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# Developing priorities for metapopulation conservation at the landscape scale: Wolverines in the Western United States

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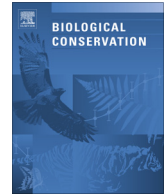
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## Developing priorities for metapopulation conservation at the landscape scale: Wolverines in the Western United States



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### ABSTRACT

Wildlife populations are often influenced by multiple political jurisdictions. This is particularly true for wide-ranging, low-density carnivores whose populations have often contracted and remain threatened, heightening the need for geographically coordinated priorities at the landscape scale. Yet even as modern policies facilitate species recoveries, gaps in knowledge of historical distributions, population capacities, and potential for genetic exchange inhibit development of population-level conservation priorities. Wolverines are an 8–18 kg terrestrial weasel (Mustelidae) that naturally exist at low densities (~5/1000 km<sup>2</sup>) in cold, often snow-covered areas. Wolverines were extirpated, or nearly so, from the contiguous United States by 1930. We used a resource selection function to (1) predict habitat suitable for survival, reproduction and dispersal of wolverines across the western US, (2) make a rough estimate of population capacity, and (3) develop conservation priorities at the metapopulation scale. Primary wolverine habitat (survival) existed in island-like fashion across the western US, and we estimated capacity to be 644 wolverines (95% CI = 506–1881). We estimated current population size to be approximately half of capacity. Areas we predicted suitable for male dispersal linked all patches, but some potential core areas appear to be relatively isolated for females. Reintroduction of wolverines to the Southern Rockies and Sierra-Nevadas has the potential to increase population size by >50% and these regions may be robust to climate change. The Central Linkage Region is an area of great importance for metapopulation function, thus warranting collaborative strategies for maintaining high survival rates, high reproductive rates, and dispersal capabilities. Our analysis can help identify dispersal corridors, release locations for reintroductions, and monitoring targets. The process we used can serve as an example for developing collaborative, landscape-scale, conservation priorities for data-sparse metapopulations.

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### 1. Introduction

As human populations expanded across the globe, many wild-life species, especially carnivores, experienced significant range loss (Fanshawe et al., 1991; Kang et al., 2010; Paquet and Carbyn, 2003). More recently, attitudes and policies have shifted to facilitate species conservation so that expansions into historical range are possible, often through reintroductions (e.g., Bangs et al., 1998; Clark et al., 2002; Raesly, 2001). Reintroductions have the

potential to improve viability of endangered species (Hebblewhite et al., 2011) and provide many other ecological benefits (Beyer et al., 2007; Dickman et al., 2009). However, in the case of wide-ranging, low-density carnivores whose populations are often threatened, they and the areas where they can exist are often managed by multiple political jurisdictions whose authorities and objectives can differ. In these situations, great gains in conservation success and financial efficiency could be made by developing geographically coordinated priorities at the scale of a viable population (Slotow and Hunter, 2009). Unfortunately, timing of range loss often occurred prior to establishment of accurate definitions of species distribution, and information on potential population numbers is simply unknown. As a result, gaps in knowledge of suitable habitat, population capacities, and potential for genetic exchange across a metapopulation can inhibit development of the most effective landscape-level priorities for aiding species recovery. The need to address these landscape-scale issues is becoming more pressing as climate change threatens to increase fragmentation of many populations (Opdam and Wascher, 2004).

The wolverine (*Gulo gulo*) is a large, terrestrial weasel (Mustelidae) weighing 8–18 kg that has an Holarctic distribution. This facultative scavenger occupies a cold, low-productivity niche (Copeland et al., 2010; Inman et al., 2012a,b) that results in sparse population densities (~5/1000 km<sup>2</sup>) and low reproductive rates (0.7 young/female > 3 yrs/yr) across its range (Golden et al., 2007; Inman et al., 2012a; Lofroth and Krebs, 2007; Persson et al., 2006). As a result, wolverine populations are relatively vulnerable due to their small size and limited capacity for growth (Brøseth et al., 2010; Persson et al., 2009). Wolverines were extirpated, or nearly so, from their historical distribution within the contiguous US by about 1930 and unregulated human-caused mortality was likely responsible (Aubry et al., 2007). Wolverines have recovered to a considerable degree (Anderson and Aune, 2008; Aubry et al., 2007; Aubry et al., 2010; Copeland, 1996; Inman et al., 2012a), however the species will 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). Wolverines were recently designated a candidate for listing in the contiguous US under the US Endangered Species Act (US Fish and Wildlife Service, 2010; US Fish and Wildlife Service, 2013).

Wolverine habitat in the contiguous US appears to consist of disjunct patches of mountainous, high alpine areas inhabited at low densities and requiring dispersal across intervening areas (Copeland et al., 2010; Inman et al., 2012a), likely 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. However, these approaches require an abundance of data that are difficult to obtain, especially in the case of rare, cryptic species such as many endangered carnivores.

While there has been much recent progress in understanding wolverine distribution and ecology in the contiguous US (Cegelski et al., 2006; Copeland et al., 2010; Inman et al., 2012a; Ruggiero et al., 2007; Schwartz et al., 2009), habitat-related tools remain coarse and estimates of potential or current population size do not exist. It is also unclear which patches of wolverine habitat in the contiguous US 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 aid decisions on whether reintroductions are warranted and, if so, which areas to prioritize. Without a more complete understanding of the spatial arrangement of habitats, their function for wolverines, and potential population numbers therein, these and other 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., 2012a).

Our objective was to develop a metapopulation framework for wolverines at the scale necessary to conserve the species in the western contiguous US. To do this we: (1) modeled relative habitat quality at the level of species distribution; (2) identified areas suitable for specific wolverine uses that are biologically important and valuable for management purposes (survival, reproduction, dispersal); and (3) related population size to predicted habitat quality 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 threatened or endangered species.

## 2. Study area

Our field research occurred in the Yellowstone Ecosystem of Idaho, Montana, and Wyoming at approximately 45° north latitude (Fig. 1). Elevations in the study area ranged from 1400 to 4200 m. Precipitation increased with elevation and varied from 32 to 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.

