

PERSSON, J. 2003. Population ecology of Scandinavian wolverines. Ph.D. dissertation, Swedish University of Agricultural Sciences, Uppsala, Sweden.

PERSSON, J. 2005. Female wolverine (*Gulo gulo*) reproduction: reproductive costs and winter food availability. Canadian Journal of Zoology 83:1453–1459.

PERSSON, J., G. ERICSSON, AND P. SEGERSTRÖM. 2009. Human-caused mortality in the endangered Scandinavian wolverine population. Biological Conservation 142:325–331.

PERSSON, J., A. LANDA, R. ANDERSEN, AND P. SEGERSTRÖM. 2006. Reproduction in Scandinavian wolverines. Journal of Mammalogy 87:75–79.

PERSSON, J., P. WEDHOLM, AND P. SEGERSTRÖM. 2010. Space use and territoriality of wolverines (*Gulo gulo*) in northern Scandinavia. European Journal of Wildlife Research 56:49–57.

PIERCE, B. M., AND V. C. BLEICH. 2003. Mountain lion (*Puma concolor*). Pp. 774–757 in Wild mammals of North America, biology, management, and conservation (G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, eds.). 2nd ed. The Johns Hopkins University Press, Baltimore, Maryland.

POOLE, K. G. 1992. Wolverine carcass collections in the western Northwest Territories, 1991–1992. Northwest Territories Department of Renewable Resources Report:1–6.

POWELL, R. A., S. W. BUSKIRK, AND W. J. ZIELINSKI. 2003. Fisher and marten (*Martes pennanti* and *Martes americana*). Pp. 635–649 in Wild mammals of North America, biology, management, and conservation (G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, eds.). 2nd ed. The Johns Hopkins University Press, Baltimore, Maryland.

PUGH, S. R., S. JOHNSON, AND R. H. TAMARIN. 2003. Voles (*Microtus* species). Pp. 349–370 in Wild mammals of North America, biology, management, and conservation. (G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, eds.). 2nd ed. The Johns Hopkins University Press, Baltimore, Maryland.

PULLIAINEN, E. 1968. Breeding biology of the wolverine (*Gulo gulo* L.) in Finland. Annales Zoologici Fennici 5:338–344.

RAEDEKE, K. J., J. J. MILLSPAUGH, AND P. E. CLARK. 2002. Population characteristics. Pp. 449–492 in North American elk: ecology and management (D. E. Toweill and J. W. Thomas, eds.). Smithsonian Institution Press, Washington, D.C.

RAUSCH, R. A., AND A. M. PEARSON. 1972. Notes on the wolverine in Alaska and the Yukon Territory. Journal of Wildlife Management 36:259–268.

ROYLE, J. A., A. J. MAGOUN, B. GARDNER, P. VALKENBURG, AND R. E. LOWELL. 2011. Density estimation in a wolverine population using spatial capture–recapture models. Journal of Wildlife Management 75:604–611.

SAMELIUS, G., ET AL. 2002. Foraging behaviours of wolverines at a large arctic goose colony. Arctic 55:148–150.

SCHWARTZ, C. C., S. D. MILLER, AND M. A. HAROLDSON. 2003. Grizzly bear (*Ursus arctos*). Pp. 556–586 in Wild mammals of North America, biology, management, and conservation (G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, eds.). 2nd ed. The Johns Hopkins University Press, Baltimore, Maryland.

SHILO, R. A., AND M. A. TAMAROVSKAYA. 1981. The growth and development of wolverines *Gulo gulo* at Novosibirsk Zoo. International Zoo Yearbook 21:146–147.

SINGER, F. J., A. HARTING, K. K. SYMONDS, AND M. B. COUGHENOUR. 1997. Density dependence, compensation and environmental effects on elk calf mortality in Yellowstone National Park. Journal of Wildlife Management 61:12–25.

STEARNS, S. C. 1992. The evolution of life histories. Oxford University Press, New York.

UNITED STATES FISH AND WILDLIFE SERVICE. 2010. Endangered and threatened wildlife and plants; 12-month finding on a petition to list the North American wolverine as endangered or threatened. Federal Register Vol. 75, No. 239, Tuesday, December 14, 2010. 78030–78061. < http://www.fws.gov/mountain-prairie/species/mammals/wolverine/75FR78030.pdf >. Accessed 14 December 2010.

VAN DIJK, J, ET AL. 2008. Diet shift of a facultative scavenger, the wolverine, following recolonization of wolves. Journal of Animal Ecology 77:1183–1190.

VANGEN, K. M., J. PERSSON, A. LANDA, R. ANDERSEN, AND P. SEGERSTRÖM. 2001. Characteristics of dispersal in wolverines. Canadian Journal of Zoology 79:1641–1649.

WITTMER, H. U., ET AL. 2005. Population dynamics of the endangered mountain ecotype of woodland caribou (*Rangifer tarandus caribou*) in British Columbia, Canada. Canadian Journal of Zoology 83:407–418.

WRIGHT, P. L., AND R. RAUSCH. 1955. Reproduction in the wolverine, *Gulo gulo*. Journal of Mammalogy 36:346–355.

YENSEN, E., AND P. W. SHERMAN. 2003. Ground squirrels (*Spermophilus* and *Ammospermophilus* species). Pp. 211–231 in Wild mammals of North America, biology, management, and conservation (G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, eds.). 2nd ed. The Johns Hopkins University Press, Baltimore, Maryland.

III

Developing a Spatial Framework and Conservation Priorities for a Wolverine Metapopulation

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Abstract

Wolverines of the contiguous United States appear to exist as a small, vulnerable metapopulation and have been designated as warranted for protection under the Endangered Species Act. Collaborative management strategies developed at the multi-state scale are essential for recovery and persistence, but wolverine data are limited. We used wolverine telemetry data along with resource selection function modeling to predict relative habitat quality across the western U.S. and differentiate areas suitable for survival, reproduction, and dispersal. We estimated potential population capacity/distribution along with current population size/distribution by relating habitat quality to population size. We then used this spatial framework to identify conservation

priorities at the multi-state scale. Our habitat model tested well with additional wolverine location datasets and k-fold cross validation (r_s = 0.94–0.99). Primary wolverine habitat (survival) existed in island-like fashion distributed across a 10 state area of ~2.5 million km^2 and we estimated capacity to be 580 wolverines (95% CI = 454–1724). We estimated current population size to be approximately half of capacity. Areas we predicted suitable for male dispersal linked all patches, but the Southern Rockies and Sierra-Nevada appear to be isolated for females. Reintroduction of wolverines to areas of historical distribution that are currently unoccupied has the potential to increase population size by >40% and includes areas that may be robust to climate change. Persistence of wolverines will require development of a permanent network of open space that ensures the ability of wolverines to disperse among many of the publically-owned mountain ranges of the western U.S. Development of a collaborative, multi-state population monitoring program is needed and our results provide an initial hypothesis of distribution and abundance to be tested and refined.

Key words: metapopulation, scale, wolverine, reintroduction, connectivity, monitor.

1. Introduction

The wolverine (*Gulo gulo*) occupies a cold, low-productivity niche (Copeland et al. 2010, Inman et al. 2012*a*, Inman et al. 2012*b*) that results in sparse population densities and low reproductive rates across its range (Golden et al. 2007, Inman et al. 2012*a*, Lofroth and Krebs 2007, Persson et al. 2006). As a result, wolverine populations are relatively vulnerable due to their low densities and limited capacity for growth (Brøseth et al. 2010, Persson et al. 2009). Historically, wolverines of the contiguous U.S. were distributed within the Rocky and Pacific Coast Mountains, including areas as far south as Colorado and California (Aubry et al. 2007). Wolverines were extirpated, or nearly so, from the contiguous U.S. by about 1930 and unregulated human-caused mortality was likely responsible (Aubry et al. 2007). Wolverines have recovered to a considerable degree, in part because the initial century of wildlife management began regulating factors such as widespread use of poisoned bait for predator control and unlimited trapping/killing. However, wolverines are expected to face a new set of habitat-related challenges in the 21st Century such as rural sprawl, roads, recreation, and climate change (Gude et al. 2007, Krebs et al. 2007, McKelvey et al. 2011, Packila et al. 2007) and will again be limited in their ability to overcome negative influences due to their niche. The species was recently designated a candidate for listing in the contiguous U.S. under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 2010).

Wolverine habitat in the contiguous U.S. appears to consist of disjunct patches inhabited at low densities and requiring dispersal across intervening areas (Copeland et al. 2010, Inman et al. 2012a), a prime example of a metapopulation (Hanski and Gaggiotti 2004). The metapopulation concept has evolved from island biogeographic theory (MacArthur and Wilson 1967) into complex estimates of population viability that are based on the spatial arrangement of habitat patches, habitat quality within and between patches, demographic rates, and dispersal (Akçakaya and Atwood 1997, Haines et al. 2006). By linking demography to habitat in a spatial framework, metapopulation analytical tools allow scenario assessments such as gauging the relative effect of one management activity vs. another on viability. While application of a complex metapopulation model for wolverine conservation in the contiguous U.S. may never be practical because it would require an abundance of data that are difficult to obtain, basic forms that are useful can be generated. This is particularly true in the early stages of conservation efforts when it is important to simply define where habitats suitable for survival, reproduction, and dispersal exist; identify who manages these habitats; determine which areas are occupied at present; and garner a reasonable assessment of population capacity and size. Most importantly, knowledge of these basic population characteristics will improve the ability to define spatially-explicit population-level strategies across jurisdictions.

While there has been much recent progress in understanding wolverine distribution and ecology in the contiguous U.S. (Cegelski et al. 2006, Copeland et al. 2010, Inman et al. 2012*a*, Ruggiero et al. 2007, Schwartz et al. 2009), habitat-related tools remain coarse and estimates of potential or current population size do not exist. Wolverine distribution at the global scale is related to areas covered in snow through mid-May in at least 1 of 7 years (Copeland et al. 2010). This spring snow model has tightened the understanding of distribution, and its parsimony makes it valuable for examining the potential for climate change to affect wolverines (McKelvey et al. 2011). However, parsimony limits its utility for some purposes. For instance, 6–25% of wolverine radio-telemetry locations from the contiguous U.S. fell outside of spring snow (Table 1 in Copeland et al. 2010) suggesting it may not capture all the elements necessary for the species; predicted corridors are limited to straight lines between patches of spring snow where major arteries of wolverine movement can flow through large cities due to a lack of intervening habitat features (Schwartz et al. 2009). Current effective population size in the contiguous U.S. has been estimated to be 35 (Schwartz et al. 2009), and it is unclear which patches of wolverine habitat in the contiguous U.S. are capable of female interchange, male interchange, or both. A better

understanding of the capacity of areas of historical distribution that remain unoccupied and the degree to which they are likely to be naturally recolonized would help with decisions on whether reintroductions are warranted and which areas to prioritize.

Without a more complete understanding of the spatial arrangement of habitats, their function for wolverines, and potential population numbers therein, metapopulation-level conservation priorities will remain undefined, leaving a host of agencies and conservation organizations without clear roles in what must be a coordinated effort across a vast geographic area (Inman et al. 2012*a*). Our objective was to develop a metapopulation framework for wolverines at the scale necessary to conserve the species in the western contiguous U.S. To do this we: 1) captured and monitored radio-marked wolverines, 2) predicted relative habitat quality at the level of distribution; 3) tested the validity of the prediction with independent wolverine location data; 4) identified areas suitable for specific wolverine uses that are biologically important and valuable for management purposes (survival, reproduction, dispersal); and 5) related population size to the habitat model in order to estimate potential and current distribution and abundance. We then use this information to identify spatially-explicit population-level conservation priorities across jurisdictions for this candidate endangered species.

2. Study Area

Our field research occurred in the Greater Yellowstone Ecosystem of Idaho, Montana, and Wyoming at approximately 45° north latitude (Fig. 1). Elevations in the study area ranged from 1,400–4,200 m. Precipitation increased with elevation and varied from 32–126 cm per year (National Oceanic and Atmospheric Administration 2007). Snow usually fell as dry powder and depths at higher elevations were often in excess of 350 cm. A variety of vegetative communities were present (Despain 1990). Low-elevation valleys contained short-grass prairie or sagebrush communities. The lower-timberline transition to forest occurred with lodgepole pine (*Pinus contorta*) or Douglas fir (*Pseudotsuga menziesii*). Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and whitebark pine (*Pinus albicaulis*) became more common with increasing elevation. Mixed forest types were common and all forest types were interspersed with grass, forb, or shrub meadows. The highest elevations were alpine tundra or talus fields where snow was present to some degree for 9 months of the year. A diverse fauna included a variety of ungulates and large carnivores (Bailey 1930, Streubel 1989).
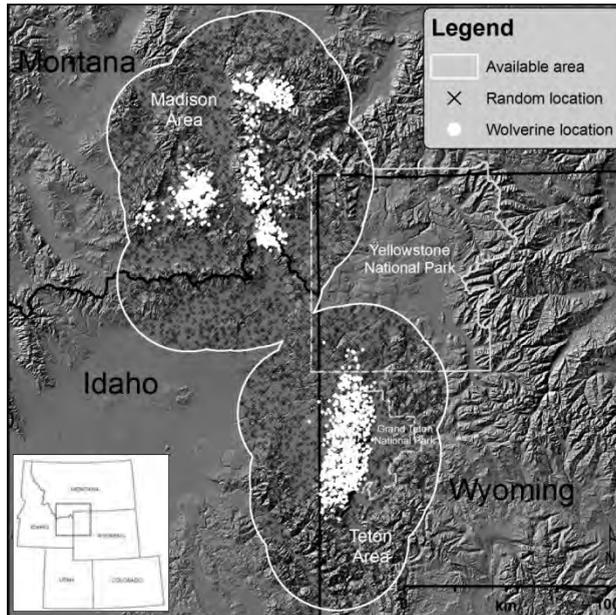
Figure 1. Study area and locations of wolverines (solid circles) and random points (x's) used to develop a resource selection function model of first order habitat selection, Greater Yellowstone Ecosystem of Montana, Idaho, and Wyoming, USA, 2001–2010.

3. Materials and Methods

3.1 Wolverine data

During 2001–2010 we captured 38 wolverines (23♀, 15♂) and equipped each with an intra-peritoneal VHF radio-transmitter (Inman et al. 2012*a*). We also opportunistically fit 18 of these wolverines (11F, 7M) with a global positioning system (GPS) collar for periods of ~3 months. The study was approved by the Animal Care and Use Committee of Montana Department of Fish, Wildlife and Parks (MFWP). We estimated VHF telemetry error to be ~300 m (Inman et al. 2012*a*). We used an approach similar to Hebblewhite et al. (2011) to train habitat models (see below) using 2,257 VHF radio telemetry locations collected from 12♀ and 6♂ wolverines resident to the Madison, Gravelly, Henry's Lake, and Teton mountain ranges. We did not use GPS collar data for model training due to the potential for bias by habitat features (D'Eon et al. 2002, Sager-Fradkin et al. 2007). We used locations of wolverines whose data were not used to train models to test the top model as described below.

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3.2 Landscape covariates

We developed a list of habitat features we believed important for wolverines (Table 1) based on our field observations and reports of food habits (Copeland and Whitman 2003, Lofroth et al. 2007), mortality sources (Boles 1977, Krebs et al. 2004), den sites (Magoun and Copeland 1998), and general habitat characteristics including the potential for avoidance of humans (Carroll et al 2001, Copeland et al. 2007, Copeland et al. 2010, Hornocker and Hash 1981, Rowland et al. 2003). We also considered the importance of caching behavior (Inman et al. 2012*b,* May 2007), and our observations of reproductive females frequently preying on marmots (*Marmota flaviventris*). We developed a set of GIS grids capable of representing these features in a first order analysis (Johnson 1980) and available across the western U.S. (Table 2). We resampled grids to 90 m resolution (Arponen et al. 2012) and calculated mean values of covariates using a 300 m window based on telemetry error.

