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Research Article

Wolverine Occupancy, Spatial Distribution, and Monitoring Design

PAUL M. LUKACS,[1] *Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, W.A. Franke College of Forestry and Conservation, University of Montana, Missoula, MT 59812, USA*

DIANE EVANS MACK, *Idaho Department of Fish and Game, McCall Subregion, 555 Deinhard Lane, McCall, ID 83638, USA*

ROBERT INMAN, *Montana Fish, Wildlife and Parks, 1420 East 6th Ave., P.O. Box 200701, Helena, MT 59620, USA*

JUSTIN A. GUDE, *Montana Fish, Wildlife and Parks, 1420 East 6th Ave., P.O. Box 200701, Helena, MT 59620, USA*

JACOB S. IVAN, *Colorado Parks and Wildlife, 317 W. Prospect Rd., Fort Collins, CO 80526, USA*

ROBERT P. LANKA,[2] *Wyoming Game and Fish Department (Retired), 5400 Bishop Blvd., Cheyenne, WY 82006, USA*

JEFFREY C. LEWIS, *Washington Department of Fish and Wildlife, 1111 Washington Street SE, Olympia, WA 98501, USA*

ROBERT A. LONG, *Woodland Park Zoo, 5500 Phinney Ave. N, Seattle, WA 98103, USA*

REX SALLABANKS, *Idaho Department of Fish and Game, 600 S. Walnut St., Boise, ID 83707, USA*

ZACK WALKER, *Wyoming Game and Fish Department, 260 Buena Vista, Lander, WY 82520, USA*

STACY COURVILLE, *Confederated Salish and Kootenai Tribe, P.O. Box 278, Pablo, MT 59855, USA*

SCOTT JACKSON, *USDA Forest Service, 26 Fort Missoula Road, Missoula, MT 59804, USA*

RICK KAHN,[3] *National Park Service (Retired), NRSS Biological Resource Management Division, 1201 Oakridge Drive, Suite 200, Fort Collins, CO 80525, USA*

MICHAEL K. SCHWARTZ, *National Genomics Center for Wildlife and Fish Conservation, USDA Forest Service, Rocky Mountain Research Station, 800 E. Beckwith Ave., Missoula, MT 59801, USA*

STEPHEN C. TORBIT,[4] *U.S. Fish and Wildlife Service (Retired), Mountain Prairie Region, Lakewood, CO 80228, USA*

JOHN S. WALLER, *Glacier National Park, P.O. Box 128, West Glacier, MT 59936, USA*

KATHLEEN CARROLL, *Department of Ecology Montana State University, P.O. Box 173460, Bozeman, MT 59717-3460, USA*

ABSTRACT In the western United States, wolverines (*Gulo gulo*) typically occupy high-elevation habitats. Because wolverine populations occur in vast, remote areas across multiple states, biologists have an imperfect understanding of this species' current distribution and population status. The historical extirpation of the wolverine, a subsequent period of recovery, and the lack of a coordinated monitoring program in the western United States to determine their current distribution further complicate understanding of their population status. We sought to define the limits to the current distribution, identify potential gaps in distribution, and provide a baseline dataset for future monitoring and analysis of factors contributing to changes in distribution of wolverines across 4 western states. We used remotely triggered camera stations and hair snares to detect wolverines across randomly selected 15-km × 15-km cells in Idaho, Montana, Washington, and Wyoming, USA, during winters 2016 and 2017. We used spatial occupancy models to examine patterns in wolverine distribution. We also examined the influence of proportion of the cell containing predicted wolverine habitat, human-modified land, and green vegetation, and area of the cluster of contiguous sampling cells. We sampled 183 (28.9%) of 633 cells that comprised a suspected wolverine range in these 4 states and we detected wolverines in 59 (32.2%) of these 183 sampled cells. We estimated that 268 cells (42.3%; 95% CI = 182–347) of the 633 cells were used by wolverines. Proportion of the cell containing modeled wolverine habitat was weakly positively correlated with wolverine occupancy, but no other covariates examined were correlated with wolverine occupancy. Occupancy rates (ψ) were highest in the Northern Continental Divide Ecosystem (ψ range = 0.8–1), intermediate in the Cascades and Central Mountains of Idaho (ψ range = 0.4–0.6), and lower in the Greater Yellowstone Ecosystem (ψ range = 0.1–0.3). We provide baseline data for future surveys of wolverine along with a design and protocol to conduct those surveys. © 2020 The Authors. The *Journal of Wildlife Management* published by Wiley Periodicals, Inc. on behalf of The Wildlife Society.

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[1]*E-mail: paul.lukacs@umontana.edu*
[2]*Current address: 1865 N 22nd St., Laramie, WY 82072, USA*
[3]*Current address: 1921 Kona Dr., Fort Collins, CO 80528, USA*
[4]*Current address: 299 Gardenia Court, Golden, CO 80401, USA*

The wolverine (*Gulo gulo*) is circumpolar and occupies tundra, taiga, boreal, and alpine areas of the northern hemisphere (Copeland and Whitman 2003). Population densities and reproductive rates are typically low relative to most carnivores (Persson et al. 2006, Royle et al. 2011). The historical distribution of wolverines in western North America extended southward into the mountainous areas of Colorado and California, but wolverines were extirpated from the contiguous United States by about 1920 (Aubry et al. 2007, Schwartz et al. 2007). Since then, populations from Canada have expanded southward reoccupying some portion of their contiguous United States historical range (Newby and McDougal 1964, Aubry et al. 2007, Moriarty et al. 2009, Packila et al. 2017).

In the western contiguous United States, wolverines exist as a set of sub-populations, likely comprised of a few hundred individuals residing in high-alpine areas that are distributed across a vast geography (Inman et al. 2013). Density is low enough that large mountain ranges such as the Tetons of western Wyoming have enough area for only about 5 home ranges and even connected areas such as the Pioneer, Beaverhead, Flint Creek, and Anaconda-Pintler mountain ranges in Montana may only have a small number of individuals at a given time (Squires et al. 2007). Few, if any, wolverines primarily reside in low elevation valleys in the western United States because wolverines tend to select higher elevations (Inman et al. 2012).