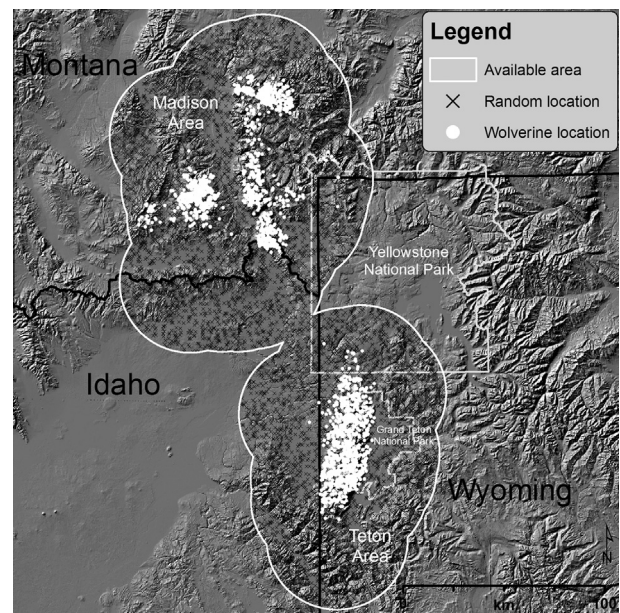


Fig. 1. Locations of wolverines (solid circles) and random points (x's) used to develop a resource selection function model of first order habitat selection, Greater Yellowstone Ecosystem of Montana, Idaho, and Wyoming, USA, 2001–2010.

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).

### 3. Materials and methods

#### 3.1. Species location data

During 2001–2010 we captured 38 wolverines (23♀, 15♂) and equipped each with an intra-peritoneal VHF radio-transmitter (Inman et al., 2012a). The study was approved by the Animal Care and Use Committee of Montana Department of Fish, Wildlife and Parks (MFWP). We attempted to relocate wolverines from the air at an approximate 10-day interval. We estimated VHF telemetry error to be ~300 m (Inman et al., 2012a). We also opportunistically fit 18 of these wolverines (11F, 7M) with a global positioning system (GPS) collar for periods of ~3 months. These collars typically collected locations at 2-h intervals for periods of a few months. We used an approach similar to Hebblewhite et al. (2011) to fit habitat models (see below) using 2257 VHF radio telemetry locations of wolverines resident to the Madison, Gravelly, Henry's Lake, and Teton mountain ranges. We did not use GPS collar data in the model selection process because they did not obtain locations on ~50% of attempts and this could have been related to habitat features (D'Eon et al., 2002; Mattisson et al., 2010). We used locations of wolverines whose data were not utilized to fit models as part of selecting a final model for use and testing the accuracy of predictions as described below.

#### 3.2. Environmental predictors

We developed a list of habitat features we believed important for wolverines (Table S1) 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, 2010; Hornocker and Hash, 1981; Rowland et al., 2003). We also considered the importance of caching behavior (Inman et al., 2012b; 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 US (Table 1). 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' (Brock and Inman, 2006). We developed an index of 'Terrain Ruggedness' following Riley et al. (1999). Based on our observations of frequent use of alpine talus, we believed this variable, or distance to it, could function as a parsimonious explanation of wolverine presence; we represented 'High-elevation Talus' by selecting all areas where latitude-adjusted elevation was >2300 m and terrain ruggedness was >100; these values differentiated rocky areas occurring in low elevation grasslands vs. alpine areas. We also measured 'Distance to High-elevation Talus.' We derived vegetation-related covariates from 30-m National Land-cover Dataset (NLCD; Homer et al., 2001). We calculated 'Tree Cover' by summing the number of treed pixels within 300 m of each grid cell. We also measured 'Distance to Tree Cover.' We calculated 'Forest 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' by averaging values for April 1 2004 and April 1 2005 because this date generally coincides with maximum snow depth for the year. 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' based on the nearest cell where April 1 snow depth was >2.5 cm (minimum snow presence). We used GIS layers developed by Carroll et al. (2001) to represent 'Road Density' and 'Interpolated Human Population Density.' Interpolation provided an approximation for the effects of human use in areas closer to urban centers (Merrill et al., 1999).

#### 3.3. Resource selection function (RSF) modeling

We estimated first order resource selection of the species at the edge of its distribution with logistic regression by comparing environmental predictors at 2257 places where the species was detected to those of 6771 (3×) random locations within the area where the species could have been detected (Carroll et al., 2001; Hebblewhite et al., 2011; Johnson, 1980; Manly et al., 2002). We delineated the area where the species could have been detected (available) with a 34.8-km buffer around our trap locations (Fig. 1), which was the average maximum distance that wolverines

**Table 1**  
Environmental predictors 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 most supported model.

Habitat covariate	Predicted association	Relevance	Source <sup>a</sup>	Resolution	References
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

<sup>a</sup> Data sources: 1 = National Elevation Dataset, US 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 = US Geological Survey, Reston, VA, USA.

were located from their initial point of capture. That area was well within the regular movement capabilities of the species but did not include large areas where we had not attempted to capture wolverines and thus did not sample for species use. Because we were at the southern edge of distribution, the available area included areas that were not likely to be suitable habitat (Inman et al., 2012a), allowing differentiation of suitable and unsuitable characteristics for the species.

We used the following approach in an attempt to model habitat with biologically meaningful terms, avoid over-fitting, and achieve adequate predictive accuracy. 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. However, we reduced the set of potential models for consideration by (1) eliminating main variables correlated >0.70 (Wiens et al., 2008), and (2) carefully considering whether each potential quadratic and interaction was both biologically relevant and explainable (Burnham and Anderson, 2002). This resulted in the retention of 10 main variables, 3 quadratic terms, and 9 interactions for further consideration. To determine models with equivalent support 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 considered models with differences in BIC scores <2 to have equivalent support (Burnham and Anderson, 2002) and used additional wolverine location datasets to select a best model for use from among these final candidates and their weighted average.