We derived topographic-related covariates from 30-m National Elevation Data (Caruso 1987). Because the model was targeted for a broad region, we used latitude-adjusted elevation (LAE; Brock and Inman 2006). We developed an index of terrain ruggedness (TRI) based on Riley et al. (1999). We represented high-elevation talus (HITAL) by selecting all areas where LAE was >2,300 m and TRI was >100, and we measured distance to high-elevation talus (DHITAL). We derived vegetation-related covariates from 30-m National Land-cover Dataset (NLCD; Homer et al. 2001). We calculated tree cover (TREE) by summing the number of treed pixels within 300 m of each grid cell. We measured distance to the nearest treed cell (DTREE). We calculated forest edge (EDGE) by reclassifying NLCD into 3 categories: forest (deciduous, evergreen, mixed, and woody wetlands), natural non-forest (shrub-scrub, grassland-herbaceous, barren land, open water, ice-snow, and herbaceous wetland), or other (developed and agricultural), and identifying cells where forest and natural non-forest were adjacent. We derived climate-related variables from the Snow Data Assimilation System (Barrett 2003). We mapped snow depth (SNOW) by averaging values for April 1 2004 and April 1 2005. We did not include temperature as a covariate because broad trends in temperature are captured by latitude-adjusted elevation (Brock and Inman 2006). We calculated distance to snow (DSNOW) based on the nearest cell where April 1 snow depth was >2.5cm. We used GIS layers developed by Carroll et al. (2001) to represent road density (ROAD) and interpolated human population density (POP). Interpolation provided an approximation for the effects of human use in areas closer to urban centers (Merrill et al. 1999).

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.

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Table 2. *Habitat covariates used in developing a first order resource selection function model predicting relative wolverine habitat quality across the western United States. Wolverine location data for the logistic regression were obtained in the Greater Yellowstone Ecosystem of Montana, Idaho, and Wyoming, USA, 2001–2010. Positive (+) or negative (–) predicted associations are noted along with the relevance of each covariate for representing key habitat features we believed to influence wolverine presence. Geographic information system (GIS) data sources, resolution, and references are provided. Covariates noted with * were not retained by the top model.*

Habitat Covariate	Predicted Association	Relevance	Source[a]	Resolution	Reference
Latitude-adjusted elevation (LAE)	+	More low temperatures and alpine meadows	1	30 m	Brock and Inman (2006)
Terrain ruggedness index (TRI)	+	More cliffs, boulders/talus, structure	1	30 m	Riley et al. (1999)
April 1 snow depth (SNOW)	+	More deep, long-lasting snow cover	2	1 km	Barrett (2003)
*Tree cover (TREE)	+	More forest and structure	3	30 m	Homer et al. (2001)
*Forest edge (EDGE)	+	More alpine meadow and structure	3	30 m	Homer et al. (2001)
*High-elevation talus (HITAL)	+	More cold, rocky terrain	1	30 m	This study
Road density (ROAD)	–	More human presence	4	1 km	Carroll et al. (2001)
Interpolated human density (POP)	–	More human activity	4	1 km	Carroll et al. (2001)
Dist. to tree cover (DTREE)	–	Farther from forest, structure, escape cover	3	30 m	Homer et al. (2001)
Dist. to Apr 1 snow >2.5 cm (DSNOW)	–	Farther from familiar feature	2	1 km	Barrett (2003)
Dist. to high-elevation talus (DHITAL)	–	Farther from familiar feature	1	30 m	This study

[a] Data Sources: 1 = National Elevation Dataset, U.S. Geological Survey, Sioux Falls, SD, USA; 2 = Snow Data Assimilation System, National Snow and Ice Data Center, Boulder, CO, USA; 3 = National Land Cover Dataset, Earth Resources Observation and Science Data Center, Sioux Falls, SD, USA; 4 = U.S. Geological Survey, Reston, VA, USA.

3.3 Resource selection function (RSF) modeling

We estimated first order resource selection of wolverines by comparing landscape covariates at wolverine locations to those at available locations in a used-available design (Hebblewhite et al. 2011, Johnson 1980, Manley et al. 2002). We delineated the area available for wolverine use with a 34.8 km buffer around our trap locations, which was the average maximum distance that wolverines were located from their initial point of capture. That area was well within the regular movement capabilities of wolverines but did not include large areas where we had not attempted to capture wolverines and thus did not sample for wolverine use. We sampled availability of landscape covariates with 6,771 random locations within the area considered available (Fig. 1; Carroll et al. 2001, Hebblewhite et al. 2011).

Prior to analysis, we disqualified highly correlated variables and limited our set of candidate models to those that were biologically relevant and explainable (Burnham and Anderson 2002). We began with 11 covariates we believed could be predictive in distinguishing first order habitat selection by wolverines. Because of the reasonable possibility for both non-linear responses (e.g., snow depth) and interactions between variables, we considered inclusion of all quadratic terms and two-way interactions. We eliminated 75% of these 88 potential models by carefully considering whether each quadratic and interaction was both meaningful and interpretable (Burnham and Anderson 2002) and using a decision threshold of 0.70 to eliminate correlated variables (Wiens et al. 2008) and. This resulted in the retention of only 3 quadratic terms and 9 interactions for further consideration.

To select the best model among candidates, we used a forward and backward stepwise selection using the stepAIC function in R statistical software (R Development Core Team 2012, Venables and Ripley 2002). We specified the Bayesian Information Criterion (BIC) option to evaluate candidate models because BIC penalizes more for over-fitting than AIC (Boyce et al. 2002, Schwartz 1978). We used the coefficients from the top logistic regression model to index habitat quality using the equation:

$$w(x) = \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_i x_i.$$

We scaled our result from 0–1 and evaluated model fit with likelihood ratio chi-square test, residual diagnostics, and k-fold cross validation (Boyce et al. 2002, Hebblewhite et al. 2011, Hosmer and Lemeshow 2000).

3.4 Testing the top model with validation datasets

We used the k-fold procedure (Boyce et al. 2002, Hebblewhite et al. 2011) to evaluate model performance with 5 wolverine location datasets that were not used to train the model (Table 3). First, we withheld 2,935 GPS collar locations of the resident animals used to train the model and tested the model's predictive capacity within the area where it was developed. Second, we also withheld 1,165 VHF and GPS locations of 9 wolverines who we captured in the Madison/Teton study area, but who dispersed beyond this area. This test set included locations both within and beyond the area of model development, including areas ~500 km south (Colorado). The remaining three datasets were independent of the model development area and we used them as out-of-sample validation sets for testing predictive ability beyond the area of development. These were 157 historical wolverine records from the western U.S. (Aubry et al. 2007), 321 wolverine mortality locations provided by MFWP, and 365 VHF and GPS collar locations of 5 resident wolverines we captured in the Anaconda Range ~150–300 km northwest of main study area.

Table 3. *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.

3.5 Identifying areas suitable for survival, reproduction, and dispersal

We binned relative habitat quality into biologically meaningful categories that were also informative for management. Various approaches for binning have been used (Aldridge et al. 2012, Haines et al. 2006). 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. 2012*b*) and then using the 10th percentile as our cutoff. 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 utilzed during documented dispersal movements by each sex (4♀, 5♂; dispersal was delineated via radio-telemetry [Inman et al. 2012*a*]).

3.6 Estimating wolverine distribution and abundance

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). We determined total RSF predicted relative probabilities for the Yellowstone area where Inman et al. (2012*a*) estimated wolverine population size and calculated total predicted habitat required for each wolverine. We summed total predicted relative probabilities for each patch of primary wolverine habitat >100 km^2, which is the approximate minimum female home range size (Copeland 1996, Hornocker and Hash 1981, Inman et al. 2012*a*). Finally, we estimated the potential number of wolverines possible in each >100km^2 patch using the following equation:

$$\frac{\sum_{Current} \hat{w}(x)_i}{N_{Current}} = \frac{\sum_{Patch} \hat{w}(x)_i}{N_{Patch}}$$

where $N_{Current}$ is the wolverine population estimate from Yellowstone (known), $\sum_{Current} \hat{w}(x)_i$ is the sum of relative probabilities within the Yellowstone population estimate area, and $\sum_{Patch} \hat{w}(x)_i$ is the summed predicted habitat probability for habitat patch *j*. We rounded the number of wolverines estimated for each patch down to the nearest integer prior to summing by region and across the western U.S.

We estimated current population size in the area where wolverines are likely well-distributed across available habitat based on contemporary records of both male and female wolverines occupying an area (Anderson and Aune 2008, Aubry et al. 2007, Aubry et al. 2010, Copeland 1996, Inman et al. 2012*a*, Magoun et al. 2011, Murphy et al. 2011, Squires et al. 2007). We then applied the same estimation technique within the boundary. We did not include areas with isolated or dispersing individuals that may occur in places that were not likely to be reproducing as part of the larger population. 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).

4. Results

4.1 Predicting relative habitat quality and testing with independent data

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. The top model's BIC score was much lower than the null model, global model, and several simple models (Tables S1 and S2). The k-fold cross validation score for the training locations indicated an excellent model fit ($r_s = 0.98$, SE = 0.005, Fig. S1), as did the Hosmer and Lemeshow goodness of fit test $\chi^2 = 19.92$ ($P = 0.01$).

The model tested well within the study area using k-fold cross validation and a holdout dataset of GPS collar locations ($r_s = 0.997$; Table 3). When the model was extrapolated to the western U.S., it also performed well ($r_s = 0.939$–0.966; Table 3). The k-fold test with all 157 historical records from the western U.S. (Aubry et al. 2007) scored low ($r_s = 0.646$). However, the 6 historical records that scored lowest were all within the boundaries of modern cities. These records included 2 from 1870 that fell within the present city of Denver, Colorado; 3 from 1871–1885 that fell within the present city of Ogden, Utah; and 1 from 1954 that fell within the present city of Caldwell, Idaho. Habitat conditions in these areas have changed drastically since the records were made, and these areas were predicted to be low-quality habitat by our model due to high road and human population densities. When these 6 records were removed, the historical dataset also tested well ($r_s = 0.966$), lending confidence to the ability of the test to detect a mismatch between predicted habitat quality and actual wolverine locations, and to the predictive performance of the model.

4.2 Identifying areas suitable for survival, reproduction, and dispersal

Predicted habitat scores ≥0.982 represented primary wolverine habitat, i.e., areas suitable for survival and use by resident adults (Fig. 2). We classified a total of 170,997 km^2 as primary habitat in the western U.S. 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. 3). We classified areas scoring ≥0.983 as maternal habitat (Fig. 2), the total area of which was 31% of the area classified
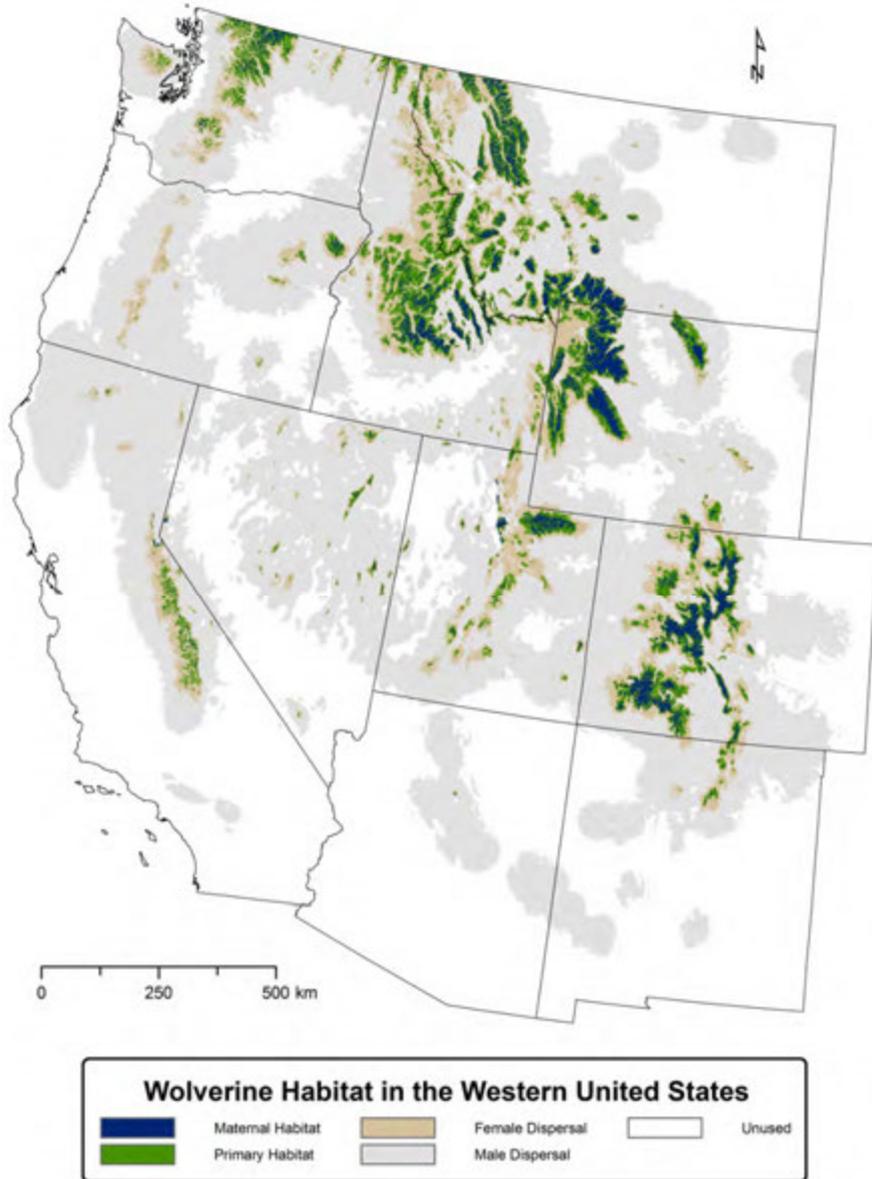
Figure 2. Areas of the western United States predicted to be maternal wolverine habitat (suitable for use by reproductive females), primary wolverine habitat (suitable for survival, i.e., use by resident adults), female dispersal habitat (suitable for relatively brief female dispersal movements), and 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.
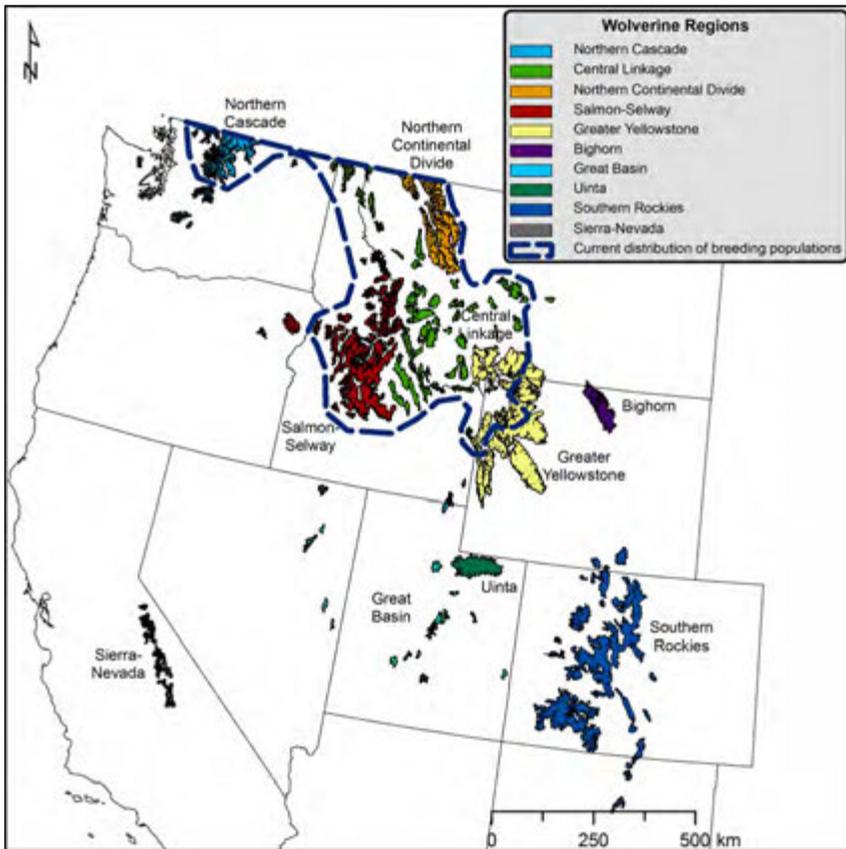
Figure 3. Major blocks (>100 km^2) of primary wolverine habitat (suitable for use by resident adults) in the western United States as predicted with a first order (species distribution) logistic regression and grouped into useful management regions. Current distribution of breeding populations based on contemporary records are also depicted with the dashed line.

as primary habitat. For patches of primary habitat >100 km^2, the quality of habitat differed internally such that percent of a patch classified as maternal habitat ranged from 0–64% (Table S3). 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. 2). 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, northwest 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. 2 and 3).