Because wolverines select high-elevation habitats, most core wolverine habitat in the western United States occurs on public lands. Young wolverines, however, often disperse long distances, including across valley bottoms, much of which is privately owned and subject to industrial, road, and housing development (Inman et al. 2012, Dilkina et al. 2016, Packila et al. 2017). Although these movements can place individuals at a greater risk to human-caused mortality (e.g., vehicle collision, incidental capture, poaching), there also is concern if wolverines avoid increasingly developed areas that once provided connectivity among important habitat. Management and conservation at the population scale include maintaining connectivity among alpine wolverine habitat in the western United States, restoring wolverines to areas of historical distribution, and monitoring the population (Inman et al. 2013).

The status of wolverines in the contiguous United States is a subject of debate. The wolverine was petitioned to be listed as an endangered species beginning in 1994, and related legal deliberations are ongoing (U.S. Fish and Wildlife Service [USFWS] 1995, 2010, 2017). Possible threats to the population identified in listing petitions and evaluations have included historical habitat loss, trapping, winter recreation, climate change, logging, road and housing development, seismic lines, mining, and wildland fire (USFWS 2017). Concerns about the effect and the uncertainties of climate change predictions on wolverine populations in the lower 48 states prompted a recognition that a better understanding of the current wolverine distribution would assist with wolverine management and conservation. The natural reestablishment, continued presence over decades during which harvest occurred, and recent expansion of the species, however, may suggest some resilience to human activities and landscape modification (Newby and McDougal 1964, Anderson and Aune 2008, Moriarty et al. 2009, Packila et al. 2017). Relatively few data exist to provide a clear understanding of whether the population distribution or status, or effects of purported threats on distribution or demographics, place the species at risk. No population monitoring program exists that is commensurate with the large scale at which the wolverine population of the western United States operates. Given this lack of monitoring, significant changes to the population distribution or status could occur and go unnoticed for years. In addition, factors contributing to any such changes would not be discernable.

Targeted monitoring is an integral component of effective wildlife management programs, serving to elucidate the status of a resource to help decide the appropriate course of action, evaluate the effectiveness of management actions relative to objectives, and provide feedback for learning to better achieve management objectives (Nichols and Williams 2006, Lyons et al. 2008). Because wolverines naturally occur at extremely low densities over large areas, monitoring is a daunting logistical task made more difficult by the species' use of remote, rugged terrain. The advent of remote wildlife camera surveys and availability of noninvasive genetic sampling have provided valuable tools for survey efforts; however, these efforts are often opportunistic, occur at small geographic extents relative to the population, and employ differing methodological approaches among survey areas that may inhibit interpretation of data to achieve meaningful population-level insights.

The field of occupancy estimation provides a structure for monitoring low-density species such as wolverines (MacKenzie et al. 2006). Occupancy models provide the opportunity to make several forms of inference. First, occupancy models provide an average estimate of the probability that a site is occupied by the species of inference. The occupancy estimate can be multiplied by the total number of sites to provide an estimate of the number of occupied sites, which gives a measure of distribution. Second, occupancy can be modeled as a function of site-specific covariates. Relationships to landscape measures provide a means of predicting occupancy of sites that have not been surveyed. They also present a way to test hypotheses about relationships between the species of interest and those covariates. Third, spatial occupancy models provide a means to use the spatial arrangement of sites to help estimate occupancy under the hypothesis that neighboring sites are likely to be more similar than distant sites (Johnson et al. 2013). Moreover, occupancy models fit in a Bayesian framework provide a straightforward approach to estimating the probability of occurrence of a species within subsets of the entire study area. Occupancy modeling has been applied to wolverine populations in Canada and Alaska (Magoun et al. 2007, Gardner et al. 2010, Whittington et al. 2015, Ray et al. 2018).

Our objectives were to develop a repeatable framework for monitoring wolverines across the western United States and to use that framework to establish a contemporary estimate of wolverine distribution. Specifically, we defined the current

distribution in Idaho, Montana, Washington, and Wyoming, identified potential gaps in distribution where restoration efforts could be considered, established a system to monitor changes over time in occupancy and genetic composition, and provided a baseline dataset that will allow use of data from future surveys to analyze factors that may influence occupancy (e.g., climate, road density) and genetic changes.

We also attempted to extract additional insights from the data, despite the design being optimized for exploring spatial distribution and, therefore, not being ideal for testing some of these subsequent hypotheses. First, we sought to understand how amount of predicted habitat defined by a composite of 2 habitat models (Copeland et al. 2010, Inman et al. 2013) influenced wolverine occurrence. We predicted that occupancy would be higher in areas comprised of more predicted habitat. Second, we wanted to understand the relationship between wolverine occupancy and human development and disturbance. We predicted that wolverine occupancy would be lower in areas with more human-modified areas. Third, we wanted to consider how vegetative productivity related to wolverine occupancy probability. We predicted that wolverine occupancy would increase with the normalized difference vegetation index (NDVI), which provided an index of green vegetation. Finally, we sought to understand how the size of predicted habitat patches influenced wolverine occupancy probability. We predicted that larger patches of contiguous predicted habitat would result in higher probability of wolverine occupancy.

STUDY AREA

We sampled areas dominated by predicted wolverine habitat within the generally accepted current extent of resident, breeding wolverine populations in the contiguous United States, including the Rocky Mountains of Montana, Wyoming, and Idaho and the Cascade Mountains in Washington (Fig. 1; Aubry et al. 2007, Copeland et al. 2010, Inman et al. 2013).

METHODS

We overlaid a 15-km × 15-km grid across a composite model of wolverine habitat comprised of persistent spring snow (Copeland et al. 2010) and habitat (Inman et al. 2013; i.e., modeled wolverine habitat). This 225-km^2 grid size is roughly equivalent to the size of resident female home ranges of wolverines in the Greater Yellowstone Ecosystem (Inman et al. 2012). We included cells that overlapped modeled wolverine habitat by ≥50% in our sampling frame, and used expert knowledge to add cells (e.g., <50% habitat within the cell but continuous with a larger block of habitat across adjacent cells) or delete cells (e.g., Olympic Peninsula with no historical wolverine occurrence) from the frame. Our final sampling frame included 633 cells across the 4 states. We used the generalized random tessellation stratified (GRTS) sampling procedure (Stevens and Olsen 2004) implemented in the R package spsurvey (Kincaid et al. 2017) to generate a spatially balanced ranked list of the 633 cells. We defined a sample size of 185 based on a power analysis conducted prior to the survey and selected the first 185 ranked grid cells to sample with remotely triggered cameras coordinated by field crews in each state (Table 1; Fig. 1).