#### 3.4. Using additional species locations to test predictive ability and select a best model among supported final candidates

We evaluated predictive ability and selected a best model for use by comparing the capability of the final candidates to score known wolverine locations from 5 test datasets that were not used to fit models (Table 2). First, we withheld all 2835 GPS collar locations of the resident animals used to fit models and tested each model's predictive capacity within the area where it was developed. Second, we also withheld 1165 VHF and GPS locations of 9 wolverines who we captured in the Madison/Teton study area, but who dispersed beyond this area (Inman et al., 2012a). 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 365 VHF and GPS collar locations of 5 resident wolverines we captured in the Anaconda Range ~150–300 km northwest of

the main study area, 321 wolverine mortality locations provided by MFWP, and 157 historical wolverine records (1870–1960) from the western US (Aubry et al., 2007). We examined overall and relative predictive ability as follows. We applied the coefficients for each final candidate model back into the GIS to obtain grids of predicted relative habitat quality on a scale from 0–1 across the western US. We then determined an appropriate area of comparison for each independent dataset, e.g., the western US for historical locations, and binned each grid into 10 equal areas (km<sup>2</sup>) to determine bin thresholds similar to the k-folds procedure (Boyce et al., 2002; Hebblewhite et al., 2011). We then determined the percentage of locations from each test dataset that fell within each bin. The bin with the highest quality predicted habitat was bin 10 and lowest was bin 1. We multiplied percentage of locations in the bin by the bin number such that a habitat prediction where 100% of test dataset locations fell within the highest scoring predicted habitat (bin 10) would receive the maximum score of 1000. A minimum score of 100 would occur in the case where all test locations fell within the lowest scoring habitat. We considered scores from 100–550 to be a poor model, 551–750 to be fair, 750–900 to be good, and 901–1000 to be excellent.

#### 3.5. Identifying areas suitable for survival, reproduction, and dispersal

We partitioned relative habitat quality into biologically meaningful categories that are also informative for management. Various approaches for partitioning have been used (Aldridge et al., 2012; Haines et al., 2006). We defined primary wolverine habitat as areas suitable for long-term survival (use by resident adults) by setting the decision threshold at a sensitivity (correct prediction of presence) of 0.95. This threshold is conservative in that it would tend to avoid excluding potential habitat (Pearson et al., 2004). In order to capture some of the variability in predicted habitat quality at maternal sites, 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., 2012b) and then using the 25th percentile as our cutoff. We delineated areas suitable for use by dispersing wolverines (used briefly, i.e. on the order of days or weeks rather than months or years, 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♂; dispersal was delineated via radio-telemetry [Inman et al., 2012a]).

#### 3.6. Estimating species distribution and abundance

We estimated potential and current distribution and abundance of wolverines by linking the RSF to an estimate of wolverine population size occurring in a portion of Greater Yellowstone where wolverines were reproducing and habitats appeared to be satu-

**Table 2**

Summary and predictive ability of wolverine location datasets used to (A) develop resource selection function models of relative habitat quality at Johnson's (1980) first order, or (B) test the predictive ability of the those models garnering support along with their weighted average, Western contiguous United States, 2001–2010.

Dataset	Years collected	# Locations	Predictive ability (100–1000)		
			Model 1	Model 2	Weighted average
<i>(A) Model development</i>					
Resident VHF telemetry	2001–2010	2257	$r_s = 0.983$	$r_s = 0.986$	
<i>(B) Model validation testing</i>					
GPS collar locations of residents used to fit models	2004–2008	2835	911 <sup>a</sup>	876	912
Disperser VHF and GPS locations	2001–2009	1165	884	890 <sup>a</sup>	884
Anaconda Range resident VHF and GPS locations	2008–2009	365	842	857 <sup>a</sup>	847
Contemporary Montana Records	1975–2005	321	925	928 <sup>a</sup>	925
Historical Records (Aubry et al., 2007)	1870–1960	157	918	920 <sup>a</sup>	918

<sup>a</sup> Highest scoring model for each test dataset.

**Table 3**  
Wolverine resource selection function (RSF) model results for first order prediction of relative habitat quality. The five models with most support are compared in addition to the global model (all covariates), the null model, and several simple intuitive potential models. Greater Yellowstone Ecosystem of Montana, Idaho, and Wyoming, USA, 2001–2010. Predictive environmental variables retained were latitude-adjusted elevation (LAE), terrain ruggedness index (TRI), April 1 snow depth (SNOW), road density (ROAD), interpolated human density (POP), distance to high-elevation talus (DHITAL), distance to tree cover (DTREE), distance to April 1 snow >2.5 cm (DSNOW) along with their quadratic terms and interactions.

Rank/model	K	BIC	ΔBIC	Weight
1 LAE + TRI + SNOW + ROAD + POP + DHITAL + DTREE + DSNOW + TRI <sup>2</sup> + LAE:ROAD + LAE:DTREE + SNOW:POP	13	6856.71	–	0.70
2 LAE + TRI + SNOW + ROAD + POP + DHITAL + DTREE + DSNOW + TRI <sup>2</sup> + LAE:ROAD + LAE:DTREE + SNOW:POP + SNOW <sup>2</sup>	14	6858.41	1.71	0.30
3 LAE + TRI + SNOW + ROAD + POP + DHITAL + DTREE + DSNOW + TRI <sup>2</sup> + LAE:ROAD + LAE:DTREE + SNOW:POP + SNOW <sup>2</sup> + HITAL	15	6867.22	10.51	0.00
4 LAE + TRI + SNOW + ROAD + POP + DHITAL + DTREE + DSNOW + TRI <sup>2</sup> + LAE:ROAD + LAE:DTREE + SNOW:POP + SNOW <sup>2</sup> + HITAL + HITAL:DTREE	16	6867.22	19.01	0.00
5 LAE + TRI + SNOW + ROAD + POP + DHITAL + DTREE + DSNOW + TRI <sup>2</sup> + LAE:ROAD + LAE:DTREE + SNOW:POP + SNOW <sup>2</sup> + HITAL + HITAL:DTREE + TRI:DTREE	17	6867.22	24.72	0.00
Global model	23	6931	74	–
LAE + TRI + SNOW + LAE <sup>2</sup> + TRI <sup>2</sup> + SNOW <sup>2</sup>	7	7058	202	–
LAE + LAE <sup>2</sup>	3	7675	818	–
LAE	2	7726	869	–
TRI + TRI <sup>2</sup>	3	8192	1,335	–
TRI	2	8436	1,579	–
SNOW + SNOW <sup>2</sup>	3	9195	2,338	–
SNOW	2	9706	2,849	–
Null model	1	10163	3,306	–