4.3 Estimating wolverine distribution and abundance

We estimated potential wolverine 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 4, Fig. 3). Sixty-one percent of this population capacity occurred in the combined Greater Yellowstone, Salmon-Selway, Central Linkage, and Northern Continental Divide ecosystems (Table 4, Fig. 3). Estimated population capacity for individual patches ranged from 0–99 (Table S3). 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) in the Salmon-Selway, Central Linkage, Northern Continental Divide, and portions of the Greater Yellowstone and Northern Cascade ecosystems (Table 4, Fig. 3).

Table 4. Estimates of wolverine population capacity and current population size by region (as in Fig. 3) 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 (Inman et al. 2012*a*).

5. Discussion

We developed a prediction of relative habitat quality for wolverines in the western contiguous U.S., identified areas suitable for survival, reproduction, and dispersal; and estimated current and potential population distribution and

abundance. The model tested well with independent location datasets suggesting it is robust to extrapolation and useful for developing collaborative conservation strategies at the multi-state scale necessary for this species.

We defined primary habitat as areas suitable for survival/use by resident adults. All areas where wolverine populations have been studied with radio-telemetry in the western U.S. contained significant areas of predicted primary habitat (Aubry et al. 2010, Copeland 1996, Hornocker and Hash 1981, Murphy et al. 2011, Squires et al. 2007). We predicted suitable habitat in areas as far south as northern New Mexico, supporting the conclusion of Frey (2006). Our estimate of primary habitat and the spring snow model of Copeland et al. (2010) matched fairly well, concurring across 96% of the western U.S. This level of agreement derived from different approaches, i.e., a global-scale bioclimatic envelope and a regional telemetry-based RSF, suggests that distribution of wolverine habitat is fairly well described. The major difference between the two models occurs in the Pacific Coastal Ranges of Oregon and northern California. Here the snow model suggests there are areas large enough to hold female territories in nearly continuous fashion from the Canadian border into southern California (Figure 8A in Copeland et al. 2010, Figure 2B in McKelvey et al. 2011); the patches are certainly within observed dispersal range of males and females. Our estimate of primary habitat is far more conservative in this area (Fig. 2). Some evidence lends support to the more conservative prediction. First, there were only 2 historical records of wolverines from Oregon and northern California whereas there were 29 from Washington and 58 from the Sierra-Nevada of central California (Aubry et al. 2007). Second, genetic information suggests wolverines of the Sierra-Nevada were isolated for >2,000 years (Schwartz et al. 2007). Our primary habitat model is more consistent with these pieces of information in that it suggests the amount and quality of habitat in Oregon and northern California is too limited to support survival and reproduction (Fig. 2). On the other hand, our prediction of primary habitat and population capacity in the Sierra-Nevada may be overly-conservative given that Aubry et al. (2007) located 57 historical records there (however those records occurred over an extended period ~1800–1930). Under either habitat model, it is difficult to reconcile the scarcity of historical records between southern Washington and the Sierra-Nevada along with the isolated genetics of the Sierra-Nevada and the number of historical records from within the Sierra-Nevada. Clearly, a better understanding of the ability of the habitats within Oregon and northern California to sustain reproducing wolverines or not would benefit efforts to conserve wolverines in the western U.S.

Maternal sites occurred in areas of higher quality habitat suggesting potential utility in distinguishing among patches more or less suitable for

reproduction. Percentage of maternal habitat within primary habitat patches varied widely (0–64%; Table S3). Patch quality in term of reproductive capacity could have important implications for metapopulation conservation strategies. For instance, the Nevada, Elkhorn, and Boulder mountains (Fig. S2) sit in a central position relative to 3 major blocks of habitat in the northern U.S. Rockies and could play an important role in gene flow among these areas. This would be particularly true if reproduction is occurring there because dispersing young could be a vector for genetic exchange among the major blocks of habitat. However, the amount of high-quality maternal habitat in these ranges is limited enough that reproduction may not occur there. If this were the case, taking management action to emphasize the ability of these ranges to produce dispersers could be futile. Differences in reproductive capacity of patches could help identify and prioritize linkage corridors throughout the metapopulation by weighting in order to better represent potential gene flow.

Male biased dispersal is typical for carnivores (Dobson 1982, Greenwood 1980, Pusey 1987), and male wolverines tend to disperse more frequently and farther, on average, than females (Flagstad et al. 2004, Inman et al. 2012*a*, Vangen et al. 2001). While our results could have shown that females used as low or lower quality areas as males, we observed males using lower scoring areas than females. All primary habitat patches fell within the limits of male dispersal that we estimated, however, this was not the case for females. The majority of primary habitat patches in Idaho, Montana, western Wyoming, and Utah were connected or very nearly so for females (<3 km; Fig. 2). However three large patches of primary habitat appear isolated for females based on the currently available data – the Bighorn Range of northeastern Wyoming, the Southern Rockies of Colorado, and the Sierra-Nevada of California (Figs. 2 and 3). Our results suggest that there are no areas of complete redundancy (all are linked for males), but of course other factors such as distance and degree of isolation would influence the rate at which exchange might occur. Our result also suggests that natural range expansion to the Sierra-Nevada, Southern Rockies, and Bighorns may be limited if possible at all for females.

For purposes of discussion, we grouped patches of wolverine habitat into regions based on capacity, connectivity, and land ownership pattern, all of which would tend to result in similar management issues at a regional scale (Fig. 3). It appears that 4 areas can likely function as major population cores where primary habitats exist as large blocks of relatively contiguous, publically-owned lands that include significant portions of designated wilderness or national park and are capable of supporting >25 wolverines. These were the Northern Continental Divide, Salmon-Selway, Greater Yellowstone, and Southern Rockies Regions (Fig. 3). Four areas appear to be

capable of functioning as minor population cores given that they are relatively contiguous blocks of public land but were more isolated and had less capacity (≥10 and <25); these were the Northern Cascade, Bighorn, Uinta, and Sierra-Nevada Regions (Figs. 2 and 3). However, we note that our estimate of primary habitat and capacity in the Sierra-Nevada may be low due to the confounding information discussed above, and the Sierras may be capable of functioning as a major core. In addition, while the Northern Cascades Region contained only 6% of estimated population capacity and does not appear to be well-linked to other major cores in the U.S., it is contiguous with large areas of wolverine habitat in British Columbia (Lofroth and Krebs 2007). However, these areas of British Columbia were rated as low quality wolverine habitat (Lofroth and Krebs 2007). The Central Linkage and Great Basin Regions consisted of smaller patches of primary habitat (<10 wolverines per individual patch) where intervening areas are often in private ownership or connectivity for females was limited (Figs. 2 and 3).

Our results clearly demonstrate that suitable habitat for resident adults and reproduction occurs in island-like fashion here at the southern periphery of the species distribution, and that wolverines are dependent on dispersal among patches of habitat across a vast geographic scale. The small wolverine metapopulation of the western contiguous U.S. is subject to the cumulative 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) 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 (Fig. 2). Maintaining high adult female survival and reproductive rates in the CLR would likely benefit metapopulation connectivity and gene flow. Recent changes to wolverine trapping regulations in Montana were designed with this landscape-level goal in mind. However, successfully achieving gene flow in the northern U.S. 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 movements through the CLR decades from now. Clearly, geographically coordinated goals will be key to successfully conserving this wolverine metapopulation.

Given the accelerated development of private lands in valley bottoms across the western U.S. in recent decades (Brown et al. 2005, Gude et al. 2007, Gude et al. 2008, Johnson and Beale 1994), 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 (Schwartz et al. 2010). Because housing developments and roads are relatively permanent and unregulated compared to human activities that might affect wolverine survival and reproductive rates (e.g., trapping and winter recreation [Krebs et al. 2004, Krebs et al. 2007]), working to establish natural areas in the locations most suitable for wolverine dispersal and movements of other wildlife species needs to be a priority. The CLR appears to be a logical priority for wolverine connectivity efforts given the position and ownership pattern.

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. Our analysis suggests that the Southern Rockies represent 23% of total wolverine population capacity, and it does not appear to be currently occupied by a breeding population (Aubry et al. 2007). The northern tier of states (MT, ID, WA) have yielded fairly consistent records of wolverines since the 1940's (Aubry et al. 2007), but wolverine presence was not confirmed for nearly a century within Colorado, Utah, or California (Aubry et al. 2007). Recent records of wolverines in California during 2008 and Colorado during 2009 were both instances of individual males that were either documented via camera and DNA (Moriarty et al. 2009) or radio-tracked while dispersing (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 California or Colorado for nearly a century, and our analysis suggests that female dispersal to either is likely to be rare if possible at all (Fig. 2). As such, active restorations would likely 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 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).

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 (Table S3).

6. Conclusion

Wolverine habitat in the western contiguous U.S. exists in island-like fashion distributed across 10 states (~2.5 million km^2) and appears to have the capacity for approximately 600 individuals. Our estimate of current population size was approximately half of capacity and was limited to portions of four states. Because the geographic scale for conserving this metapopulation is so large, management actions must be conceived and implemented in a nested fashion across multiple states and numerous management jurisdictions. Significant positive steps toward wolverine persistence could be made by 1) restoring wolverines to areas of historical range that are currently unoccupied by breeding females, 2) securing connectivity within and among core areas, and 3) establishing a collaborative population monitoring program. Restoration of wolverines to the Southern Rockies could increase current population size by an estimated 42% along with improving the redundancy, resiliency, and genetic diversity of the metapopulation. The Southern Rockies are also predicted to be relatively robust for wolverines as climate change occurs over the next 50 years (McKelvey et al. 2011, Peacock 2011). The Central Linkage Region is a logical priority for securing connectivity because of the nature of its habitat and land ownership along with the fact that the Northern U.S. Rockies (Northern Continental Divide, Salmon-Selway, Greater Yellowstone,

and Central Linkage Regions) include 3 of the 4 major wolverine core areas, the majority of the current wolverine population, and connections to larger populations in Canada. Our model can facilitate efforts to identify and prioritize connectivity by providing a base layer that accounts for habitat features occurring between patches of primary habitat. Our analysis also provides an initial hypothesis for wolverine distribution and abundance within the western contiguous U.S. that can facilitate development of a collaborative metapopulation monitoring program.

Acknowledgements

References

Akçakaya, H.R., and J.L. Atwood. 1997. A habitat-based metapopulation model of the California gnatcatcher. *Conservation Biology* 11(2):422–434.

Aldridge, C.L., D.J. Saher, T.M. Childers, K.E. Stahlnecker, and Z.H. Bowen. 2012. Crucial nesting habitat for Gunnison sage-grouse: a spatially explicit hierarchical approach. *Journal of Wildlife Management* 76(2):391–406.

Anderson, N.J. and K.E. Aune. 2008. Fecundity of female wolverine in Montana. *Intermountain Journal of Science* 14(1–3):17–30.

Arponen, A., J. Lehtomäki, J. Leppänen, E. Tomppo, and A. Moilanen. 2012. Effects of connectivity and spatial resolution of analyses on conservation prioritization across large extents. *Conservation Biology* 26(2):294–304.

Aubry, K. B., K.S. McKelvey, and J.P. Copeland. 2007. Distribution and broadscale habitat relations of the wolverine in the contiguous United States. *Journal of Wildlife Management* 71(7):2147–2158.

Aubry, K.B., J. Rohrer, C.M. Raley, E.C. Lofroth, S. Fitkin. 2010. *Wolverine distribution and ecology in the North Cascades Ecosystem, 2010 Annual Report*. U.S. Forest Service, Pacific Northwest Research Station, Olympia, Washington, USA.

Bailey, V. 1930. *Animal life of Yellowstone National Park*. Charles C. Thomas, Springfield, Illinois, USA.

Barrett, A. 2003. National Operational Hydrologic Remote Sensing Center Snow Data Assimilation System (SNODAS) Products at National Snow and Ice Data Center. Digital Media. *National Snow and Ice Data Center Special Report 11*. National Snow and Ice Data Center, Boulder, Colorado, USA.

Boles, B.K. 1977. Predation by wolves on wolverines. *Canadian Field-Naturalist* 91(1):68–69.

Boyce, M.S., and L.L. McDonald. 1999. Relating populations to habitats using resource selection functions. *Trends in Ecology and Evolution* 14(7):268–272.

Boyce, M.S., P.R. Vernier, S.E. Nielsen, and F.K.A. Schmiegelow. 2002. Evaluating resource selection functions. *Ecological Modelling* 157:281–300.

Brock, B.L., and R.M. Inman. 2006. Use of latitude-adjusted elevation in broad-scale species distribution models. *Intermountain Journal of Sciences* 12:12–17.

Brown, D.G., K.M. Johnson, T.R. Loveland, and D.M. Theobald. 2005. Rural land-use trends in the conterminous United States, 1950–2000. *Ecological Applications*. 15(6):1851–1863.

Burnham, K.P. and D.R. Anderson. 2002. *Model Selection and Multimodel Inference: A Practical Information–theoretic Approach. Second edition*. Springer Science + Business Media, LLC, New York, New York, USA.

Carroll, C., R.F. Noss, and P.C. Paquet. 2001. Carnivores as focal species for conservation planning in the rocky mountain region. *Ecological Applications* 11:961–980.

Caruso, V.M. 1987. Standards for digital elevation models. Technical papers; 1987 American Society for Photogrammetry and Remote Sensing annual convention; *Volume 4, Cartography Technical Papers of the American Society of Photogrammetry Annual Meeting 1987*:159–166.

Cegelski, C.C., L.P. Waits, N.J. Anderson, O. Flagstad, C. Strobeck, and C.J. Kyle. 2006. Genetic diversity and populations structure of wolverine (*Gulo gulo*) populations at the southern edge of their current distribution in North America with implications for genetic viability. *Conservation Genetics* 7:197–211.

Copeland, J. 1996. *Biology of the wolverine in central Idaho*. MSc Thesis, University of Idaho, Moscow, USA.

Copeland, J.P., and J.S. Whitman. 2003. Wolverine. Pages 672–682 *in* G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. *Wild mammals of North America, biology, management, and conservation. Second edition*. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Copeland, J.P., J.M. Peek, C.R. Groves, W.E. Melquist, K.S. McKelvey, G.M. McDaniel, C.D. Long, and C.E. Harris. 2007. Seasonal habitat associations of the wolverine in central Idaho. *Journal of Wildlife Management* 71(7):2201–2212.