Camera Stations

Our sampling occurred during 4 1-month intervals beginning 1 December and ending 31 March. All sampling occurred during winter 2016–2017 in Washington, Idaho, and Montana. Wyoming split sampling geographically and temporally, sampling the southern half of their cells in winter 2015–2016 and the remaining cells in winter 2016–2017 coincident with the other states. Prior to 1 December, we

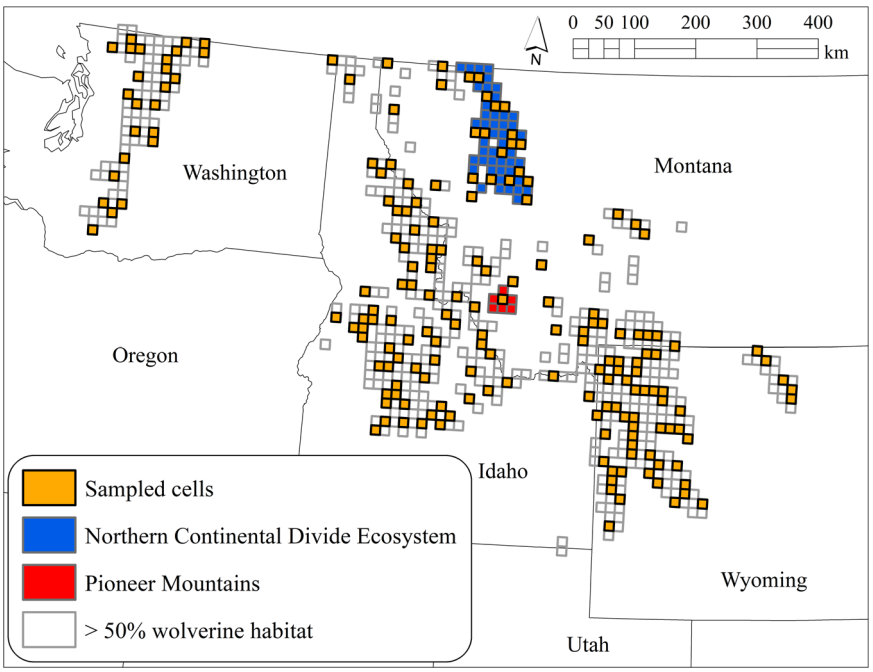

Figure 1. Sampling frame and selected cells (yellow) for the wolverine survey across Washington, Idaho, Montana, and Wyoming, USA, 2016–2017. The Pioneer Mountains are indicated in red and the Northern Continental Divide is indicated in blue as examples for small area estimation.

Table 1. Summary statistics for a multi-state wolverine camera trapping survey during winters of 2016 (WY only) and 2017.

State	Cells	Wolverine photo detections	Survey cells with detections	Supplemental cells with detections	Cells with sex identification[a]
ID	59	10,165	21	1	14
MT	48	7,114	23	24	32
WA	26	3,622	9	4	4
WY	52	1,740	6	2	3
Total	185	22,641	59	31	53

[a] Official survey and supplemental cells.

placed 1 camera station in each 15-km × 15-km sampling cell. All cameras were located within modeled habitat. Beyond that, we established a ruleset that prioritized centrality within the cell, access throughout the winter, high-quality wolverine microsite, outside designated wilderness, greater distance to adjacent stations, and greater distance to roads and trails. Cameras that fell within wilderness areas followed a Minimum Requirements Decision Guide (MRGD) analysis approved by United States Forest Service Regional Foresters in Regions 1, 2, 4, and 6 in 2017. No cells sampled in 2015–2016 occurred in wilderness.

We deployed 2 types of camera stations (i.e., a camera plus all associated sampling accessories). Both types of stations consisted of a single camera (Reconyx PC800 Hyperfire, Holman, WI, USA) cabled to a tree and pointed at a bait or lure tree approximately 4–6 m away. Accessible stations, those that could be reached throughout the winter, included meat bait (roadkill game or beaver [*Castor canadensis*] carcasses) wired to the bait tree 1–1.5 m above winter snow height, a long call scent lure for wolverine (Western States Wolverine Working Group 2018), a lynx (*Lynx canadensis*) lure (Western States Wolverine Working Group 2018), and gun brushes (cylindrical, wire-bristled, brushes) to snag hair for DNA (Kendall and McKelvey 2008). We revisited accessible stations monthly to refresh bait and scent, collect hair samples, collect photo data, replace camera batteries as needed, and move components higher up the tree as snow accumulated. Visits were approximately 30 days apart and based on date of deployment. Inaccessible stations were those too remote to visit in winter; we deployed these stations in late fall and did not revisit them until snow receded the following summer. In place of bait, we used a scent dispenser (R. A. Long, Woodland Park Zoo, Seattle, WA, USA) that dripped liquid wolverine lure onto a cow femur bone each day. We intentionally deployed inaccessible station components 2.5–3.5 m high in anticipation of snow accumulation. We mounted cameras at inaccessible stations sideways to orient the detection zone vertically rather than horizontally to encompass the greater distance from ground level to scent dispenser.

Camera settings (e.g., number of photos/trigger, quiet period between triggers, sensor sensitivity) were standardized across the study area and did not differ between accessible and inaccessible stations (Western States Wolverine Working Group 2018). We used 2 gun brush arrays at all stations. A group of 4 brushes was centered approximately 0.3 m below the bait or bone. We incorporated a second gun brush array approximately 0.4 m above ground level on the bait or lure tree to increase the likelihood of incidentally detecting Canada lynx. We secured gun brushes to the bait or lure tree with a corrugated plastic collar (P. Figura, California Department of Fish and Game, personal communication) or similar belt-type fastener (e.g., web belt). The state wildlife agencies in Idaho, Montana, Washington, and Wyoming approved the protocols used in this study.