rated or nearly so with resident adult territories (Inman et al., 2012a). Following Boyce and McDonald (1999) and Hebblewhite et al. (2011), we determined total RSF predicted relative probabilities for the Yellowstone area where Inman et al. (2012a) estimated wolverine population size (which included residents and subadults/transients) and calculated total RSF-predicted habitat per wolverine. We then summed total predicted relative probabilities for each individual patch of primary wolverine habitat (as defined by the cutoff values described above) within the western US that was >100 km<sup>2</sup>, i.e., the approximate minimum female home range size (Copeland, 1996; Hornocker and Hash, 1981; Inman et al., 2012a). Finally, we estimated the potential number of wolverines possible in each of these >100-km<sup>2</sup> patches using the following equation:

$$\frac{\sum \hat{w}(x)_{\text{Yellowstone}}}{N_{\text{Yellowstone}}} = \frac{\sum \hat{w}(x)_{\text{Patch}}}{N_{\text{Patch}}}$$

where  $N_{\text{Yellowstone}}$  is the wolverine population estimate from Yellowstone (known/measured),  $\sum \hat{w}(x)_{\text{Yellowstone}}$  is the sum of predicted relative habitat probabilities within the Yellowstone population estimate area, and  $\sum \hat{w}(x)_{\text{Patch}}$  is the sum of predicted relative habitat probabilities for the wolverine habitat patch where wolverine population capacity ( $N_{\text{Patch}}$ ) was to be estimated. We rounded the number of wolverines estimated for each patch down to the nearest integer prior to summing by region and across the western US. By using the 100 km<sup>2</sup> minimum patch size, this method could predict wolverines in areas too small for males. However female use of these areas could be important (Dias, 1996; Boughton, 1999), so we checked our potential to over-predict by removing estimated wolverines from patches that were <400 km<sup>2</sup> and >10 km from a 400 km<sup>2</sup> patch; this was based on resident male home range size and movements between patches (Persson et al., 2010; Inman et al., 2012a).

We also used the above estimation technique to predict current population size for the area where male and female wolverines are likely well-distributed across available habitat. This assumed habitat occupation at similar densities to the study area of Inman et al. (2012a) which appeared reasonable for our purposes based on the history of available wolverine records, evidence of reproduction, and contemporary studies (Anderson and Aune, 2008; Aubry et al., 2007, 2010, Copeland, 1996, Copeland and Yates, 2008, Inman et al., 2012a, Murphy et al., 2011; Newby and Wright, 1955; Newby and McDougal, 1964; Squires et al., 2007). 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 (Inman et al., 2009, Magoun et al., 2011; Moriarty et al., 2009, Murphy et al., 2011). In order to facilitate discussion of landscape-level management strategies, we subjectively categorized patches of primary habitat >100 km<sup>2</sup> 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 location data

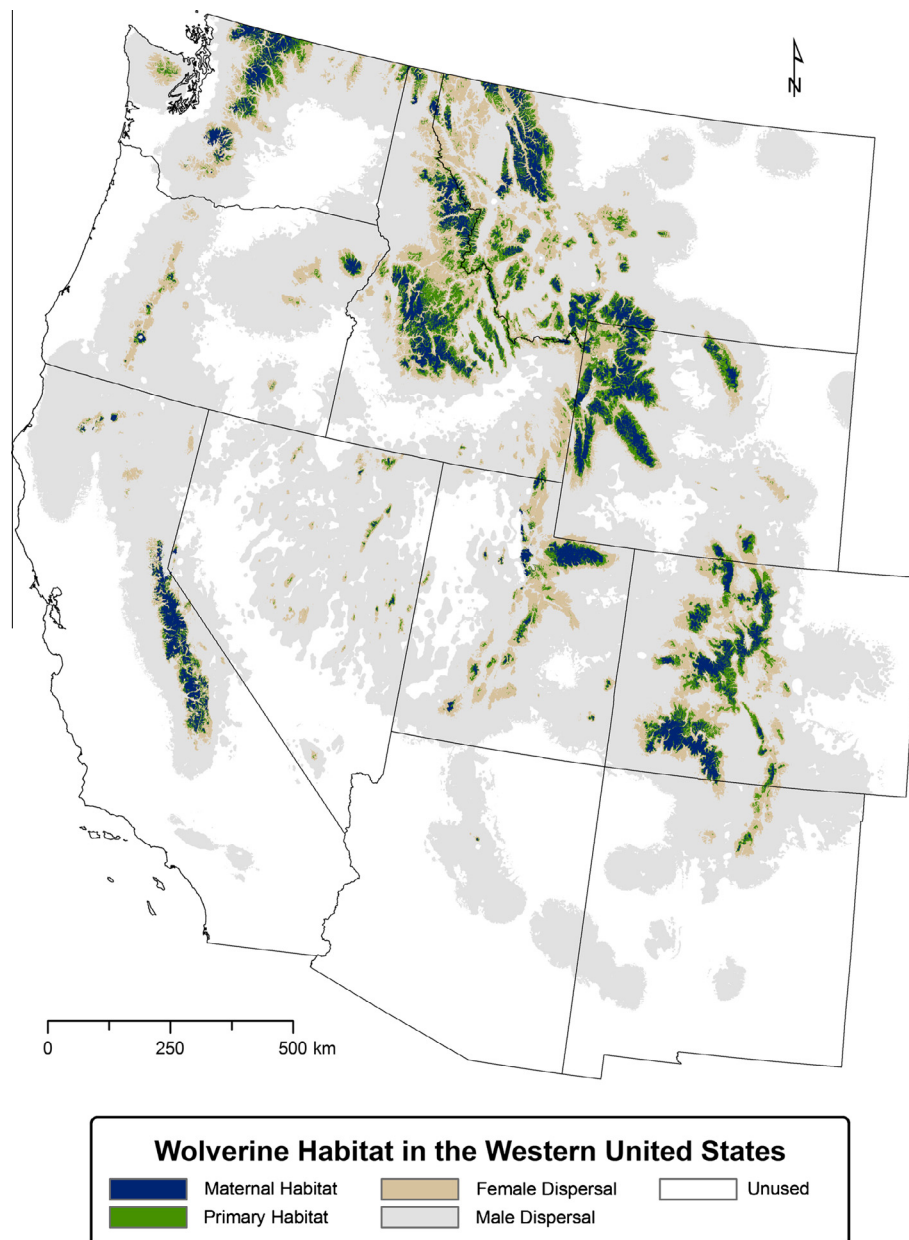
Two models garnered support with ΔBIC scores <2 (Table 3). These models performed much better than the null model, global model, and several simple and intuitive models (Table 3). Model 2 differed from model 1 only by the inclusion of ‘Snow Depth’ as a quadratic term. We used model 2 as our final model because it tested best overall with the additional wolverine location datasets relative to model 1 and the weighted average of models 1 and 2 (Table 2). The k-fold cross validation score for the locations used

to fit model 2 indicated an excellent fit ( $r_s = 0.986$ ,  $SE = 0.003$ , Fig. S1). Model 2 also scored good or excellent with all test datasets suggesting its predictive capability was sufficient for use (Table 2). In general, wolverines were distributed in 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 (Table S2).