Copeland, J.P., K.S. McKelvey, K.B. Aubry, A. Landa, J. Persson, R.M. Inman, J. Krebs, E. Lofroth, H. Golden, J.R. Squires, A. Magoun, M.K. Schwartz, J. Wilmot, C.L. Copeland, R.E. Yates, I. Kojola, R. May. 2010. The bioclimatic envelope of the wolverine (*Gulo gulo*): do climatic constraints limit its geographic distribution? *Canadian Journal of Zoology* 88(3): 233–246.

D'Eon, R.G., R. Serrouya, G. Smith, and C.O. Kochanny. 2002. GPS radio telemetry error and bias in mountainous terrain. *Wildlife Society Bulletin* 30:430–439.

Despain, D.G. 1990. *Yellowstone vegetation: consequences of environment and history in a natural setting*. Roberts Rinehart, Boulder, Colorado, USA.

Dobson, F.S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behaviour* 30:1183–1192.

Flagstad, Ø., E. Hedmark, A. Landa, H. Brøseth, J. Persson, R. Andersen, P. Segerström, and H. Ellegren. 2004. Colonization history and noninvasive monitoring of a reestablished wolverine population. *Conservation Biology* 18:676–688.

Frey, J.K. 2006. Inferring species distributions in the absence of occurrence records: An example considering wolverine (*Gulo gulo*) and Canada lynx (*Lynx canadensis*) in New Mexico. *Biological Conservation* 130:16–24.

Golden, H.N., J.D. Henry, E.F. Becker, M.I. Goldstein, J.M. Morton, D. Frost, Sr., and A.J. Poe. 2007. Estimating wolverine (*Gulo gulo*) population size using quadrat sampling of tracks in snow. *Wildlife Biology* 13(Suppl. 2):52–61.

Greenwood, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28:1140–1162.

Gude, P.H., A.J. Hansen, and D.A. Jones. 2007. Biodiversity consequences of alternative future land use scenarios in Greater Yellowstone. *Ecological Applications* 17:1004–1018.

Gude, P., R. Rasker, and J. van den Noort. 2008. Potential for future development on fire-prone lands. *Journal of Forestry* June:198–205.

Haines, A.M., M.E. Tewes, L.L. Laack, J.S. Horne, and J.H. Young. 2006. A habitat-based population viability analysis for ocelots (*Leopardus pardalis*) in the United States. *Biological Conservation* 132:424–436.

Hanski, I. and O.E. Gaggiotti. 2004. *Ecology, Genetics, and Evolution of Metapopulations*. Elsevier Academic Press, Burlington, Massachusetts, USA.

Hebblewhite, M., D.G. Miquelle, A.A. Murzin, V.V. Aramilev, and D.G. Pikunov. 2011. Predicting potential habitat and population size for reintroduction of the Far Eastern leopards in the Russian Far East. *Biological Conservation* 144:2403–2413.

Homer, C., C. Huang, L. Yang, B. Wylie, and M. Coan. 2001. Development of a 2001 National Land-cover Database for the United States. *Photogrammetric Engineering and Remote Sensing* 70:829–840.

Hornocker, M.G., and H.S. Hash. 1981. Ecology of the wolverine in Northwestern Montana. *Canadian Journal of Zoology* 59:1286–1301.

Hosmer, D.W., and S. Lemeshow. 2000. *Applied Logistic Regression. Second edition*. John Wiley & Sons, New York, New York, USA.

Inman, R.M., M.L. Packila, K.H. Inman, B.C. Aber, R. Spence, and D. McCauley. 2009. *Greater Yellowstone Wolverine Program, Progress Report, December 2009*. Wildlife Conservation Society, North America Program, General Technical Report, Bozeman, Montana, USA.

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*a*. Spatial ecology of wolverines at the southern periphery of distribution. *Journal of Wildlife Management* 76(4):778–792.

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

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.

Johnson, K.M., and C.L. Beale. 1994. The recent revival of widespread population growth in nonmetropolitan areas of the United States. *Rural Sociology* 59(4):655–667.

Krebs, J., E.C. Lofroth, and I. Parfitt. 2007. Multiscale habitat use by wolverines in British Columbia, Canada. *Journal of Wildlife Management* 71(7):2180–2192.

Krebs, J., E. Lofroth, J. Copeland, V. Banci, D. Cooley, H. Golden, A. Magoun, R. Mulders, and B. Schultz. 2004. Synthesis of survival rates and causes of mortality in North American wolverines. *Journal of Wildlife Management* 68:493–502.

Lofroth, E.C., and J. Krebs. 2007. The abundance and distribution of wolverines in British Columbia, Canada. *Journal of Wildlife Management* 71(7):2159–2169.

Lofroth, E.C., J.A. Krebs, W.L. Harrower, and D. Lewis. 2007. Food habits of wolverine, *Gulo gulo*, in montane ecosystems of British Columbia. *Wildlife Biology* 13(Suppl. 2):31–37.

MacArthur, R.H., and E.O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey, USA.

Magoun, A.J., and J.P. Copeland. 1998. Characteristics of wolverine reproductive den sites. *Journal of Wildlife Management* 62:1313–1320.

Magoun, A.J., P. Valkenburg, C.D. Long, and J.K. Long. 2011. *Monitoring wolverines in northeast Oregon – 2011, Final Report*. The Wolverine Foundation, Inc., Kuna, Idaho, USA.

Manly, B.F.J., L.L. McDonald, D.L. Thomas, T.L. McDonald, and W.P. Erickson. 2002. *Resource Selection by Animals, Statistical Design and Analysis for Field Studies, Second edition*. Kluwer Academic Publishers, Dordrecht, Netherlands.

May, R. 2007. *Spatial ecology of wolverines in Scandinavia*. PhD Dissertation. Norwegian University of Science and Technology, Trondheim, Norway.

McKelvey, K.S., J.P. Copeland, M.K. Schwartz, J.S. Littell, K.B. Aubry, J.R. Squires, S.A. Parks, M.M. Elsner, and G.S. Mauger. 2011. Climate change predicted to shift wolverine distributions, connectivity, and dispersal corridors. *Ecological Applications* 21(8):2882–2897.

Merrill, T., D.J. Mattson, R.G. Wright, and H.B. Quigley. 1999. Defining landscapes suitable for restoration of grizzly bears (*Ursus arctos*) in Idaho. *Biological Conservation* 87:231–248.

Moriarty, K.M., W.J. Zielinski, A.G. Gonzales, T.E. Dawson, K.M. Boatner, C.A. Wilson, F.V. Schlexer, K.L. Pilgrim, J.P. Copeland, M.K. Schwartz. 2009. Wolverine confirmation in

California after nearly a century: native or long-distance immigrant? *Northwest Science* 83(2):154–162.

Murphy, K., J. Wilmot, J. Copeland, D. Tyers, J. Squires, R.M. Inman, M.L. Packila, and D. McWhirter. 2011. *Wolverine conservation in Yellowstone National Park: Final report*. YCR-2011-02. National Park Service, Yellowstone National Park, Yellowstone Center for Resources, Yellowstone National Park, Wyoming.

National Oceanic and Atmospheric Administration. 2007. *Western Regional Climate Center*. Historic temperature and precipitation data for Ennis, Montana, 1948–2006. <http://www.wrcc.dri.edu/index.html>

Packila, M.L., R.M. Inman, K.H. Inman, and A.J. McCue. 2007. Wolverine road crossings in western Greater Yellowstone. Chapter 7 *in Greater Yellowstone Wolverine Study, Cumulative Progress Report, May 2007*. Wildlife Conservation Society, North America Program, General Technical Report, Bozeman, Montana, USA.

Peacock, S. 2011. Projected 21st century climate change for wolverine habitats within the contiguous United States. *Environmental Research Letters* 6 (2011) 014007 (9pp).

Persson, J., A. Landa, R. Andersen, P. Segerström. 2006. Reproductive characteristics of female wolverines (*Gulo gulo*) in Scandinavia. *Journal of Mammalogy* 87(1):75–79.

Persson, J., G. Ericsson, and P. Segerström. 2009. Human caused mortality in the endangered Scandinavian wolverine population. *Biological Conservation* 142:325– 331.

Pusey, A.E. 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends in Ecology and Evolution* 2:295–299.

R Development Core Team. 2012. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Riley, S.J., S.D. DeGloria, and R. Elliot. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. *Intermountain Journal of Sciences* 5:23–27.

Rowland, M.M., M.J. Wisdom, D.H. Johnson, B.C. Wales, J.P. Copeland, and F.B. Edelmann. 2003. Evaluation of landscape models for wolverines in the interior Northwest, United States of America. *Journal of Mammalogy* 84:92–105.

Ruggiero, L.F., K.S. McKelvey, K.B. Aubry, J.P. Copeland, D.H. Pletscher, and M.G. Hornocker. 2007. Wolverine conservation and management. *Journal of Wildlife Management* 71(7):2145–2146.

Sager-Fradkin, K.A., K.J. Jenkins, R.A. Hoffman, P.J. Happe, J.J. Beecham, and R.G. Wright. 2007. Fix success and accuracy of global positioning system collars in old-growth temperate coniferous forests. *Journal of Wildlife Management* 71(4):1298–1308.

Schwartz, C.C., M.A. Haroldson, and G.C. White. 2010. Hazards affecting grizzly bear survival in the Greater Yellowstone Ecosystem. *Journal of Wildlife Management* 74(4):654–667.

Schwartz, G. 1978. Estimating the dimension of a model. *Annals of Statistics*. 6:461–464.

Schwartz, M.K., K.B. Aubry, K.S. McKelvey, K.L. Pilgrim, J.P. Copeland, J.R. Squires, R.M. Inman, S.M. Wisely, and L.F. Ruggiero. 2007. Inferring geographic isolation of wolverines in California using historical DNA. *Journal of Wildlife Management* 71(7):2170–2179.

Schwartz, M.K., J.P. Copeland, N.J. Anderson, J.R. Squires, R.M. Inman, K.S. McKelvey, K.L. Pilgrim, L.P. Waits, and S.A. Cushman. 2009. Wolverine gene flow across a narrow climatic niche. *Ecology* 90(11):3222–3232.

Squires, J.R., J.P. Copeland, T.J. Ulizio, M.K. Schwartz, and L.F. Ruggiero. 2007. Sources and patterns of wolverine mortality in western Montana. *Journal of Wildlife Management* 71(7):2213–2220.

Streubel, D. 1989. *Small mammals of the Yellowstone Ecosystem*. Roberts Rinehart, Boulder, Colorado, USA.

United States Fish and Wildlife Service. 2010. Endangered and Threatened Wildlife and Plants; 12-Month Finding on a Petition To List the North American Wolverine as Endangered or Threatened. *Federal Register* Vol. 75, No. 239, Tuesday, December 14, 2010. 78030–78061.

Vangen, K.M., J. Persson, A. Landa, R. Andersen, and P. Segerström. 2001. Characteristics of dispersal in wolverines. *Canadian Journal Zoology* 79:1641–1649.

Venables, W.N. and Ripley, B.D. 2002. *Modern Applied Statistics with S. Fourth edition*. Springer, New York, USA.

Wiens, T.S., B.C. Dale, M.S. Boyce, and G.P Kershaw. 2008. Three-way k-fold cross-validation of resource selection functions. *Ecological Modelling* 212:244–255.

Supplemental Materials

Table S1. *Top wolverine resource selection function model for relative habitat quality at the first order developed in the Greater Yellowstone Ecosystem of Montana, Idaho, and Wyoming, USA, 2001–2010.*

Coefficient	Estimate	Std. Error
LAE	2.081e-03	1.444e-04
TRI	2.346e-02	3.169e-03
SNOW	3.167e-04	8.641e-05
ROAD	-2.768e+00	6.928e-01
POP	-3.151e-01	1.005e-01
DHITAL	-1.281e-04	1.532e-05
DTREE	-1.500e-02	2.995e-03
DSNOW	-1.777e-03	7.869e-04
TRI^2	-7.403e-05	1.577e-05
LAE:ROAD	1.175e-03	2.903e-04
LAE:DTREE	4.500e-06	1.048e-06
SNOW:POP	2.291e-04	7.538e-05

Table S2. *Wolverine resource selection function (RSF) model results for first order prediction of relative habitat quality. The top model is compared to the global model (all covariates), the null model, and several simple models, Greater Yellowstone Ecosystem of Montana, Idaho, and Wyoming, USA, 2001–2010.*

Model	k	LL	ΔBIC
1.LAE+TRI+SNOW+ROAD+POP+DHITAL+DTREE+ DSNOW+TRI^2+LAE:ROAD+LAE:DTREE+SNOW:POP	13	-3,369	.
Global Model	23	-3,361	74
LAE + TRI + SNOW + LAE^2 + TRI^2 + $SNOW^2$	7	-3,497	202
LAE+ LAE^2	3	-3,824	818
LAE	2	-3,854	869
TRI + TRI^2	3	-4,082	1,335
TRI	2	-4,209	1,579
SNOW + $SNOW^2$	3	-4,584	2,338
SNOW	2	-4,844	2,849
Null Model	1	-5,077	3,306
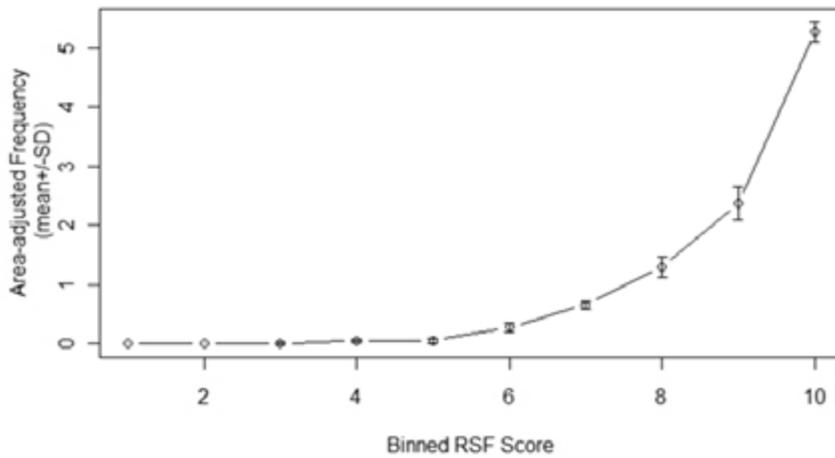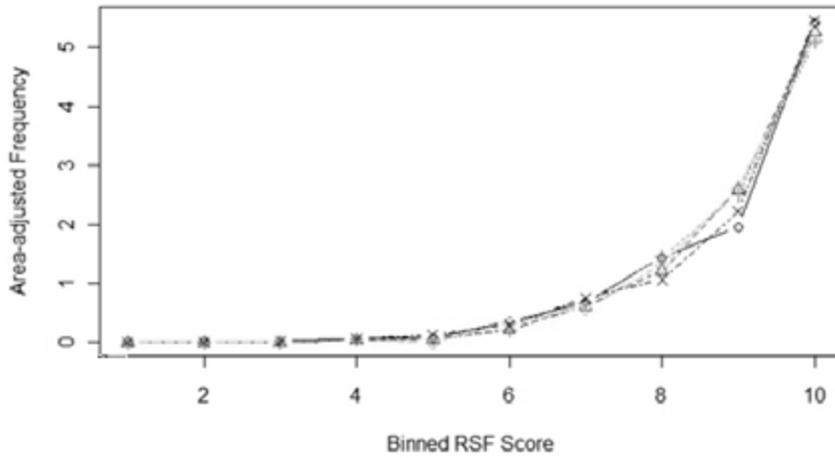
Figure S1. Plots of k-fold cross-validation assessment of model fit for data used to develop the resource selection function model, Greater Yellowstone Ecosystem of Montana, Idaho, and Wyoming, USA, 2001–2010.
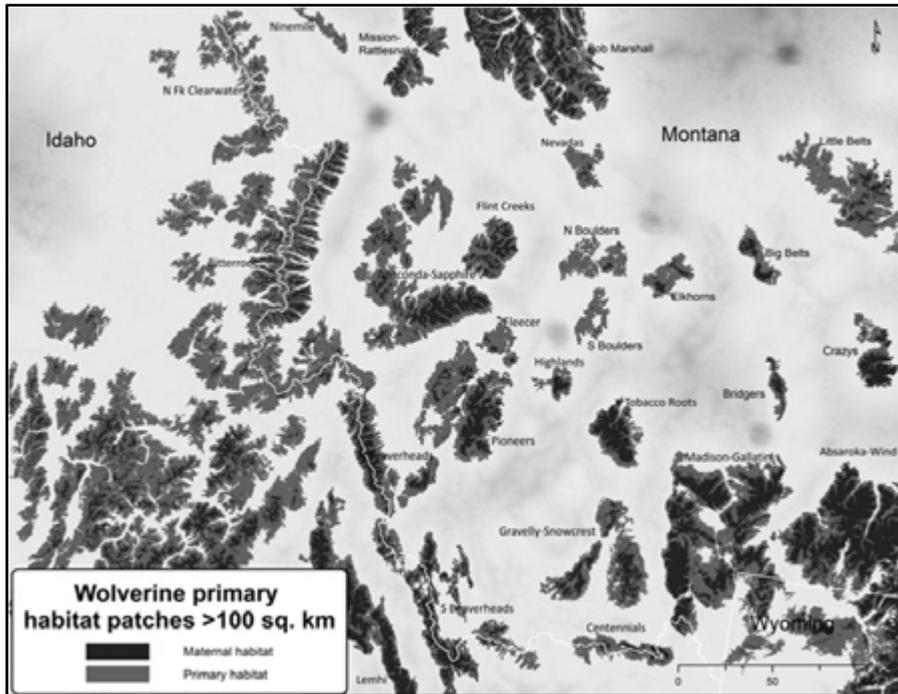
Figure S2 Proportion of high-quality maternal habitat of wolverines that occurred within patches suitable for use by resident adults differed by patch and region according to RSF modeling based on data obtained in the Yellowstone Ecosystem of Montana, Idaho, and Wyoming, 2001–2010. Relative ability of patches to function as reproductive sources and quality of habitats in-between primary habitats could be important in designing conservation strategies.