Genetic Analyses

We used a decision tree (Western States Wolverine Working Group 2018) to select hair samples from target and non-target carnivores to submit to the National Genomics Center for Wildlife and Fish Conservation (NGC), Missoula, Montana, USA. We extracted genomic DNA using the QIAGEN Dneasy Blood and Tissue kit (Qiagen, Hilden, Germany) using modifications for hair samples (Mills et al. 2000). We first identified samples to species using the 16srRNA region of mitochondrial DNA. We analyzed wolverine-positive samples with sufficient-quality DNA for haplotype (using the control region of mitochondrial DNA; Wilson et al. 2000), sex (SRX/SRY analysis designed for wolverine [Hedmark et al. 2004] with internal controls for DNA quality), and individual (using 15 microsatellite loci; Schwartz et al. 2009).

Supplemental Camera and DNA Stations

We encouraged other organizations to participate in the survey by running independent camera stations. These additional stations ranged from professional deployments by agency and non-governmental organization biologists during the course of independent carnivore research, to deployments by volunteers. Participants placed supplemental cameras in grid cells not previously selected by GRTS procedure. Professional deployments generally followed the protocol established by the 4 states. Volunteer-run stations typically followed a less rigorous protocol that allowed for a later deployment (Jan or Feb), different camera models, a shorter active period, and no DNA collection. Overall, 56 supplemental camera stations were deployed. We did not use supplemental wolverine detections as part of the occupancy estimate because they were not drawn from the GRTS sample. We mapped supplemental detections in our results, in essence replacing a predicted occupancy probability in an unsampled cell (0.0–1.0) with known presence of the species in the grid cell (1.0).

Statistical Analysis

We imported photos collected from our sampling effort into CPW PhotoWarehouse (Ivan and Newkirk 2016) for

storage, organization, and to facilitate efficient identification of species within them. Two independent observers in each state classified each image to species. Observers flagged images when they did not agree, and a referee (usually the project manager for the state) reviewed them to determine identification. We analyzed the wolverine photo data using non-spatial and spatial occupancy estimation methods (MacKenzie et al. 2006, Johnson et al. 2013). We fit occupancy models to the sampled sites and imputed the remaining sites that we did not sample (excluding supplemental camera data) using a Bayesian implementation of the occupancy models (Kéry and Schaub 2012, Johnson et al. 2013). For the purposes of analysis, we divided the survey period into 4, 30-day sampling occasions beginning 1 December of the survey year so that we then had a 4-occasion encounter history for each camera site.

Based on *a priori* hypotheses developed by a panel of wolverine experts and the survey design team prior to implementation of the survey, we considered 4 covariates for probability of occupancy (ψ) in the non-spatial occupancy models. We included proportion of the cell containing predicted wolverine habitat, proportion of the cell containing human-modified land as defined by Theobald (2013), mean integrated NDVI (Pettorelli 2013), and size of habitat block (count of contiguous cells of predicted habitat). The habitat models used contain important wolverine habitat correlates such as snow. We chose not to include individual covariates contained in these models because we already reduced the observed range of the covariates to areas where wolverines are likely to occupy. Therefore, an analysis based on our monitoring design would greatly reduce power to detect a relationship with those covariates. We centered all covariates to have mean = 0 and scaled to have variance = 1. We included the covariates as a logit-linear function of ψ. We used normally distributed prior distributions for the intercept and slopes of the logit-linear model with mean = 0 and precision (τ) = 0.001. We fit a single model including all covariates on ψ.

We considered 3 forms of the detection probability parameter (p) in the non-spatial occupancy model. We held p constant, allowed p to vary by month, and included a binary indicator of whether a camera site was in an accessible area (included bait and was resupplied monthly) or in inaccessible area (included a scent dispenser and was not revisited during the survey period). We used normally distributed prior distributions for the intercept and slopes of the logit-linear model with mean = 0 and precision (τ) = 0.001.

We recognize that wolverines are highly mobile and our sampling frame did not align exactly with home ranges of individuals. Thus, we violated the assumption of closure one must make when estimating occupancy. Consequently, our estimate of ψ should be interpreted as the probability that a given cell (or camera station) was used by ≥1 wolverine during the course of the survey, and p is the joint probability that an individual was both available and detected during a given occasion.

We fit non-spatial occupancy models in JAGS (Plummer 2003). We ran each model for 10,000 iterations of 3 chains with 5,000 iterations discarded as burn-in. We examined trace plots of chains and used the $\hat{R}$ statistic to test for Markov chain Monte Carlo (MCMC) chain convergence. We used Bayesian *P*-values to determine adequacy of model fit.

We fit spatial occupancy models to account for variation in occupancy probability across the study area that our covariates could not explain (Johnson et al. 2013). We considered only predicted wolverine habitat as a covariate on ψ for the spatial model and we held detection probability constant based on results from the non-spatial model. We fit the spatial occupancy model in R using the stocc package (Johnson et al. 2013). We used a threshold of 20 km for the spatial model and an independent conditional autoregressive function (Johnson et al. 2013). We ran the MCMC chains for 100,000 iterations.

We estimated local scale, mountain range in our example, occupancy and numbers of occupied cells to provide an example of small area estimation from this survey. To estimate the probability that ≥1 cell in a set of cells was occupied, we used the imputed occupancy of each cell in the set from all of the MCMC replicates. We then summed the number of times ≥1 cell was occupied and divided by the number of MCMC replicates. To estimate the number of occupied cells, we summed the number of occupied cells in the set and divided by the number of MCMC replicates. As an example of the probability of ≥1 occupied cell, we used 7 cells covering the Pioneer Mountains (Fig. 1). As an example of the number of occupied cells we used the Northern Continental Divide Ecosystem (Fig. 1).