#### 4.2. Identifying areas suitable for survival, reproduction, and dispersal

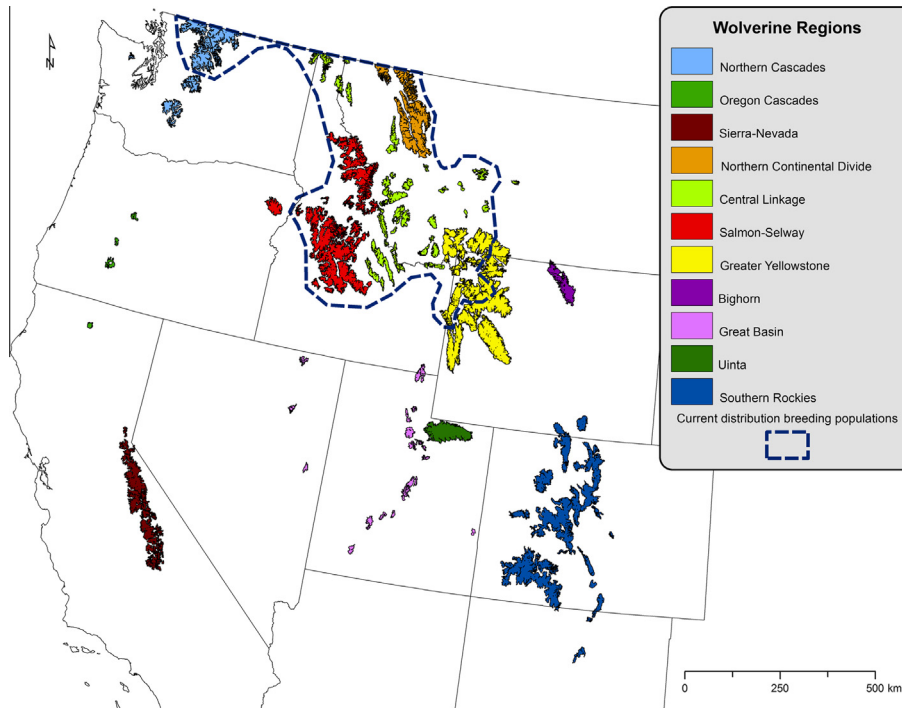
Using model 2, predicted habitat scores  $\geq 0.967$  represented primary wolverine habitat, i.e., areas suitable for survival and use by resident adults (Fig. 2). We classified a total of 164,125 km<sup>2</sup> as primary habitat in the western US. Ninety-three percent of primary habitat existed in 111 patches >100 km<sup>2</sup> that were distributed

across 10 of the 11 western states (Fig. 3). Seven patches were >5000 km<sup>2</sup> and occurred in the Northern Continental Divide, Salmon-Selway, Greater Yellowstone, Southern Rockies, Northern Cascades, and Sierra-Nevada regions (Fig. 3). We classified areas scoring  $\geq 0.968$  as maternal habitat (Fig. 2). Small differences in scores categorizing habitat classes were the result of the 0–1 scale used in the GIS and mapped across the entire western US; some habitats were so poor for wolverines that meaningful differences for wolverines all occurred at the upper end of the scale. The total area of predicted maternal habitat was 48% of the area classified as primary habitat. For patches of primary habitat >100 km<sup>2</sup>, the quality of habitat differed internally such that percent of a patch classified as maternal habitat ranged from 0% to 84% (Table S3). The lowest habitat value used by dispersing wolverines was 0.966 for females and 0.933 for males, and we used these to map



**Fig. 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 in the Greater Yellowstone Ecosystem, of Montana, Idaho, and Wyoming, USA, 2001–2010.





**Fig. 3.** Major blocks (>100 km<sup>2</sup>) 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.

**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 collected in the Yellowstone region 2001–2010.

Region	Population capacity estimate (95% CI) <sup>a</sup>	Current population estimate (95% CI) <sup>a</sup>
Northern Cascade	48 (37–138)	37 (29–103)
N. Continental Divide	49 (38–138)	49 (38–138)
Salmon–Selway	124 (97–352)	119 (93–338)
Central Linkage	50 (38–173)	50 (38–172)
Greater Yellowstone	146 (119–412)	63 (51–175)
Southern Rockies	137 (108–390)	0
Sierra–Nevada	45 (35–128)	0
Uinta	21 (17–58)	0
Bighorn	12 (10–35)	0
Great Basin	11 (6–48)	0
Oregon Cascade	1 (1–9)	0
Western United States	644 (506–1881)	318 (249–926)

<sup>a</sup> Estimate of capacity within each primary habitat patch >100 km<sup>2</sup> was rounded down to the nearest integer and then summed by region. Estimates based on model 2 and a 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., 2012a).

areas suitable for dispersal for each sex (Fig. 2). Areas we predicted suitable for male dispersal linked all primary habitat patches >100 km<sup>2</sup> but this was not the case for females.

#### 4.3. Estimating distribution and abundance

Using model 2, we estimated the potential wolverine population capacity in the western contiguous US to be 644 wolverines (95% CI = 506–1881) in the hypothetical case where all available primary habitat patches >100 km<sup>2</sup> were occupied at densities measured in Greater Yellowstone (Table 4, Fig. 3). We note that Inman et al. (2012a) suggested a reasonable upper limit for the population

estimate was approximately half the upper 95% CI (Table 4). The potential to overestimate due to patches being smaller than a male home range was negligible overall (639 vs. 644) and concentrated in the Great Basin Region (Table S3). Fifty-seven percent of total 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 to 88 (Table S3). We estimated that the Southern Rockies represent 21% of total population capacity. We estimated current population size to be 318 wolverines (95% CI = 249–926) in the Northern Continental Divide and portions of the Salmon–Selway, Central Linkage, Greater Yellowstone, and Northern Cascade ecosystems (Table 4, Fig. 3). Estimated population capacities were similar under model 1 and the weighted average model with the exception of the Sierra–Nevadas (Table S4).