Table S3. *Estimates of wolverine population capacity and proportion maternal habitat by region and primary habitat patch in the western contiguous United States based on resource selection function habitat modeling of wolverine radio-telemetry data. Numbers presented are based on a population estimate of 15.2 wolverines (95% CI = 12.3–42.0) where 11 individuals were known to be on the 3,669 km^2 area and 20 was considered a reasonable upper limit (Inman et al. 2012a). The estimate of capacity within each primary habitat patch >100 km^2 was rounded down to the nearest integer and then summed by region.*

Region	Primary Habitat Patch >100 km^2	Population Capacity	95% CI	Proportion Maternal Habitat
Northern		**51**	**41–143**	**0.39**
Continental Divide	Bob Marshall Wilderness	36	29–99	0.39
	Glacier National Park	10	8–29	0.43
	Whitefish Range	5	4–15	0.31
Greater		**135**	**109–381**	**0.49**
Yellowstone	Absaroka-Wind Ranges	99	80–275	0.54
	Henrys Lake Mountains	0	0–2	0.49
	Madison-Gallatin Ranges	16	13–45	0.40
	Piney Mountains	0	0–1	0.01
	Teton-Snake Ranges	7	6–21	0.37
	Wyoming-Salt Ranges	13	10–37	0.29
Salmon-Selway		**105**	**84–310**	**0.22**
	Bitterroot Range	21	17–59	0.14
	Boston Mountain	1	0–2	0.01
	Elkhorn Ridge Mountains	0	0–2	0.10
	Farrow Mountain	1	1–3	0.12
	Gospel Hump Mountains	2	1–5	0.05
	Little Salmon River Mountains	1	1–4	0.09
	Lochsa Mountains	2	1–5	0.03
	Mallard Peak	0	0–1	0.02
	North Fork Clearwater Mountains	5	4–15	0.05
	North Fork Payette Mountains	3	3–10	0.15
	Panther Creek Mountains	0	0–2	0.04
	Salmon-Pioneer-Smoky Mountains	44	36–123	0.36
	Steamboat Creek Mountains	1	0–3	0.03
	Secesh River Mountains	0	0–2	0.05
	Seven Devils Mountains	1	1–3	0.11
	Soldier Mountains	0	0–2	0.11
	S Fork Salmon River Mountains	16	13–44	0.15
	Trinity Mountain	0	0–2	0.10
	Wallowa Mountains	4	3–13	0.26
	Yellowjacket Mountains	3	3–10	0.23

Region	Primary Habitat Patch >100 km^2	Population Capacity	95% CI	Proportion Maternal Habitat
Central Linkage		**75**	**53–236**	**0.28**
	Anaconda-Sapphire Ranges	8	7–24	0.26
	Beaverhead Mountains Central	1	0–3	0.25
	Beaverhead Mountains North	4	3–12	0.32
	Beaverhead Mountains South	4	3–11	0.46
	Big Belt Mountains	1	0–3	0.30
	Big Snowy Range	0	0–2	0.20
	Bloody Dick Range	1	0–2	0.22
	Boulder Mountains North	1	1–5	0.03
	Boulder Mountains South	1	0–3	0.01
	Bridger Range	0	0–2	0.29
	Cabinet Mountains East	2	1–6	0.25
	Cabinet Mountains South	1	0–2	0.02
	Cabinet Mountains West	1	1–5	0.10
	Centennial Range	2	1–5	0.21
	Crazy Mountains	2	1–5	0.49
	Elkhorn Mountains	1	1–3	0.15
	Fleecer Mountain	1	0–3	0.07
	Flint Creek Range	2	2–7	0.35
	Garfield Mountain	1	1–3	0.15
	Gravelly Range	3	2–9	0.25
	Gypsy Peak	1	1–3	0.10
	Highland Range	0	0–2	0.28
	John Long Mountains North	0	0–1	0.01
	John Long Mountains South	1	1–4	0.09
	Lemhi Range	8	6–22	0.52
	Little Belt Mountains	5	4–15	0.12
	Little Belt Mountains South	0	0–2	0.14
	Lost River Range	4	3–12	0.59
	Mission Mountains	3	2–8	0.31
	Nevada Mountains	1	0–3	0.08
	Ninemile Range	0	0–1	0.04
	Pioneer Range	7	5–19	0.27
	Purcell Mountains	1	0–3	0.13
	Rattlesnake Mountains	1	1–3	0.28
	Selkirk Range	3	3–10	0.12
	Snowcrest Range	1	1–4	0.32

Region	Primary Habitat Patch >100 km^2	Population Capacity	95% CI	Proportion Maternal Habitat
..Central Linkage	Tendoy Mountains	0	0–2	0.17
	Tobacco Root Range	2	2–6	0.53
	Wapaloosie	0	0–1	0.03
Bighorn		**15**	**12–42**	**0.30**
Uinta		**19**	**15–52**	**0.37**
Southern Rockies		**131**	**104–387**	**0.38**
	Battlement Mesa	0	0–1	0.01
	Culebra Range	3	2–9	0.28
	Flat Top Mountains	8	6–22	0.19
	Front Range	65	53–180	0.47
	Front Range West	0	0–1	0.07
	Gore Range	0	0–1	0.00
	Grand Mesa East	0	0–1	0.02
	Grand Mesa West	0	0–2	0.09
	Huntsman Mountain	0	0–1	0.19
	Pikes Peak	0	0–2	0.29
	Red River Mountains	0	0–1	0.08
	San Juan Range	40	32–112	0.40
	San Juan West	0	0–1	0.15
	Sangre de Christo Range	4	3–13	0.45
	Santa Fe Mountains	1	1–5	0.10
	Sierra Madre Central	0	0–2	0.06
	Sierra Madre Main	5	4–14	0.33
	Sierra Madre North	1	1–4	0.14
	Sierra Madre West	0	0–1	0.07
	Snowy Range	3	2–9	0.11
	Wet Mountains	0	0–2	0.07
	Wheeler Peak	1	0–3	0.05
Northern Cascade		**35**	**27–105**	**0.21**
	Mount Baker	0	0–1	0.14
	Mount Prophet	0	0–1	0.13
	Mount Rainier	1	1–4	0.24
	Mount Rainier East	0	0–1	0.07
	Mount Rainier Nelson Ridge	0	0–1	0.03
	North Cascades Range Glacier Peak	11	9–31	0.18
	North Cascades Range Pasayten	17	14–48	0.29
	Olympic Mountains	0	0–1	0.00

Region	Primary Habitat Patch >100 km^2	Population Capacity	95% CI	Proportion Maternal Habitat
..Northern Cascade	Skagit Range	3	2–8	0.16
	Wenatchee Mountains Central	2	1–5	0.07
	Wenatchee Mountains East	0	0–2	0.09
	Wenatchee Mountains West	1	0–2	0.02
Sierra-Nevada		**7**	**5–29**	**0.11**
	John Muir Wilderness 1	2	1–6	0.15
	John Muir Wilderness 2	0	0–1	0.13
	John Muir Wilderness 3	1	1–4	0.13
	Sequoia-Kings Canyon 1	2	1–6	0.09
	Sequoia-Kings Canyon 2	0	0–1	0.08
	Sonora Peak	0	0–1	0.08
	Yosemite 1	0	0–2	0.14
	Yosemite 2	0	0–1	0.04
	Yosemite 3	2	2–7	0.11
Great Basin		**7**	**4–39**	**0.17**
	Bear River Range Northeast	0	0–2	0.02
	Bear River Range Southwest	1	0–2	0.18
	East Humboldt Range	0	0–1	0.14
	Escalante Mountains	0	0–2	0.01
	Jarbridge Mountains	1	0–3	0.17
	La Sal Mountains	0	0–1	0.33
	Meade Peak	0	0–1	0.04
	Monroe Peak	0	0–1	0.04
	Mount Belknap	1	0–3	0.20
	Mount Terrel	0	0–1	0.10
	Roan Cliffs	0	0–1	0.00
	Ruby Mountains	1	1–4	0.15
	Salt Lake South	1	1–4	0.64
	Schell Creek Range	0	0–2	0.24
	Snake Range	0	0–1	0.26
	Strawberry Peak	0	0–1	0.01
	Wasatch Plateau Central	0	0–1	0.03
	Wasatch Plateau East	0	0–1	0.00
	Wasatch Plateau West	2	2–7	0.09
Western Contiguous U.S.		**580**	**454–1724**	

IV

Wildlife as Public Domain:
Endangered Status, Connectivity, and Critical Habitat of the Wolverine

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Abstract

Wolverines (*Gulo gulo*) are a candidate threatened or endangered species in the contiguous United States where a metapopulation of a few hundred individuals is distributed within high-elevation, alpine habitats across several states. Successful dispersal is essential for population persistence and there is a clear need to identify and prioritize suitable corridors among mountain ranges. We used Circuitscape to produce a scalable index of potential dispersal corridors across the western U.S. We also examined the degree to which important corridors were in public vs. private ownership and discuss approaches and institutional adaptations necessary to conserve these areas and wolverines over the coming century. Locations with the greatest potential for wolverine dispersal/gene flow were most concentrated in an area of western Montana referred to as the Central Linkage Region. Approximately half of the highest scoring lands were in private ownership, therefore there is need to develop a network of privately owned natural areas that complements the ability of publicly-owned habitats to achieve species persistence. However, designating corridors as "critical habitat" and attempting to enforce development limitations within areas that contain large amounts of private land would likely be a poor choice for wildlife conservation. Instead, a financial incentive program that encourages private landowners to maintain their lands as permeable open space is needed. Such a system will require funding in excess of that available at present. Therefore the continued viability of the wolverine in the contiguous United States, a candidate endangered species threatened by climate change

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and other modern impacts derived from all of society, depends on a fundamental shift in the way conservation of wildlife and habitat are approached and financed. We suggest broadening the constituency that is invested in and rewarded by wildlife conservation and therefore supportive of the public trust doctrine and state wildlife Institution by 1) assuring sportsmen that their activities will remain a primary component of an expanded state wildlife Institution, 2) extending the mandatory and dedicated user-based funding paradigm to wildlife biodiversity and outdoor enthusiasts along with investing in related infrastructure, and 3) integrating the non-wildlife-oriented public (>60% of citizens) by developing programs that link biodiversity to water quality monitoring as part of applied components of public school science and math curricula.

1. Introduction

Wildlife in the United States is a public resource owned by no one and held in trust by government for the benefit of present and future generations (Bean and Rowland 1997). But wildlife depend on habitat, and although public lands in the western United States are vast and well distributed, their boundaries were delineated based on human use potential, not on their value to wildlife. For example, the 1872 boundary of Yellowstone National Park was intended to encompass scenic and geothermal wonders, the 1905 National Forest boundaries of the Yellowstone area were based on their utility for timber production, and federal lands passed into state ownership exist in checkerboard fashion. While some thought was given to wildlife conservation, it was not the primary objective and, even if it had been, the state of knowledge regarding critical habitat features for the native fauna was incomplete.

Modern wildlife studies have revealed critical movements for a wide variety of species. For instance, pronghorn (*Antilocapra americana*) whose summer range lies within Grand Teton National Park migrate along a very specific traditional route (now the first federally designated migration corridor in the U.S.) to reach low elevation areas of winter range that are critical for overwinter survival (Berger et al. 2006). During this annual, one-way migration of 150 km, the pronghorn must cross a variety of public land jurisdictions and numerous privately owned parcels (Beckmann et al. 2012). These private lands fall under individual jurisdiction and are therefore subject to the potential for housing development or other activities that could inhibit or even sever a migration route that has existed for millennia (Berger et al. 2006). As such, the continued existence of an iconic western species within a

publically owned National Park depends in part on what occurs within private lands lying far outside the park boundary and public domain.

While the routes that some ungulate populations utilize during seasonal migrations are often fairly specific and conspicuous, the movements of other species are equally important but far more variable and difficult to ascertain. For example, successful dispersal of carnivores that exist at low densities plays a critical role by minimizing inbreeding, reducing competition for resources and mates among related individuals, maintaining genetic heterozygosity, and influencing distribution, abundance, and metapopulation dynamics (MacArthur and Wilson 1967, Dobson and Jones 1985, Waser 1996, Hanski and Gilpin 1997, Paetkau et al. 1998, Swenson et al. 1998, Gandon and Michalakis 2001, Proctor et al. 2004). The timing of these dispersal movements is less predictable, and traditional routes are not learned and repeated over generations as they can be for migratory ungulates. Rather, dispersing carnivores typically move as individuals across unfamiliar areas (Beier 1993, Inman et al. 2004). As a result, documenting dispersal-specific movements of carnivores is difficult and rarely achieved even though they are essential.