Finally, we examined our survey design to determine what level of effort (number of cells) is needed to achieve varying levels of precision. To do so, we used our survey as a baseline level of effort. We then considered surveys with 0.5, 0.75, 1.25, and 1.5 times as much effort. We sampled from our data with replacement to obtain a sample corresponding to those levels of effort. We then calculated the mean coefficient of variation on the estimated number of occupied sites (based on repeated sampling at each effort level 10 times) as a measure of resulting precision.

RESULTS

Across all 4 states we obtained results from 183 of the 185 official survey camera and DNA stations. One camera in Idaho was stolen and 1 camera in Montana burned in a wildfire. We detected wolverines in 59 of these 183 cells (34%; Table 1; Fig. 2). We detected wolverines at 50 stations with both cameras and DNA, 11 stations with camera only, and in 1 cell with DNA only (we collected genetic material from a track in route to checking the camera station). We obtained 439,834 photos during the survey, of which 22,641 photos contained wolverines. At many stations, the bulk of the photos were from the same wolverine repeatedly passing in front of the camera over a

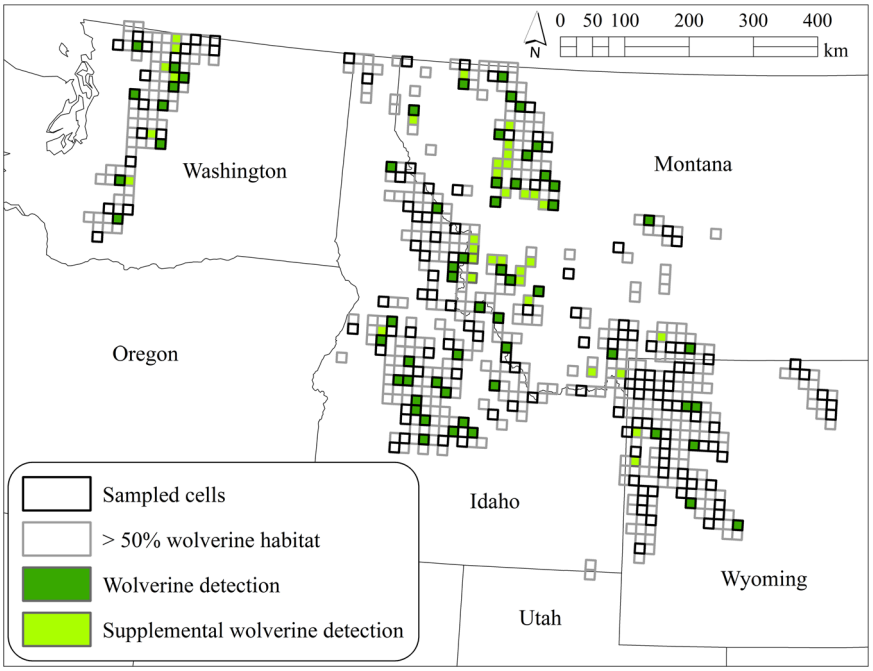

Figure 2. Wolverine detections across a 4-state area, USA, in winters 2016 and 2017.

short time. Wolverines were detected via camera or DNA at another 31 supplemental stations for 93 cells with positive detections (Fig. 2).

We obtained 1,439 DNA samples and identified the species of 81% of these samples (Table 2). We identified (detected) wolverine from 240 DNA samples obtained during the survey period, which included 202 samples from 51 official survey stations and 38 samples from 18 supplemental stations. Of these wolverine-positive samples, 145 (60%) were of sufficient quality to determine sex and to identify individual. Both males and females were broadly distributed (Fig. 3). We identified 26 unique females and 24 unique males. Mitochondrial DNA analysis of the control region showed regional structuring. All of the wolverine samples in Montana, Wyoming, and Idaho were haplotype Wilson A, the most abundant and widely occurring wolverine haplotype in North America (Wilson et al. 2000, Schwartz et al. 2009, McKelvey et al. 2014). In contrast, all the samples in Washington assigned to haplotype Wilson C.

Table 2. Species detected from DNA analysis of hair samples obtained at camera stations and number of detections for each species in the western United States, 2016–2017.

	Number of detections		
	Official	**Supplemental**	**Total**
Wolverine	202	38	240
Lynx	17	1	18
Fisher (*Pekania pennanti*)	16	0	16
Marten (*Martes americana*)	449	24	473
Red fox (*Vulples vulpes*)	97	7	104
Other species	302	12	314
DNA did not amplify	253	21	274
Total	1,336	103	1,439

Occupancy models fit the data well. The model converged for all parameters ($\hat{R} < 1.002$ for each parameter). There was no evidence of lack of fit for the model (Bayesian *P*-value = 0.568). Correlation among covariates was low (≤0.21) between all pairs of covariates.

We estimated detection probability per month to be 0.47 (95% CI = 0.39–0.54) in the non-spatial model. The overall probability of a wolverine being detected at least once at a site that was occupied during the survey period was 0.92. There was evidence of lower detection probability in December, but the overall high detection rate did not result in any change in estimated occupancy with different forms of the detection model. There was no evidence of a difference in detection for sites that were run with the accessible versus inaccessible protocols ($\beta = -0.19 \pm 0.56$ [SE]).

Mean occupancy was 0.33 (95% CI = 0.27–0.39) in the non-spatial model. Proportion of predicted habitat in the cell was weakly positively associated with occupancy ($\beta = 0.26 \pm 0.18$ [SE]; Table 3). All of the other covariates (% human-modified, NDVI, and patch size) showed no relationship with occupancy. Based on this occupancy estimate, the expected number of cells used by wolverines during the survey period was 208 (95% CI = 169–249). When the supplemental cells were included, the estimated number of occupied cells was 231 (95% CI = 194–271).

The spatial occupancy model produced a detection probability estimate of 0.42 ± 0.03, which was slightly lower than the non-spatial model. Despite the small reduction, the chance of detecting a wolverine at least once in an occupied cell (0.89) remained high.