## 5. Discussion

We developed a prediction of relative habitat quality for a data-sparse carnivore that had been eliminated from much of its historical range prior to clear establishment of distribution and potential population capacity. Our prediction of habitat tested well with independent location datasets suggesting it is robust to extrapolation and useful for developing collaborative conservation strategies across the large geographic area necessary for conserving the species in the western contiguous US. The method we used could be applied to a wide variety of species where information on historical range, population capacity, or relative connectivity of habitat patches is lacking but needed to make conservation decisions. This may be particularly true at the periphery of a species distribution where suitable habitats may become more fragmented.

We defined primary habitat as areas suitable for survival/use by resident adults, which we believe is a good approximation for historical distribution of wolverines in the Western contiguous

US. All additional areas where wolverine populations have been studied with radio-telemetry in the Western US contained significant areas of predicted primary habitat (Aubry et al., 2010; Copeland, 1996; Copeland and Yates, 2008; 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 well, concurring across >96% of the western US. 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 spring 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)) and the patches are certainly within observed dispersal range of males and females. Our estimate of primary habitat is more conservative in this area (Fig. 2), likely due to the relatively low latitude-adjusted elevations of these areas and general lack of steep, rocky terrain despite their being snow-covered in May. The presence of only 2 historical records of wolverines from Oregon and northern California (compared to 29 from Washington and 58 from the Sierra-Nevadas) lends some support to the more conservative prediction (Aubry et al., 2007). While previous genetic analyses suggested the Sierra-Nevadas were isolated for >2000 years (Schwartz et al., 2007), other analyses suggest that may not be the case (McKelvey et al., submitted for publication). Additional information on the ability of habitats within western Oregon and northern California to sustain reproducing wolverines or not would benefit efforts to conserve the species in the western US.

Maternal sites occurred in areas of higher quality habitat suggesting potential utility in distinguishing among patches more or less suitable for reproduction. Patch quality in terms of reproductive capacity could have important implications for metapopulation conservation strategies. For instance, the Nevada and Elkhorn mountains sit in a central position relative to 3 major blocks of habitat in the northern US 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 proportion of maternal habitat could help identify and prioritize linkage corridors throughout the metapopulation by factoring in the reproductive capacity of individual patches in order to better represent potential gene flow. Similar information on other species could help prioritize actions that would help maintain guild-level 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 than females (Flagstad et al., 2004; Inman et al., 2012a; Vangen et al., 2001). Our sample sizes were small, however we observed males using lower scoring areas than females even though our results could have shown that females used as low or lower quality areas as males. This may have been related to our distance-related variables and males being more inclined to disperse. It is also possible that with additional data the extent of female dispersal habitat could increase. Based on our current results, all primary habitat patches fell within the limits of male dispersal that we estimated (Fig. 2). However, this was not the case for females. Nearly all primary habitat patches

in Montana, Idaho, western Wyoming, and Utah were connected or very nearly so for females (<5 km; Fig. 2). But 3 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-Nevadas 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-Nevadas, Southern Rockies, and Bighorns may be limited if possible at all for females.

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 6 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 ~50+ wolverines; these were the Northern Cascade, Northern Continental Divide, Salmon-Selway, Greater Yellowstone, Southern Rockies, and Sierra-Nevada Regions (Fig. 3). While the Northern Cascades Region contained only 7% of estimated population capacity and does not appear to be well-linked to other major cores in the US, it is contiguous with large areas of wolverine habitat in British Columbia. However, these areas of British Columbia were rated as low quality wolverine habitat (Lofroth and Krebs, 2007). The Uinta and Bighorn Regions may function as minor population cores. The Central Linkage, Great Basin, and Oregon Cascades 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). Total capacity of the Central Linkage Region is as large as a major core.

Suitable habitat for resident adults and reproduction occurs in island-like fashion here at the southern periphery of the species distribution, and it is clear that wolverines are dependent on dispersal among patches of habitat across a vast geographic scale. The small wolverine metapopulation of the western contiguous US 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 US Rockies. 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 US 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 US in recent decades (Brown et al., 2005; Gude et al., 2007, 2008; Johnson and Beale, 1994), maintaining a network of natural areas among the patches of suitable reproductive habitat will be critical for natural, 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 reason-

able 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. Road density was retained in a negative relationship with wolverine occurrence. 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 (Krebs et al., 2004, 2007), developing incentives for maintaining natural areas on privately owned lands needs to be a priority. The CLR is a natural starting point for these efforts given its unique location and ownership pattern. Establishing connectivity for wolverines would also benefit many other species including mountain lions (*Puma concolor*), black bears (*Ursus americanus*), and grizzly bears (*Ursus arctos*) because of the large scale at which wolverines require connectivity and that fact that doing so would link much of the forested public land of Idaho, Montana, and Wyoming. Further work on dispersal is needed to improve our understanding of factors limiting these critical movements for wolverines and other species.

Restoring wolverines to unoccupied areas of historical range could substantially increase population size, genetic diversity, and resiliency and could function to establish refugia for the species as climate change occurs. Our analysis suggests that the Southern Rockies represent 21% 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 1940s (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 so infrequent (if possible) that it may be of limited value in establishing or maintaining populations (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 US. Given the restricted number of haplotypes in the northern US 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-Nevadas, it is possible that by 2100 these areas may be some of the best remaining wolverine habitat within the contiguous US (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. Clearly there is 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 (Table S3) that can be refined by future surveys.