The wolverine (*Gulo gulo*) is one such carnivore, and may represent the terrestrial extreme regarding the size of area over which a population is required to successfully disperse in the contiguous U.S. (Paper III). Suitable habitat for resident adults is limited to high-elevation, alpine areas that occur in island-like fashion, forming a prime example of a metapopulation (MacArthur and Wilson 1967, Hanski and Gilpin 1997). Large territorial requirements of individuals result in low densities (4 wolverines/1,000 km^2), such that full occupation of all suitable habitat would yield a population of ~600 individuals across Montana, Idaho, Wyoming, Utah, Colorado, Washington, Oregon, and California (Paper III). Clearly, the persistence of this candidate endangered species (U.S. Fish and Wildlife Service 2010) depends upon its continued ability to disperse among the mountain ranges of the western U.S., and similar to the pronghorn example, this population that spends the majority of its time on public lands (Inman et al. 2012*a*) must at times disperse across private lands that are subject to a growing level of human influence (Johnson 2001, Gude et al. 2007).

As the wildlife profession works to conserve presently undeveloped private lands so that they continue to function for wildlife, there is a clear need to identify and prioritize areas that are most valuable (Western Governors' Association 2008). This need is of particular importance in the case of the wolverine given its status as a candidate endangered species and the vast geographic area over which the population functions. Undertaking an effort to maintain a network of natural areas that facilitates wolverine dispersal

throughout the western U.S. will necessarily involve many entities, each of which works at a different geographic scale. For instance, a locally oriented land trust may be interested in the highest priority for conservation easements within a county, whereas the federal highway department may want to identify the top tier candidates for wildlife crossing structures in a multi-state area. As such, the most useful tool for identifying and prioritizing conservation areas will be scalable, i.e., it will be able to account for the potential of a particular piece of land to contribute to dispersal/gene flow of the entire metapopulation while being informative at a more local level.

In their most recent report on funding non-game wildlife conservation, the Association of Fish and Wildlife Agencies (2011) recommend determining justifications for non-game conservation that can inform and substantiate the funding need to Congress, state legislatures, and others. The work needed to be done to conserve wolverines through the 21st century (e.g., landscape-level connectivity) 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 (Jacobson et al. 2010).

Our objectives were to 1) develop a scalable GIS layer that indexes the value of lands for contributing to wolverine dispersal/gene flow throughout the metapopulation of the western contiguous U.S., 2) determine the degree to which the most valuable areas for wolverine dispersal are in public vs. private ownership, and 3) discuss the steps needed to conserve areas of private land necessary for the persistence of wolverine and improve conservation of non-game wildlife over the coming century.

2. Materials and Methods

2.1 Circuitscape

We utilized a wolverine habitat suitability model 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. We followed the methodology of Bergen et al. (unpublished manuscript) but used wolverine-specific inputs at specific decision points (details below). Circuitscape is based on electrical flow theory where dispersing animals (modeled as electrical charges) move between source habitats (modeled as + and - poles) through a landscape modeled as a resistor network or resistivity surface (McRae et al. 2006, McRae et al. 2008). We

chose the Circuitscape approach because 1) Circuitscape does not require the arbitrary selection of a single beginning and ending point with source patches as other approaches do (e.g., least-cost-path), 2) Circuitscape more accurately reflects animal dispersal because it does not limit potential movements to a single path between two patches, and 3) Circuitscape is capable of accounting for accumulated dispersals by incorporating information about a patch's position relative to the size and position of other patches/source habitats.

2.2 Defining source habitats and the intervening resistance layer

We used a wolverine habitat suitability layer developed for the western United States that represented the biological requirements of wolverines, i.e., food, competition for food, escape cover, den sites, and dispersal potential. This model identified patches of primary wolverine habitat (areas suitable for use by resident adults), and yielded a relative suitability score in the intervening spaces (Paper III). We included as source areas all patches of primary wolverine habitat that were >241 km^2. We based this lower limit for source patch size on a wolverine density estimate of 4.1 wolverines per 1,000 km^2 of primary wolverine habitat (Inman et al. 2012a, Paper III). Based on observed wolverine movements via radio-telemetry, we also appended "satellite" patches of primary/source habitat that were >100 km^2 (minimum female home range size) and within 5 km of a >241 km^2 source patch. To control for "dipole" interactions, satellite and larger source patches were connected via the least cost path between the two polygons of one pixel width. Our analysis treats all patches of suitable habitat as if they are occupied by reproductive females, which would only be the case if areas of historical distribution were reoccupied or restored. We did not consider potential source areas from north of the Canadian border in the analysis.

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). This produced a transit cost or "resistance" surface of values between 0 and 10,000, where 0 yielded the least resistance and 10,000 the most resistance. Squaring resistance values has the effect of magnifying differences in poor quality habitat relative to high quality habitat.

2.3 Corridor generation and allocating dispersal potential by source

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, Inman et al. 2012a), and B) were within direct line of sight of each other and shared at least one

compass degree of direct exposure; Fig. 1). We used capacity for female territories as a proxy for relative potential for production of dispersers. 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 neighboring patches in inverse proportion to their individually recorded resistances.

2.4 Identifying connectivity areas

We conducted our analysis with the four-way approach at 360 m resolution after preliminary investigations suggested that larger pixels did not retain sufficient detail. This resulted in 31 million raster cells for the western U.S. We used pairwise mode to generate current and resistance. We then summed the values of all calibrated corridors to estimate relative importance to metapopulation-level dispersal for each 360 m pixel. Because Circuitscape output includes charges occurring across source habitats, and the focus of this study was to estimate the significance of corridors (not source habitats), we replaced corridor charge values that occurred within source habits with values of zero. We then classified all pixels as percentiles of conductance, which approximates wolverine dispersal/gene flow potential.
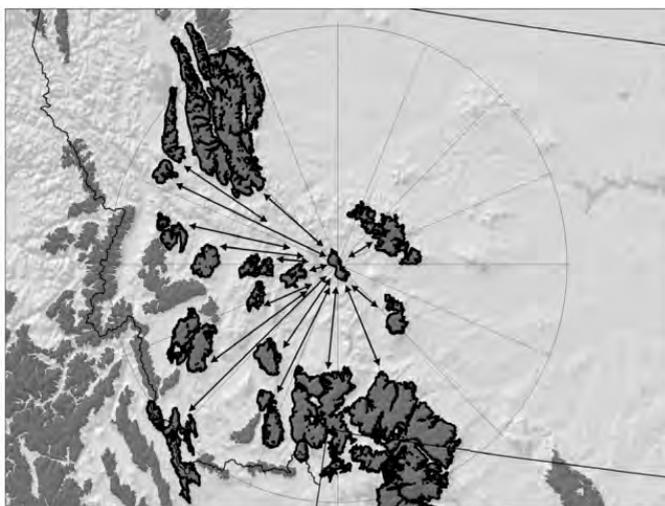

Figure 1. Circuitscape corridors were calculated between source habitat patches for wolverines if they were within the 250 km dispersal distance (fine circle) and shared ≥1 degree of direct exposure. In this example, paired source habitats are bold outlined and bi-direction corridors are depicted with arrowed paths.

3. Results

Seventy-seven source habitat patches averaged 2,100 km^2 (range = 266–25,247 km^2, SD = 3,831 km^2), and total area of source habitat was <5% of the 11 state area of the western U.S. When binned by percentile based on area, i.e., each percentile represented an equal number of km^2, areas with the greatest potential for dispersal/gene flow (≥98.5th percentile) were concentrated in the southern and central portions of western Montana and along Montana's borders with Idaho and Wyoming proximate to this area (Fig. 2). 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. Southwestern Colorado also contained areas of higher gene flow potential at the scale of the western U.S. (Fig. 2).

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. The vast majority of privately owned 98.5th percentile wolverine connectivity habitat occurred in western Montana.

Our result was scalable and can identify highest priority areas at the multi-state level or within a local geography. The CLR stands out as important for wolverine gene flow among the largest patches of source habitat in the western U.S.; when results were scaled down to this region and binned by percentile based on area, those areas scoring >88.5th percentile linked the 3 major ecosystems (Fig. 3). When scaled down to a local area, e.g., the Madison Valley, Montana (Fig. 4), areas with the greatest potential for dispersal/gene flow were concentrated in the southern end of the Madison Valley between the Madison, Gravelly and Centennial Ranges; across Norris Hill between Ennis and Norris, Montana; and along the mountain pass between Ennis and Virginia City, Montana.
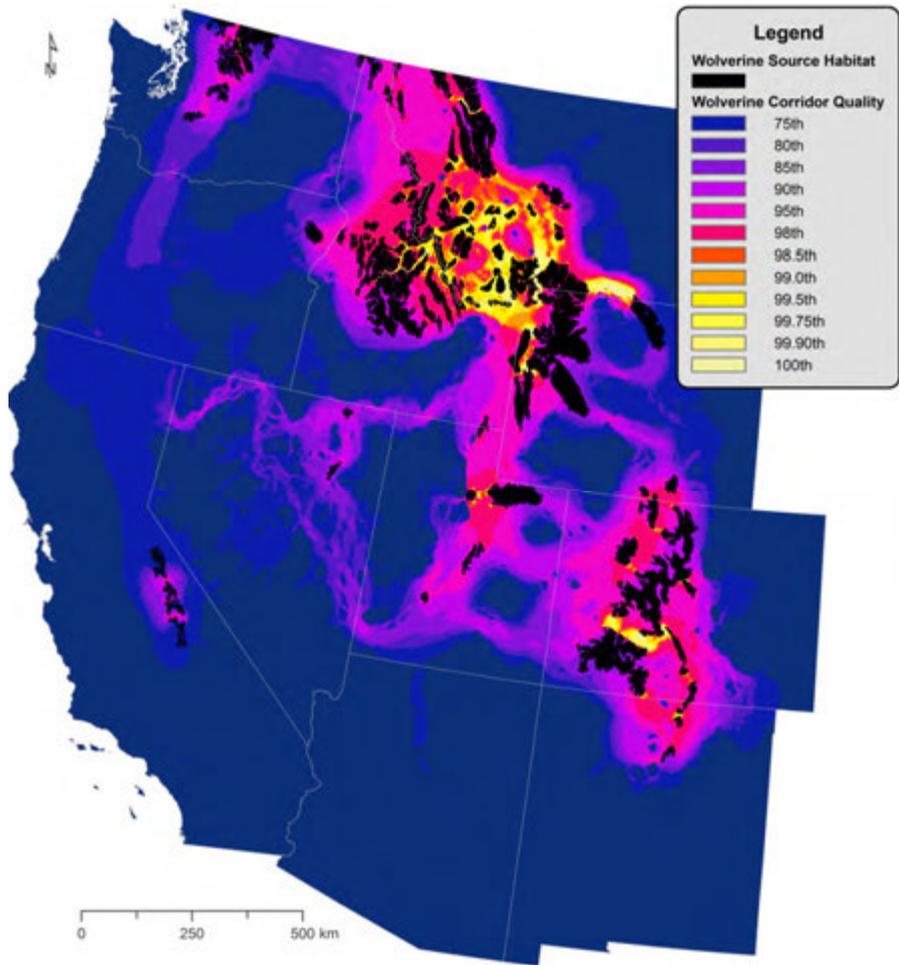
Figure 2. Relative value of lands across the western United States for wolverine dispersal and gene flow as determined by Circuitscape corridor analysis. Circuitscape is based on the theory of electrical current flow between "poles" across a "resistance surface." In this analysis, patches of wolverine habitat of high enough quality for use by resident adults are "sources" that represent an electrical pole (black patches). Relative corridor quality, i.e., "conductance" or dispersal/gene flow potential, across the metapopulation 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.
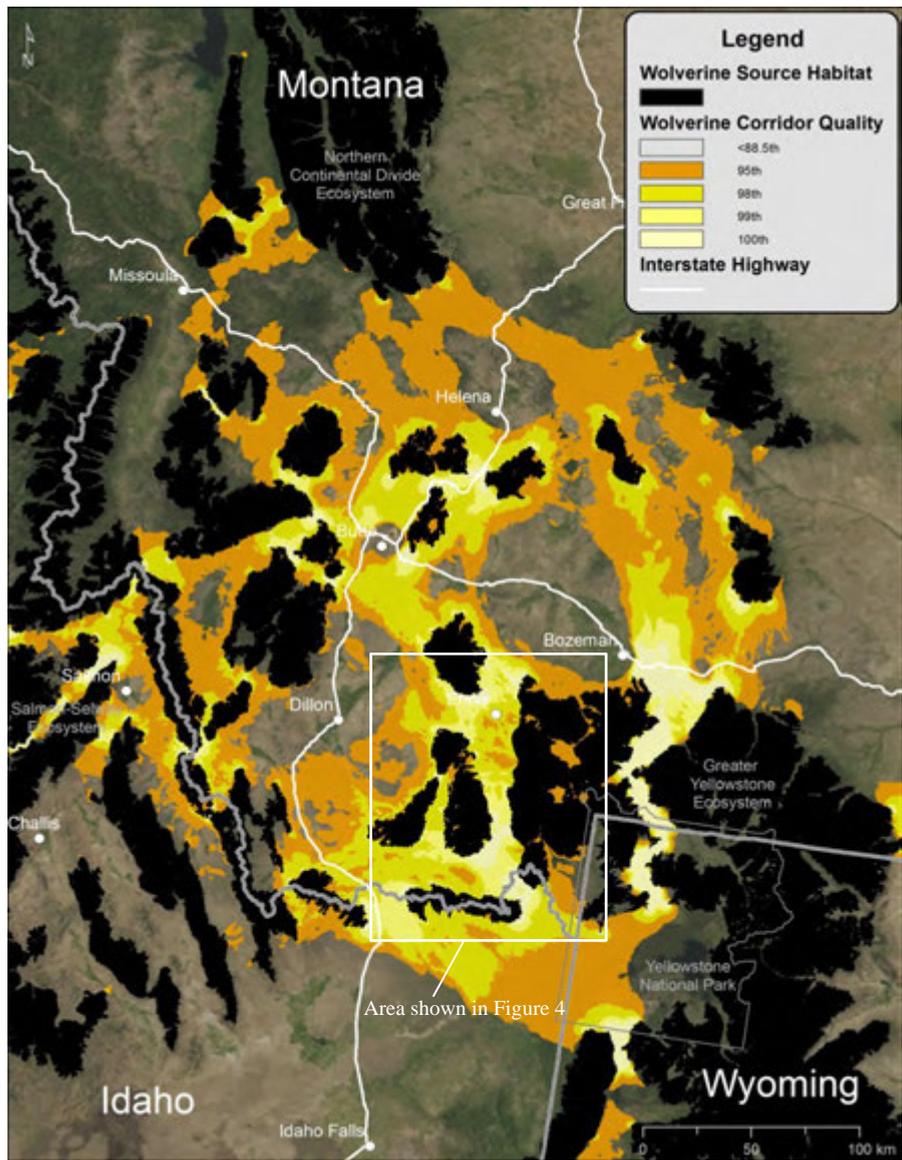
Figure 3. The Central Linkage Region, an area positioned in-between the three major blocks of publically owned wild lands in the northern U.S. Rocky Mountains (Greater Yellowstone, Salmon-Selway, and Northern Continental Divide Ecosystems), is an area of importance for wolverine dispersal. The results of the metapopulation-level analysis for potential wolverine dispersal/gene flow are scalable to this smaller region as shown here.
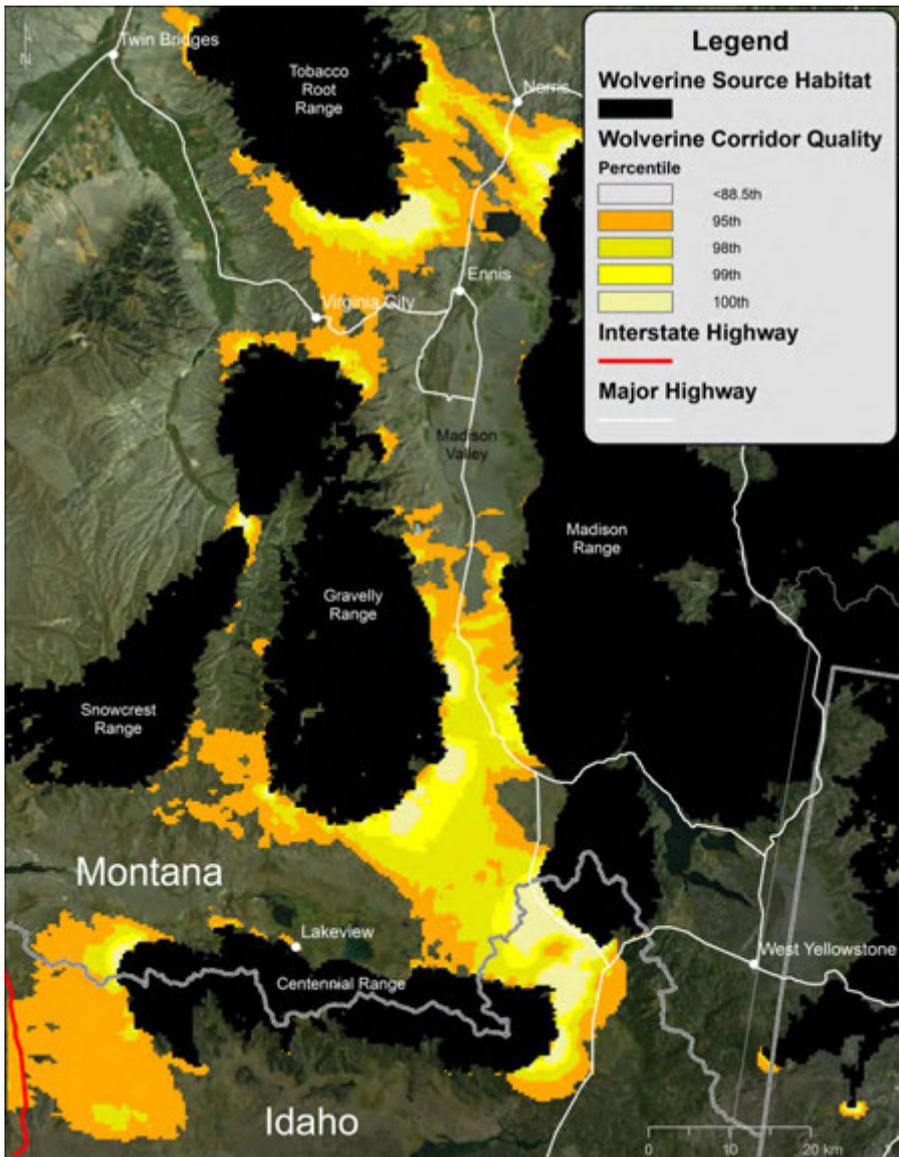
Figure 4. Wolverine dispersal/gene flow potential scaled to the Madison River Valley of southwestern Montana. Results of the analysis can be scaled-down to any sized area of interest, but retain the metapopulation "perspective" regarding potential dispersal/gene flow significance.