The spatial occupancy model allowed patterns in wolverine occupancy across space to emerge (Fig. 4). Occupancy probability was highest in the Northern Continental Divide Ecosystem (ψ per cell range = 0.8–1), intermediate in

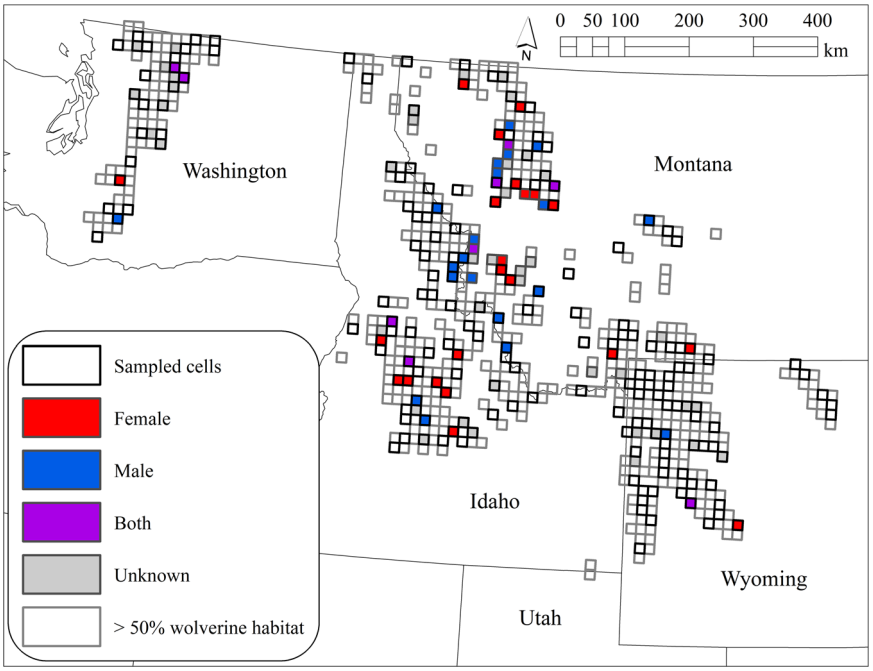

Figure 3. Sex of wolverines detected by DNA at generalized random tessellation stratified-selected and supplemental stations in Idaho, Montana, Washington, and Wyoming, USA, winters 2016 and 2017.

the Cascades and Central Mountains of Idaho (ψ range = 0.4–0.6), and lower in the Greater Yellowstone Ecosystem (ψ range = 0.1–0.3). Similarly, by state, Montana had the highest occupancy probability ($\psi = 0.6$), Idaho and Washington were intermediate ($\psi = \sim 0.4$), and Wyoming was lower ($\psi = 0.15$; Table 4). Uncertainty at the individual cell level was high, but overall inferences to patterns in occupancy were strong. Coefficients of variation ranged from 0.15 for the entire study to 0.1 to 0.3 for the state-level estimates.

We estimated local-scale occupancy as an example of small area estimation from this study. In the Pioneer Mountains, where 1 cell was sampled, the estimated probability of ≥ 1 cell out of the 7 in the mountain range being occupied was 0.06 ± 0.2 (SD). In the Northern Continental Divide Ecosystem, where 18 of the 66 cells covering the ecosystem were sampled, the estimated number of occupied cells was 59 ± 8 (SD).

The bootstrap analysis of survey effort showed precision increased as a function of the square root of sample size as expected by statistical theory (Fig. 5). A survey with half the number of cells would produce a coefficient of variation of 0.16 and 1.5 times the effort reduced the coefficient of variation to 0.08. The lack of evidence of a difference between bait and scent dispensers also provides guidance on reducing survey costs because whichever method costs less could be used.

Table 3. Posterior distribution summaries for parameters from non-spatial occupancy models for wolverines in Idaho, Montana, Washington, and Wyoming in 2016 and 2017.

			Quantile				
Parameter[a]	$\bar{x}$	**SD**	**2.5**	**25**	**50**	**74**	**97.5**
Detection							
Intercept	0.47	0.04	0.39	0.44	0.47	0.50	0.55
Bait or scent	−0.20	0.56	−1.28	−0.58	−0.21	0.19	0.89
Occupancy							
Intercept	−0.73	0.18	−1.08	−0.85	−0.73	−0.62	−0.39
Habitat	0.26	0.18	−0.09	0.13	0.25	0.38	0.62
Human	0.16	0.18	−0.18	0.04	0.16	0.28	0.54
NDVI	0.17	0.18	−0.18	0.05	0.17	0.28	0.52
Cluster	−0.02	0.18	−0.37	−0.14	−0.02	0.09	0.33

[a] Habitat is the proportion of predicted wolverine habitat in the cell, human is the proportion of human-modified land in the cell, NDVI is the normalized difference vegetation index, and cluster is the count of contiguous cells of predicted habitat.

DISCUSSION

We present an evaluation of the distribution of wolverines in a 4-state region of the western United States for the first time since historical extirpation nearly a century ago. The results provide a population-scale evaluation of occupancy for wolverines in the western United States, confirming much of what experts in local areas suspected or knew about wolverine distribution but had never studied at this large scale. Moreover, the results demonstrate expansion into areas such as the southern Cascade Mountains in Washington and Wind River Range in Wyoming as compared to records of wolverines from 1995–2005 presented by Aubry et al. (2007). The survey results provide a strong baseline for future work and a quantitative assessment to compare future change in wolverine distribution. We have identified areas of potential wolverine habitat with low occupancy, such as northern Idaho, the Wyoming Range, and Big Horn Mountains. We also demonstrated that all of the large areas of predicted wolverine habitat contain wolverines.