## 6. Conclusion

We used telemetry data and an RSF to identify metapopulation conservation priorities for a candidate threatened or endangered species that had been extirpated from its historical range prior to establishment of distribution or population numbers. Wolverine habitat in the western contiguous US exists in island-like fashion distributed across 10 states (~2.5 million km<sup>2</sup>) and appears to have the capacity for approximately 650 individuals. Because the geographic scale for conserving this metapopulation is so large, management actions must be conceived and implemented across multiple states and numerous management jurisdictions. We suggest conservation priorities are (1) Securing connectivity in the Central Linkage Region, (2) Restoring populations to (a) the Southern Rockies and (b) the Sierra-Nevadas, and (3) establishing a metapopulation monitoring program. 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 US Rockies include most of the major core areas, the majority of the current 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. Because of the scale over which wolverine connectivity needs to be maintained and the fact that doing so would link much of the public land of the western US, developing incentives for retaining private lands in a state that facilitates animal movement is important and would likely benefit numerous terrestrial species. Our estimate of current population size was approximately half of capacity and was limited to portions of four states. Restoration of wolverines to the Southern Rockies and Sierra-Nevadas could increase current population size by an estimated 57% along with improving the redundancy, resiliency, and genetic diversity of the metapopulation. Our analysis can help identify potential release sites based on habitat quality. Our analysis also provides an initial hypothesis for wolverine distribution and abundance within the western contiguous US that can aid development of a collaborative metapopulation monitoring program. The process we used may serve as an example for developing conservation priorities for other data-sparse metapopulations where range contractions have likely occurred.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2013.07.010>.

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Table S1. Habitat features we considered important for wolverines in the analysis of first order habitat selection within the Yellowstone Region and subsequently modeled at a multi-state scale across the western United States.

<b>Key component</b>	<b>Habitat feature</b>	<b>Significance</b>
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 from 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

Table S2. Coefficients and standard errors for wolverine model 2 resource selection function for relative habitat quality at the first order developed in the Greater Yellowstone Ecosystem of Montana, Idaho, and Wyoming, USA, 2001–2010. Predictive environmental variables were Latitude-adjusted Elevation (LAE), Terrain Ruggedness Index (TRI), Snow Depth (SNOW), Road Density (ROAD), Interpolated Human Density (POP), Distance to High-elevation Talus (DHITAL), Distance to Tree Cover (DTREE), Distance to Snow >2.5 cm (DSNOW).

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<b>Coefficient</b>	<b>Estimate</b>	<b>SE</b>
LAE	2.036e-03	1.454e-04
TRI	2.355e-02	3.167e-03
SNOW	1.220e-03	3.499e-04
ROAD	-2.940e+00	6.998e-01
POP	-3.255e-01	1.024e-01
DHITAL	-1.217e-04	1.538e-05
DTREE	-1.480e-02	2.990e-03
DSNOW	-1.428e-03	7.737e-04
TRI <sup>2</sup>	-7.477e-05	1.576e-05
SNOW <sup>2</sup>	-4.598e-7	1.725e-07
LAE:ROAD	1.250e-03	2.931e-04
LAE:DTREE	4.445e-06	1.047e-06
SNOW:POP	2.375e-04	7.674e-05

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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 collected in the Yellowstone region 2001–2010. Numbers presented here are based on model 2 and a population estimate of 15.2 wolverines (95% CI = 12.3–42.0) from the Yellowstone study area of Inman et al. (2012a) where 11 individuals were known to be on the area and 20 was considered a reasonable upper limit. The estimate of capacity within each primary habitat patch  $>100 \text{ km}^2$  was rounded down to the nearest integer and then summed by region. Patches that were smaller than minimum male home range size ( $400 \text{ km}^2$ ) and  $>10 \text{ km}$  from a  $400 \text{ km}^2$  patch are noted with an \*.

<b>Region</b>	<b>Primary habitat patch <math>&gt;100 \text{ km}^2</math></b>	<b>Population capacity</b>	<b>(95% CI)</b>	<b>Proportion maternal habitat</b>
<b>Bighorn</b>		<b>12</b>	<b>(10–35)</b>	
	Bighorn Range	12	(10–35)	0.36
<b>Central Linkage</b>		<b>50</b>	<b>(38–173)</b>	
	Anaconda-Sapphire Ranges	7	(5–20)	0.33
	Beaverhead Mountains Central	0	(0–1)	0.19
	Beaverhead Mountains North	3	(2–9)	0.39
	Beaverhead Mountains South 1	0	(0–2)	0.05
	Beaverhead Mountains South 2	2	(2–7)	0.15
	*Big Belt Mountains	0	(0–2)	0.30
	*Big Snowy Range	0	(0–1)	0.17
	Bloody Dick Range	0	(0–1)	0.11
	*Bridger Range	0	(0–1)	0.33
	Cabinet Mountains East	2	(2–6)	0.50
	Cabinet Mountains West	2	(2–7)	0.62
	Centennial Range	2	(1–6)	0.43
	*Crazy Mountains	1	(1–3)	0.38
	*Elkhorn Mountains	0	(0–2)	0.14
	Flint Creek Range	2	(1–6)	0.42
	Gravelly Range	2	(1–6)	0.26
	Greenhorn Range	0	(0–1)	0.05
	Gypsy Peak	1	(1–4)	0.29
	John Long Mountains	0	(0–1)	0.13
	Lemhi Range	7	(5–19)	0.23
	Little Belt Mountains	2	(2–7)	0.14
	Lost River Range Central	2	(1–5)	0.43
	Lost River Range North	0	(0–2)	0.11
	Lost River Range South	0	(0–2)	0.17
	Lost Trail	0	(0–1)	0.06
	Mission Mountains	3	(2–9)	0.54
	*Nevada Mountains	0	(0–1)	0.08



Table S3 continued...