4. Discussion

4.1 Metapopulation connectivity

The vast majority of area ranked highest for wolverine dispersal/gene flow occurred in an area of western Montana referred to as the Central Linkage Region (CLR). Our analysis highlights the importance of maintaining connectivity in the CLR to ensure wolverine persistence in the contiguous U.S. The CLR consists of numerous smaller mountain ranges that are in public ownership and of high enough quality to contain reproductive female wolverines (Anderson and Aune 2008, Paper III). The CLR also sits between 3 of the largest areas of source wolverine habitat in the contiguous U.S. (Paper III). The importance of the CLR connectivity areas is further highlighted by the fact that these 3 large ecosystems along with the CLR are the vast majority of suitable wolverine habitat known to be presently occupied by reproductive females (Aubry et al. 2007).

Our analysis suggests that the Southern Rocky Mountains, primarily Colorado, are more connected to the main portion of the contiguous U.S. wolverine population than the Sierra-Nevada of California. Both of these areas were within the historical range of wolverines (Aubry et al. 2007). Historical genetic data suggest that California was isolated from other wolverines in North America for an extended period of time (Schwartz et al. 2007). While both the Southern Rockies and Sierra-Nevada may play an important role for wolverines if populations returned or were restored (Cross and Servheen 2010, Paper III), 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.

4.2 Endangered status, connectivity, and critical habitat

While over 90% of source wolverine habitat in the contiguous U.S. is publicly owned (Paper III), our analysis suggests nearly half of the highest-quality wolverine connectivity habitat is privately owned. The Association of Fish and Wildlife Agencies recommended that it is imperative to engage the public about the need to maintain wildlife as a public trust, and that conservation professionals should not avoid the associated philosophical and economic debates (Prukop and Regan 2005). Here we discuss the issue of maintaining a species that belongs to the public trust but is dependent on extensive areas of privately owned lands for a specific life requisite – dispersal. We also discuss wolverine conservation in general as an example of how to meet the challenges that lie ahead in the coming century, (e.g., Jacobson et al. 2010).

Wolverines were designated a candidate threatened or endangered species in the contiguous United States and the primary threat identified was climate change (U.S. Fish and Wildlife Service 2010). Climate change has been predicted to decrease distribution and connectivity for wolverines (McKelvey et al. 2011). Warmer temperatures and less snow are at some point certain to have negative consequences for a species that is obviously adapted for life in cold, snowy conditions (Copeland et al. 2010, Inman et al. 2012*a*, Inman et al. 2012*b*). However, it is important to point out, for purposes of comparing the potential for climate change and loss of connectivity to be threats to wolverines, that the species will be justifiably listed 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; 3) a multi-decadal time-frame over which changing conditions will threaten population viability; and 4) a condition (climate change) that can be reversed (albeit slowly). In addition, because climate change is borderless, the impact could continue even if the U.S. government were to interpret the ESA in the strictest sense, citing a lack of regulatory control, and granting the U.S. Environmental Protection Agency authority to limit greenhouse gas emissions.

Because maintaining suitable habitat for wolverine dispersal is a core requisite for persistence within the contiguous U.S., we argue that loss of connectivity is as significant of a threat to wolverine persistence in the contiguous U.S. as climate change over the 50–100 year time frame used to find wolverines warranted for listing (U.S. Fish and Wildlife Service 2010). We base this on the following. First, it is possible to forecast human use development with a similar degree of certainty as can be achieved for climate change (e.g., Gude et al. 2007). Second, 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 in the wildlife literature (e.g., Seiler 2003, Schwartz et al. 2010) than the specific mechanisms regarding wolverines and climate change (Copeland et al. 2010, Inman et al. 2012*b*). Third, there is no less certainty regarding the time frame over which loss of connectivity will begin impacting individuals and populations. And finally, human development may be even less reversible than climate change; once roads and buildings have been constructed, they are highly unlikely to be removed. In addition, connectivity is an issue that is not borderless; it is addressable at a local scale. If the U.S. Fish and Wildlife Service considered dispersal corridors to be integral to wolverine persistence, and thus degradation of connectivity a threat to wolverine persistence, designating corridors as critical habitat could follow.

4.3 Regulations or incentives?

Our analysis shows that there are significant areas of private land in places where wolverine dispersal/gene flow potential is greatest. These private lands are all potentially subject to future housing development, and there is clearly a need to establish a means for maintaining some portion of them as permeable space to ensure wolverine persistence. However, establishing dispersal corridors under the legal definition of critical habitat and attempting to regulate development of private lands would most likely be a poor choice for wildlife conservation because of the backlash this would cause. Society has established a legal framework for managing wildlife (Bean and Rowland 1997), but that framework is always subject to change based on society's current perceptions and values. For example, repeated litigation attempting to maintain gray wolves on the list of federal endangered species despite having met recovery goals resulted in the United States congress removing the species from the list outside of the normal process (Bruskotter et al. 2011, Environment News Service 2011, Taylor 2011). And even the Public Trust Doctrine itself, which establishes that wildlife is owned by no one and held in trust for future generations, can be challenged or eroded (Jacobson et al. 2010).

Private property rights are a provocative issue of great financial, emotional, and cultural significance. The roots of property ownership lie at the genesis of government centuries ago, when individuals' investments in land and labor were protected from conquest with a defined and fair system that became the basis for civil society. Thus the resolution of the boundary between wildlife as public domain and the privately owned habitats that wildlife depend on is difficult. Two main approaches exist, 1) regulating uses of private property that negatively impact the public and 2) paying private property owners to achieve socially beneficial goals. The legal framework for conserving wildlife includes the possibility of federal takings of private land under eminent domain (Bean and Rowland 1997). Proponents of strong regulatory approaches exist based on their interpretation of the 'true nature' of property ownership and what rights ownership conveys (Freyfogle 2007, Echeverria and Pidot 2009). Concerns of regulatory proponents include the fear that financial incentives will undermine the ability to regulate because they legitimize the notion of absolute ownership. Regulatory proponents' arguments against payments include the idea that the public can be forced to pay more for the benefits of land conservation than necessary if it used regulation instead (Echeverria and Pidot 2009).

On the other hand, it is clear that the regulatory approach can be unfair to certain landowners (Ruhl 1998). In some cases individuals and families have chosen to invest their resources, sometimes over multiple generations, in a

parcel of rural land. Then they are informed that society has acted in ways that have pushed a species toward extinction, their land is one of the few remaining strongholds, and regulation limiting their activities and options is imminent. We suggest this approach is profoundly unfair to rural landowners and, as Ruhl (1998) suggested, creates a cultural environment susceptible to species vortex – do not be the last one to get rid of the species/habitat. If society wants to conserve wildlife, and the collective actions of society have pushed a species to the brink of extinction, then the burden of cost for conservation and restoration should be shared equally by all of society. It should not be disproportionately shouldered by those who have found value in the more natural characteristics of the land that have left it in a state still useful for wildlife today.

As Ruhl (1998) noted, promulgating this unfairness will eventually erode the very foundation of endangered species conservation in the U.S. - the endangered species act. Therefore, rather than a regulatory system, significant incentives for private landowners to maintain their properties as permeable space in perpetuity must be developed. Conservation easements are one such tool, however their incentives are generally favorable to affluent landowners who can donate use values of their lands for a modest tax break (Cheever and McLaughlin 2004). In order to conserve private lands important for wolverine persistence, distribute the financial burden for doing so equitably, and reward (rather than punish) those who have maintained lands in a more natural state regardless of their level of wealth, new financial incentives that can benefit rural counties and landowners must be developed. This wolverine-specific situation represents a larger and fundamental problem for conservation – how to successfully navigate the Institutional (Jacobson et al. 2010) shift from 20th century management of intentional human-caused mortality of game species to 21st century management of habitat loss for both game and non-game species.

4.4 Wolverines and the conservation Institution for the 21st century

In 1937, sportsmen and firearms manufacturers worked to pass the Federal Aid in Wildlife Restoration Act, better known as the Pittman-Robertson Act (PR). PR requires that 10% of the purchase price of all firearms, ammunition, and archery equipment be distributed to state wildlife agencies where each dollar is matched by 3 hunting license dollars. These and similar funds derived from the Federal Aid in Sport Fish Restoration Act of 1950 (Dingle-Johnson) contributed an average of approximately $1 billion per year to wildlife conservation during 2005–2009 (Loftus et al. 2011*a, *2011*b*). When combined with state hunting and fishing license sales, these sportsmen-generated dollars contribute approximately $2.5 billion annually to wildlife conservation and have typically formed ~90% of state wildlife agency budgets (Association of

Fish and Wildlife Agencies 2011, Loftus et al. 2011*c*). This system, the foundation of the North American Model of Wildlife Conservation, has been vastly successful in restoring many species (Organ et al. 2010). Its successes can all be linked to one fundamental aspect–a mandatory, specifically-dedicated, user-based funding system to support the work necessary meet its goals.

When the North American Model was developing at the beginning of the 20th century, unregulated and commercial harvest *were* the major conservation issues. These issues led to the extirpation of the wolverine from the contiguous U.S. (Aubry et al. 2007). But these issues and much more have largely been addressed with nearly 100 years of effort founded on a legal system and dedicated funding from sportsman's licenses and associated "user-fees" such as PR dollars. However, wolverines are emblematic of the shift in emphases necessary to meet the challenges of major conservation issues of the 21st century and how to pay for them, e.g., climate change, connectivity at the landscape scale (including road projects), and funding non-game species monitoring and habitat conservation. 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 notion of the so-called "non-consumptive user" is outdated and unrealistic.

The major conservation challenges wolverines face are of daunting financial significance under the current wildlife funding paradigm. For instance, if the 100,000 acres of private land most suitable for wolverine connectivity (i.e., 2% of the top 1.5% which is the top 3/100[ths] of one percent) were available for purchase at an average of $1,500/acre (R. Dilschneider, Prudential Real Estate, pers. comm.), total cost would be $150 million. If we assume the cost for protecting lands with easements (forfeiture of development rights and potential profits thereof) is 1/3 of the purchase price, $50 million is needed. (We note here that the cost via 'take' under eminent domain would require payment at market value and incur future management costs. We also note that the regulatory approach would require enforcement and court costs in perpetuity). Adding the cost of constructing road structures that facilitate wildlife crossings in these same wolverine-focused areas would likely fall in the realm of $100 million. If similar to lynx (*Lynx canadensis*), the cost for reintroduction to the southern Rockies is likely on the order of $2 million over 10 years. That cost would double if the Sierra-Nevadas of California were also a restoration site. Multi-state monitoring of this rare animal that resides in the most rugged and inaccessible terrain of North America will require on the order of $350,000/year. Adding research to determine whether winter recreation

impacts wolverine reproduction or not (Carlton et al. 2000, Krebs et al. 2007) could cost an additional $250,000/year for 10 years.

Under the above scenario, actions specific to wolverines (reintroductions, monitoring, winter recreation research) will require approximately $1 million/year over the coming decade. If we include wolverine necessities that benefit other species also, i.e., achieving long-term connectivity at the landscape scale the cost increases to the order of $10 million/year over a 20-year time frame. This figure represents a tremendous departure from the status quo, and it exemplifies the need to broaden the funding base of state wildlife agencies in order to match the growing set of responsibilities that society is now asking them to provide. Given that sportsmen generate $2.5 billion annually for conservation and they comprise only 16% of total U.S. population and only 42% of those who participate in some form of wildlife related recreation (United States Fish and Wildlife Service 2012), achieving sufficient levels of funding for these new tasks is not impossible. However, it will require the participation of a broader segment of society.

Jacobson (2008), Jacobson and Decker (2006), and Jacobson et al. (2007, 2010) provide a thorough and thoughtful assessment of the history and future direction of the state wildlife agencies, or "SWA Institution," that have governing authority over wildlife. Their purpose was "to encourage wildlife professionals to think about the extent and nature of change needed to position the Institution for greatest effectiveness in the future." They recommend 4 ideal components of the future Institution: 1) Broad-based funding, 2) Trustee-based governance, 3) Multidisciplinary science as basis for recommendations from professional staff, and 4) Involvement of diverse stakeholders and partners. While we generally agree, we offer some additional thoughts and nuances that may be important for success.