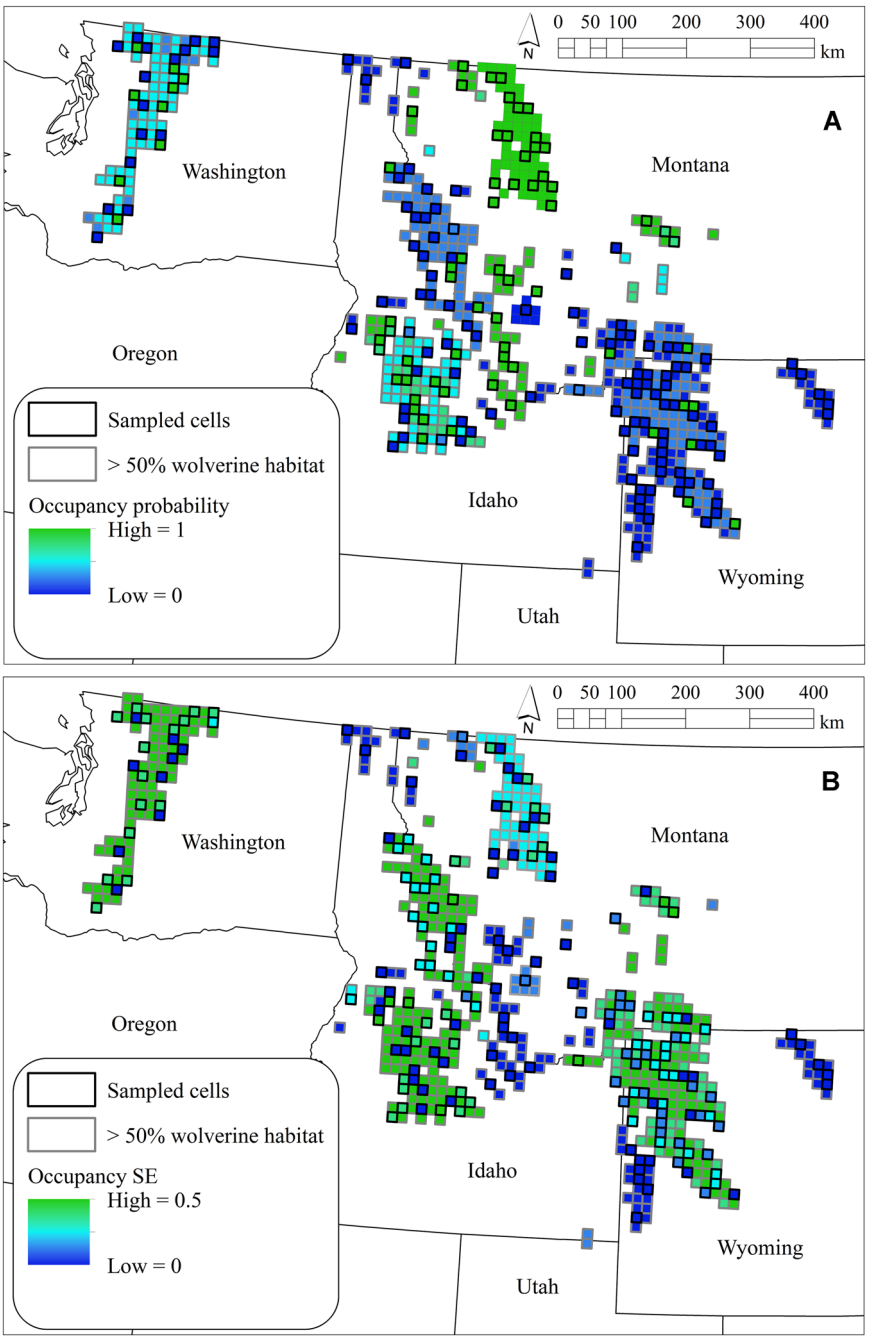

Figure 4. Results from a spatial occupancy model for wolverine occupancy in Idaho, Montana, Washington, and Wyoming, USA, 2016 and 2017. The color ramp represents probability of occupancy on plot (A) and standard error on plot (B). Cells with detected wolverines are shown as an occupancy = 1 and standard error = 0.

Table 4. Wolverine occupancy model estimates, lower credible limit (LCL), and upper credible limit (LCL) by state from the spatial occupancy model. Estimates were based on the total number of available sampling cells within each of the 4 states, 2016–2017.

		Occupied cells			Occupancy probability		
State	Cells	Estimate	LCL	UCL	Estimate	LCL	UCL
ID	189	87	65	112	0.46	0.34	0.59
MT	194	117	85	132	0.60	0.44	0.68
WA	93	40	21	62	0.43	0.23	0.67
WY	157	24	11	41	0.15	0.07	0.26
Total	633	268	182	347	0.42	0.29	0.55

Our results demonstrate that wolverine occupancy varies across ecosystems in the western United States. The Northern Continental Divide Ecosystem in Montana showed the highest predicted occupancy, with nearly complete use of 15-km × 15-km cells in the Glacier National Park and Bob Marshall Wilderness complex. Central Idaho and the Cascade Mountains in Washington showed an intermediate occupancy rate. The Greater Yellowstone Ecosystem had a lower occupancy, with the rate further decreasing to the south (Wyoming Range) and east (Big Horn Mountains). The spatial variation in occupancy opens several questions about why wolverines may be more

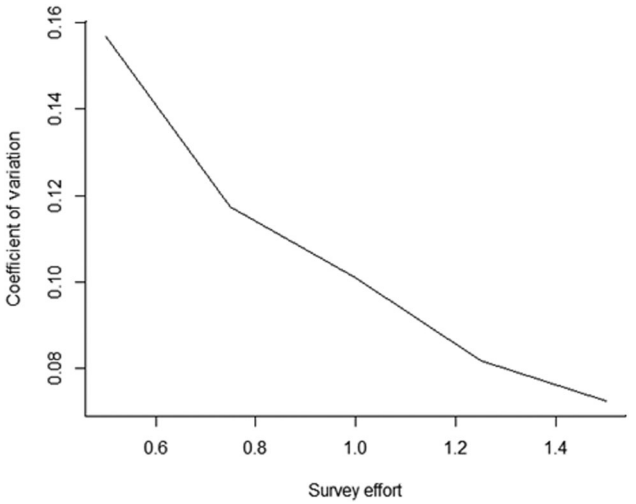

Figure 5. Resulting coefficient of variation on the estimated number of occupied sites for wolverine monitoring as a function of effort in Idaho, Montana, Washington, and Wyoming, USA, 2016 and 2017. Survey effort = 1 represents the study reported in this paper (183 camera stations). Effort is represented as a proportion of that survey.

prevalent in northern Montana than southern Wyoming. Hypotheses for these differences include slow recovery from population extirpation in the nineteenth century starting from the north where they are more abundant and moving south and habitat differences allowing for denser populations in the north (Anderson and Aune 2008). In addition, it is possible that we sampled some areas that are not suitable wolverine habitat in the Greater Yellowstone Ecosystem. Predicted habitat between the 2 models that were combined to create our sampling frame diverged most in the Greater Yellowstone Ecosystem, specifically the interior of Yellowstone National Park. Historical records (Aubry et al. 2007) and recent surveys (Murphy et al. 2011) have consistently indicated the interior of Yellowstone Park does not have resident wolverines despite residents nearby for decades. Sampling of areas that were incorrectly predicted as habitat could have produced lower estimates in that ecosystem.