Region	Primary habitat patch >100 km <sup>2</sup>	Population capacity	(95% CI)	Proportion maternal habitat
<b>Central Linkage...</b>				
	Pioneer Range East	2	(2–7)	0.34
	Pioneer Range West	3	(2–8)	0.15
	*Purcell Mountains	0	(0–1)	0.30
	Rattlesnake Mountains	1	(1–4)	0.69
	Selkirk Range	3	(3–10)	0.38
	Snowcrest Range	1	(1–4)	0.18
	South Anaconda	0	(0–2)	0.06
	Tobacco Root Range	2	(1–5)	0.53
<b>Great Basin</b>				
	Bear River Range	2	(2–8)	0.46
	*Blowhard Mountain	1	(0–2)	0.73
	*Jarbridge Mountains	1	(0–2)	0.24
	*La Sal Mountains	0	(0–1)	0.37
	*Monroe Peak	0	(0–1)	0.12
	*Mount Belknap	1	(1–4)	0.38
	*Mount Terrel	0	(0–1)	0.37
	*Ruby Mountains	0	(0–2)	0.29
	*Schell Creek Range	0	(0–2)	0.39
	*Strawberry Peak	0	(0–1)	0.06
	Wasatch Central	2	(1–6)	0.84
	*Wasatch North East	0	(0–1)	0.27
	*Wasatch North West	0	(0–2)	0.57
	Wasatch Plateau East	0	(0–1)	0.10
	Wasatch Plateau West	3	(2–9)	0.37
	*Wasatch South East	0	(0–2)	0.09
	*Wasatch South West	1	(0–3)	0.44
<b>Greater Yellowstone</b>				
	Absaroka-Teton Ranges	88	(71–244)	0.54
	Henrys Lake Mountains	0	(0–2)	0.32
	Madison-Gallatin Ranges	22	(18–63)	0.43
	Wind River Range	22	(18–62)	0.54
	Wyoming-Salt Ranges	14	(12–41)	0.57
<b>Northern Cascade</b>				
	Gilbert Peak	1	(0–3)	0.57
	Mount Aix	1	(1–3)	0.60
	Mount Baker	7	(5–20)	0.72
	Mount Rainier	4	(3–12)	0.84
	Mount Stewart	5	(4–16)	0.46

Table S3 continued...

Region	Primary habitat patch >100 km <sup>2</sup>	Population capacity	(95% CI)	Proportion maternal habitat
<b>Northern Cascade...</b>				
	*Olympic Mountains	0	(0–1)	0.10
	Pasayten	29	(23–80)	0.55
	Tiffany Mountain	1	(1–3)	0.07
<b>Northern Continental Divide</b>				
	Bob Marshall Wilderness	36	(29–100)	0.68
	Bob Marshall Wilderness 2	0	(0–1)	0.36
	Glacier National Park	9	(7–26)	0.47
	Whitefish Range North	3	(2–9)	0.52
	Whitefish Range South	1	(0–2)	0.05
<b>Coastal Oregon</b>				
	*Diamond Peak	0	(0–1)	0.25
	*Mount Mazama	1	(1–4)	0.52
	*Mount Shasta	0	(0–2)	0.75
	*Sister Mountains	0	(0–2)	0.35
<b>S Rockies</b>				
	Bald Mountain	1	(0–2)	0.02
	Blanca Peak	1	(0–2)	0.35
	Culebra Range	3	(2–8)	0.35
	Flat Top Mountains	8	(6–23)	0.50
	Front Range	59	(48–165)	0.47
	Grand Mesa	3	(2–9)	0.40
	Huntsman Mountain	0	(0–1)	0.27
	*Pikes Peak	0	(0–1)	0.14
	San Juan Range	43	(35–120)	0.62
	Sangre de Christo Range	3	(2–8)	0.28
	Santa Fe Mountains	1	(1–5)	0.24
	Sierra Madre Range	11	(9–32)	0.51
	Snowy Range	3	(2–10)	0.38
	Twin Cone	1	(1–3)	0.03
	Venado Peak	0	(0–1)	0.00
<b>Sierra-Nevada</b>				
	John Muir Wilderness North	0	(0–1)	0.60
	John Muir Wilderness South	7	(5–19)	0.72
	Kings Canyon	1	(1–4)	0.80
	Sequoia	8	(6–23)	0.58
	Tahoe	0	(0–1)	0.84
	Yosemite	29	(23–80)	0.76

Table S3 continued...

<b>Region</b>	<b>Primary habitat patch &gt;100 km<sup>2</sup></b>	<b>Population capacity</b>	<b>(95% CI)</b>	<b>Proportion maternal habitat</b>
<b>Salmon-Selway</b>		<b>124</b>	<b>(97–352)</b>	
Allen Mountain		2	(2–7)	0.12
Bitterroot Range		19	(15–54)	0.45
Clearwater		16	(13–45)	0.63
Farrow Mountain		0	(0–1)	0.00
Gospel Hump Mountains		0	(0–1)	0.01
Salmon Mountain		1	(1–4)	0.06
Salmon-Smoky Mountains		72	(58–200)	0.50
Seven Devils Mountains		1	(0–2)	0.04
Soldier Mountains		1	(0–2)	0.25
Trinity Mountain		1	(0–3)	0.51
Wallawa Mountains		5	(4–14)	0.58
War Eagle Mountain		2	(1–6)	0.15
Widow Mountain		1	(1–5)	0.63
Yellowjacket Mountains		3	(2–8)	0.05
<b>Uinta</b>		<b>21</b>	<b>(17–58)</b>	
Uinta		21	(17–58)	0.68
<b>Western Contiguous United States</b>		<b>644</b>	<b>(506–1881)</b>	

Table S4. Comparison of estimates of wolverine population capacity resulting from resource selection function models with  $\Delta\text{BIC}$  scores  $<2$  and their weighted averages by region (as in Fig. 3) in the western contiguous United States. Habitat models based on wolverine telemetry data collected in the Yellowstone region 2001–2010.

Region	Population capacity estimate (95% CI) <sup>a</sup>		
	Model 2	Model 1	WtdAvg
Northern Cascade	48 (37–138)	35 (27–105)	32 (24–99)
N. Continental Divide	49 (38–138)	51 (41–143)	52 (42–147)
Salmon–Selway	124 (97–352)	105 (84–310)	105 (85–314)
Central Linkage	50 (38–173)	75 (53–236)	73 (52–237)
Greater Yellowstone	146 (119–412)	135 (109–381)	141(113–395)
Southern Rockies	137 (108–390)	131 (104–387)	134 (105–396)
Sierra–Nevada	45 (35–128)	7 (5–29)	5 (3–20)
Uinta	21 (17–58)	19 (15–52)	19 (16–54)
Bighorn	12 (10–35)	15 (12–42)	15 (12–43)
Great Basin	11 (6–48)	7 (4–39)	7 (4–41)
Oregon Cascade	1 (1–9)	0 (0–0)	0 (0–0)
Western United States	644 (506–1881)	580 (454–1724)	583 (456–1746)

<sup>a</sup> Estimate of capacity within each primary habitat patch  $>100 \text{ km}^2$  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. 2012a).

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.