Some have suggested that the user-pay system has resulted in Institutional resource dependency such that the SWA Institution may have become an 'iron triangle' that privileges a minority special interest group, i.e., sportsmen (Beck 1998, Gill 2004, Nie 2004, Jacobson 2008). We suggest it is important that all wildlife enthusiasts recognize that they are the minority special interest group– only 38% of U.S. citizens >16 years of age participated in any form of wildlife-related recreation during 2011, and this included activities as passive as watching wildlife around their home (U.S. Fish and Wildlife Service 2012). The percentage of citizens willing to pay for maintaining native biodiversity is even smaller as evidenced by the failure to achieve the full goal of the Teaming With Wildlife initiative and a continuing struggle to fund conservation of habitats and non-game species like the wolverine (Jacobson et al. 2007, 2010, Association of Fish and Wildlife Agencies 2011). It is important to recognize

this all-inclusive minority status because the PTD upon which conservation is founded is not guaranteed in perpetuity. As Jacobson et al. (2010) point out, courts have failed to uphold the PTD, and there is a tension between the government's general obligation to act for public benefit and the obligation it has to uphold the PTD in the case of wildlife. If wildlife were ever viewed by the majority as something that no longer benefits the public, the foundation of our conservation system (PTD) could disappear. In our view, consolidation to strengthen the PTD will be most effective if it builds out across 3 groups: traditional wildlife supporters (sportsmen), wildlife biodiversity and outdoor enthusiasts, and the non-wildlife-oriented public.

The first step toward effective consolidation is framing the discussion of SWA "change" in terms that are not confrontational to sportsmen, and, as Jacobson et al. (2010) begin to suggest, making it clear that traditional activities will be maintained. The SWA Institution does not necessarily have to "reform to maintain legitimacy with society," as Jacobson (2008, p. 3) and Jacobson et al. (2010) assume. While it is true that society's perspectives on wildlife and their desires for SWAs are changing, it is also true that the game and fish model and its user-based funding sources have proven successful over time. In addition, while hunting and fishing may not be significant among the recreational activities of large urban populations, they are culturally pervasive over a vast majority of the landmass of North America and of such deeply ingrained significance that several states have amended their constitutions to make them a right (e.g., Virginia, Idaho). In fact, the PTD is legally founded on the right to utilitarian access to resources (*Martin v. Waddell*, 41, U.S. 234). One option for SWAs is to simply dial-back to a set of game-related goals and cover those expenses with traditional revenues. However, this potential outcome would lead to great inefficiencies and a fractured and difficult environment for meeting many modern conservation goals such as those needed to conserve wolverines. In addition, confrontation does not appear to be necessary to broaden the scope of SWAs. Jacobson et al. (2007) found in interviews with leaders of SWAs that the restricted non-game programs of most were related to deficient funding rather than an unwillingness to expand responsibilities. So, we emphasize the need to discuss change in terms of "expanding the historically successful model" as opposed to "reforming to maintain legitimacy (change or die)." As the diversity of perspectives within the wildlife profession discusses these issues, we should think carefully about whether we couch it in terms of "resource dependence and an associated iron triangle that blocks non-traditional users from decision processes," or "a polygon of effective partners that can grow."

The second step toward effective consolidation is expanding the mission of SWAs to be able to meet the desires of a new and growing segment of the public that is interested in wildlife (Jacobson et al. 2010). 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 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 interest or support diminishes for any reason. Sportsmen along with wildlife biodiversity and outdoor enthusiasts are the people most interested in conservation and therefore probably most reliable. 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 funding, facilities development, new constituents, and improved support for conservation (Jacobson 2008, Ch. 4).

The third step toward consolidation to strengthen the PTD is defining the mission in terms that the public that is not interested in wildlife desires to support. 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. The potential long-term benefits from this step range from a broader acceptance of science in deriving solutions, to improved health (e.g., knowledge of and concern for water quality), and higher wages (via improved science, biology, and technology education). Defining mission in these terms offers an opportunity to bolster support for the PTD in a more significant way than with any other group.

5. Conclusion

Wildlife in the United States is a public resource owned by no one and held in trust by government for the benefit of present and future generations (Bean and Rowland 1997). Wildlife depend on habitat, and our examination of the wolverine provides a clear example of the need to develop a network of

privately-owned natural areas that complements the ability of publicly-owned habitats to achieve species persistence. An incentive-based system, as opposed to a regulatory approach such as critical habitat, will be required in order to distribute the financial responsibilities fairly and equitably. Such a system will require funding in excess of that available at present. 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.

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References

Anderson, N.J. and K.E. Aune. 2008. Fecundity of female wolverine in Montana. *Intermountain Journal of Science* 14(1–3):17–30.

Association of Fish and Wildlife Agencies. 2011. *President's Task Force on Wildlife Diversity Funding*. Final Report, September 1, 2011. http://www.fishwildlife.org/files/President_s TaskForceonWildlifeDiversity_Funding_FINAL-REPORT.pdf >

Aubry, K. B., K.S. McKelvey, and J.P. Copeland. 2007. Distribution and broadscale habitat relations of the wolverine in the contiguous United States. *Journal of Wildlife Management* 71(7):2147–2158.

Bean, M.J., and M.J. Rowland. 1997. *The Evolution of National Wildlife Law, Third Edition*. Praeger Publishers, Westport, Connecticut, USA.

Beck, T.D.I. 1998. Citizen ballot initiatives: A failure of the wildlife management profession. *Human Dimensions in Wildlife* 3:21–28.

Beckmann, J.P., K. Murray, R.G. Seidler, and J. Berger. 2012. Human-mediated shifts in animal habitat use: sequential changes in pronghorn use of a natural gas field in Greater Yellowstone. *Biological Conservation* 147:222–233.

Beier, P. 1993. Determining minimum habitat areas and habitat corridors for cougars. *Conservation Biology* 7:94–108.

Bergen, S., J. Beckman, and R.M. Inman. Unpublished manuscript. *Using circuit theory-based models to assess potential linkage zones for bears between Greater Yellowstone and the northern Rockies.*

Berger, J., S.L. Cain, and K.M. Berger. 2006. Connecting the dots: an invariant migration corridor links the Holocene to the present. *Biology Letters* 2006(2):528–531.

Bruskotter, J.T., S.A. Enzler, and A. Treves. 2011. Rescuing wolves from politics: Wildlife as a public trust resource. *Science* 333(6051):1828–1829.

Carlton, D.C., D. Gaillard, M. Senatore, M. Friedman, R. Fenner, and G. Macfarlane. 2000. *Petition for a rule to list the wolverine (Gulo gulo luscus) as Threatened or Endangered under the Endangered Species Act, 16 U.S.C. Sec. 15312 et seq. (1973 as amended) within the contiguous United States*. Biodiversity Legal Foundation, Louisville, Colorado, USA.

Cheever, F. and N.A. McLaughlin. 2004. Why environmental lawyers should know (and care) about land trusts and their private land conservation transactions. *Environmental Law and Review* 34:10223–10233.

Copeland, J.P., K.S. McKelvey, K.B. Aubry, A. Landa, J. Persson, R.M. Inman, J. Krebs, E. Lofroth, H. Golden, J.R. Squires, A. Magoun, M.K. Schwartz, J. Wilmot, C.L. Copeland, R.E. Yates, I. Kojola, R. May. 2010. The bioclimatic envelope of the wolverine (*Gulo gulo*): do climatic constraints limit its geographic distribution? *Canadian Journal of Zoology* 88(3): 233–246.

Cross, M., and C. Servheen. 2010. *Climate change impacts on wolverines and grizzly bears in the Northern U.S. Rockies: Strategies for conservation*. Wildlife Conservation Society and United States Fish and Wildlife Service, Workshop summary report, October 9–10, 2009, Missoula, Montana, USA.

Dobson, F.S, and W.T. Jones. 1985. Multiple causes of dispersal. *American Naturalist* 126:855–858.

Echeverria, J. and J. Pidot. 2009. Drawing the line: Striking a principled balance between regulating and paying to protect land. *Environmental Law Reporter* 39:10868–10880.

Environment News Service. 2011. Congress Pulls Wolves Off Endangered Species List. April 14, 2011. http://www.ens-newswire.com/ens/apr2011/2011-04-14-093.html

Freyfogle, E.T. 2007. Private property–correcting the half-truths. *Planning and Environmental Law* 59(10):3–11.

Gandon, S., and Y. Michalakis. 2001. Multiple causes of the evolution of dispersal. Pages 155–167 *in* J. Clobert, E. Danchin, A.A. Dhondt, and D.J. Nichols, editors. *Dispersal*. Oxford University Press, Oxford. UK.

Gill, R.B. 2004. Challenges of change: Natural resource management professionals engage their future. Pages 35–46 in M. J. Manfredo, J. J. Vaske, B. L. Bruyere, D. R. Field, and P. Brown, Jr., editors. *Society and natural resources: A summary of knowledge*. Modern Litho. Jefferson, Michigan, USA.

Gude, P.H., A.J. Hansen, and D.A. Jones. 2007. Biodiversity consequences of alternative future land use scenarios in Greater Yellowstone. *Ecological Applications* 17:1004–1018.

Hanski, I.A., and M.E. Gilpin, editors. 1997. *Metapopulation Biology: Ecology, Genetics, and Evolution*. Academic Press, San Diego, California, USA.

Hornocker, M.G., and H.S. Hash. 1981. Ecology of the wolverine in Northwestern Montana. *Canadian Journal of Zoology* 59:1286–1301.

Inman, R.M., R.R. Wigglesworth, K.H. Inman, M.K. Schwartz, B.L. Brock, and J.D. Rieck. 2004. Wolverine makes extensive movements in the Greater Yellowstone Ecosystem. *Northwest Science* 78:261–266.

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*a*. Spatial ecology of wolverines at the southern periphery of distribution. *Journal of Wildlife Management* 76(4):778–792.

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

Jacobson. C.A. 2008. *Wildlife conservation and management in the 21st century: Understanding challenges for institutional transformation*. PhD Dissertation, Cornell University, Ithaca, New York, USA.

Jacobson, C.A., and D.J. Decker. 2006. Ensuring the future of state wildlife management: Understanding challenges for institutional change. *Wildlife Society Bulletin* 34(2):531–536.

Jacobson, C.A., D.J. Decker, and L. Carpenter. 2007. Securing alternative funding for wildlife management: Insights from agency leaders. *Journal of Wildlife Management* 71(6):2106–2113.

Jacobson, C.A., J.F. Organ, D.J. Decker, G.R. Batcheller, and L. Carpenter. 2010. A conservation institution for the 21st century: Implications for state wildlife agencies. *Journal of Wildlife Management* 74(2):203–209.

Johnson, V.K. 2001. Trends in rural residential development in the Greater Yellowstone Ecosystem since the listing of the grizzly bear, 1975–1998. *Yellowstone Science*. Spring:2–9.

Krebs, J., E. Lofroth, and I. Parfitt. 2007. Multiscale habitat use by wolverines in British Columbia, Canada. *Journal of Wildlife Management* 71(7):2180–2192.

Loftus, A., R. Southwick, B. Byrne, and L. Bragg. 2011*a*. *Financial returns to Industry from the Federal Aid in Wildlife Restoration Program*. <http://www.southwickassociates.com /clients/client-project-links/ >

Loftus, A., R. Southwick, B. Byrne, and L. Bragg. 2011*b*. *Financial returns to Businesses from the Federal Aid in Sport Fish Restoration Program*. < http://www.southwickassociates.com /clients/client-project-links/ >

Loftus, A., R. Southwick, B. Byrne, and L. Bragg. 2011*c*. *The benefits to business from hunting and fishing excise taxes*. < http://www.southwickassociates.com/clients/client-project-links/ >

MacArthur, R.H., and W.O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, N.J.

McKelvey, K.S., J.P. Copeland, M.K. Schwartz, J.S. Littell, K.B. Aubry, J.R. Squires, S.A. Parks, M.M. Elsner, and G.S. Mauger. 2011. Climate change predicted to shift wolverine distributions, connectivity, and dispersal corridors. *Ecological Applications* 21(8):2882–2897.

McRae, B.H. 2006. Isolation by resistance. *Evolution* 60(8):1551–1561.

McRae, B.H., B.G. Dickson, T.H. Keitt, and V.B. Shah. 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology* 89(10):2712–2724.

McRae, B.H., and V.B. Shah. 2009. *Circuitscape user's guide*. The University of California, Santa Barbara. Available at: http://www.circuitscape.org.

Nie, M. 2004. State wildlife policy and management: The scope and bias of political conflict. *Public Admin. Rev.* 64:221–233.

Organ, J.F., S.P. Mahoney, and V. Geist. 2010. Born in the hands of hunters: The North American Model of Wildlife Conservation. *The Wildlife Professional* 4(3):22–27.

Paetkau, D.H., G.F. Shields, and C. Strobeck. 1998. Gene flow between insular, coastal, and interior populations of brown bears in Alaska. *Molecular Ecology* 7:1283–1292.

Proctor, M.F., B.N. McLellan, C. Strobeck, and R.M.R. Barclay. 2004. Gender-specific dispersal distances of grizzly bears estimated by genetic analysis. *Canadian Journal of Zoology* 82:1108–1118.

Prukop, J. and R.J. Regan. 2005. In my opinion: The value of the North American model of wildlife conservation–an International Association of Fish and Wildlife Agencies position. *Wildlife Society Bulletin* 33(1):374–377.

Ruhl, J. B. 2009. The Endangered Species Act and Private Property: A Matter of Timing and Location. *Cornell Journal of Law and Public Policy* 8:37–53.

Schwartz, C.C., M.A. Haroldson, and G.C. White. 2010. Hazards affecting grizzly bear survival in the Greater Yellowstone Ecosystem. *Journal of Wildlife Management* 74(4):654–667.

Schwartz, M.K., K.B. Aubry, K.S. McKelvey, K.L. Pilgrim, J.P. Copeland, J.R. Squires, R.M. Inman, S.M. Wisely, and L.F. Ruggiero. 2007. Inferring geographic isolation of wolverines in California using historical DNA. *Journal of Wildlife Management* 71(7):2170–2179.

Seiler, A. 2003. *The toll of the automobile: Wildlife and roads in Sweden*. PhD Dissertation, Swedish University of Agricultural Sciences, Uppsala, Sweden.

Swenson, J.E., F. Sandergren, and A. Söderberg. 1998. Geographic expansion of an increasing brown bear population: evidence for presaturation dispersal. *Journal of Animal Ecology* 67: 819–826.

Taylor, P. 2011. Budget's Wolf Delisting Opens Pandora's Box of Species Attacks, Enviro Groups Warn. *New York Times*, April 13, 2011. http://www.nytimes.com/gwire/2011/04/13/13 greenwire-budgets-wolf-delisting-opens-pandoras-box-of-s-99159.html

United States Fish and Wildlife Service. 2010. Endangered and Threatened Wildlife and Plants; 12-Month Finding on a Petition To List the North American Wolverine as Endangered or Threatened. *Federal Register* Vol. 75, No. 239, Tuesday, December 14, 2010. 78030–78061.

United States Fish and Wildlife Service. 2012. *2011 National Survey of Fishing, Hunting, and Wildlife-Associated Recreation*, National Overview, Issued August 2012. http://library. fws. gov/ Pubs/nat_survey2011-national-overview-prelim-findings.pdf>

Vangen, K.M., J. Persson, A. Landa, R. Andersen, and P. Segerström. 2001. Characteristics of dispersal in wolverines. *Canadian Journal Zoology* 79:1641–1649.

Waser, P.M. 1996. Patterns and consequences of dispersal in gregarious carnivores. Pages 267–295 *in* J. L. Gittleman, editor. *Carnivore Behavior, Ecology, and Evolution. Volume 2*. Cornell University Press, Ithaca, New York, USA.

Western Governors' Association. 2008. *Western Governors' Association Wildlife Corridors Initiative, June 2008 Report*. < http://www.westgov.org/wildlife >

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This thesis focuses on wolverine ecology and conservation in the western United States. The thesis covers the wolverine's niche, scale of effective management, and conservation priorities; it also examines the institutional system in place for delivering conservation actions for non-game species like wolverines. The analyses presented include home range size, movement rates, social organization, density, dispersal, reproductive chronology, habitat selection, and connectivity. This thesis provides information that can facilitate recovery and management of this candidate endangered species.

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