We estimated occupancy for wolverines in winter. At other times of year, wolverines may use a broader area than they do during the winter. For example, wolverines tended to travel greater distances in spring and summer in northwestern Montana (Hornocker and Hash 1981). Copeland et al. (2007) reported that wolverines in Idaho used higher elevations in summer than in the winter. Their results suggest that our sampling frame would encompass much of the summer and winter habitat. Finally, absence of bears (*Ursus* spp.) in winter presents a major advantage for winter surveys. Bears tend to consume baits quickly when they are active.

We examined the relationship of several covariates to wolverine occupancy. Testing habitat relationships was a secondary objective of this study; therefore, we designed our sampling to optimize precision for of an overall occupancy estimate, not to detect covariate relationships. The study design predisposed us to have low power to detect covariate relationships. We found no association with vegetative productivity, human disturbance, and habitat patch size. Our sampling design may have limited our ability to detect those effects because the sampling frame was based off models of predicted wolverine habitat. The models placed the sampling frame in areas with higher elevations, less human disturbance, and more forest than the 4 states surveyed contain in general. The restricted range of covariate values observed may have had more influence on the lack of importance than any other reason. In addition, the scale of the sampling cell, 15 km × 15 km, also averages over a large area of variable conditions; therefore, single values of covariates at that scale may show dampened relationships as compared to fine-scale resource selection.

We provided a survey protocol for future surveys. The protocol is statistically rigorous and viable in rugged, winter field conditions. We established a sampling frame based on prior knowledge of wolverine habitat use from den locations (Copeland et al. 2010), telemetry studies (Inman et al. 2012), and expert opinion. We demonstrated that cells selected using a probability sampling scheme can be surveyed even in remote wilderness areas. The camera and lure protocol we used was very effective for detecting wolverines given they were present.

The Bayesian analyses used for this survey provide a direct method for small area estimation and the broader scale results presented here. The analysis provided a posterior distribution for each cell in the survey area. These posterior distributions can be used to estimate the proportion of a given area occupied by wolverines or the probability that any given set of cells is occupied by wolverines. For example, if managers in a specific national forest wanted to know the probability of ≥1 wolverine occurring on that forest, the posterior distributions for each cell in the national forest could be combined to answer the question. If more certainty is required about the extent of wolverine occupancy in a given area than would be provided by a random selection of cells across the larger frame, certain areas can be sampled more intensively. For example, we estimated a 0.06 probability that a wolverine used the Pioneer Mountains in Montana during the survey, based on 1 sampled cell in this local area, and a wolverine was detected in this mountain range by a supplemental camera station shortly after the survey period ended. This was not totally unexpected, however, because the uncertainty in this estimate (0.2) was high and could be reduced with more intensive sampling. As long as the more intensive local sampling is randomized in coordination with selection of the broader study design, estimates and models of occupancy and detection probability can proceed in the same analysis.

This wolverine survey provides a demonstration of collaboration at the species-distribution scale for proactive conservation. Representatives from multiple state wildlife agencies, the Forest Service, National Park Service, USFWS, Confederated Salish and Kootenai Tribes, nongovernmental agencies, and 2 universities worked together from project development to implementation to analysis. Wolverine populations function at a scale far larger than

that for which any 1 entity has jurisdiction or could afford to operate (Ellis et al. 2014). Multi-agency collaboration provided a strong result and created a framework for future monitoring. We suggest that this collaborative process is useful for other species.

This occupancy survey and modeling approach has been designed to feed directly into a wolverine conservation program focused on maintaining the distribution of wolverines throughout suitable habitat. The occupancy models resulting from this survey can be used to generate maps of the estimated area occupied by wolverines at large and small scales, provide quantitative and spatial predictions of the effects of management actions on wolverine occupancy that can be used to inform actions by state and federal decision makers, and provide a framework for repeated monitoring to evaluate the effects of management in the future, after decisions are implemented. For this survey and analysis, we considered the effects of predicted habitat (from existing models), human development, vegetation productivity, and habitat patch sizes on wolverine occupancy. Future iterations and analyses can also estimate the effects of incidental and regulated harvest, translocations, habitat conservation focused on maintaining connectivity among high-elevation habitats, and even loss of snowpack due to climate change on wolverine occupancy. Although it will not provide a direct test of the effects of climate change on wolverine populations, our work has shown that we can assess changes in occupancy in relation to changes in the number and distribution of occupied cells within our study area. These additional factors represent primary uncertainties about the effects of human actions on wolverine distribution across large spatial scales into the future. Therefore, this occupancy modeling approach could be used in the design of an adaptive management program whereby uncertainty in the definition of suitable wolverine habitat and effects of management on wolverine occupancy can be reduced over time. We can explore the utility of such a program via expected value-of-information analyses, estimating the extent to which the conservation of wolverines can be improved by implementation of adaptive management to reduce uncertainty (Runge et al. 2011) and design future implementations of this survey framework for this purpose. Because of the large-scale nature of this survey effort and the partnerships built to implement it, we have an unprecedented opportunity to work on wolverine conservation across their range in the contiguous United States (and perhaps beyond), with coordination among all the government agencies with jurisdictional responsibilities.

MANAGEMENT IMPLICATIONS

Wildlife managers now have a strong baseline estimate of wolverine occupancy in a 4-state rejoin at the southern edge of wolverine distribution. The information provides a starting point to evaluate changes through time. The survey design also provides a strong foundation for future efforts to understand wolverine distribution throughout the region.

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