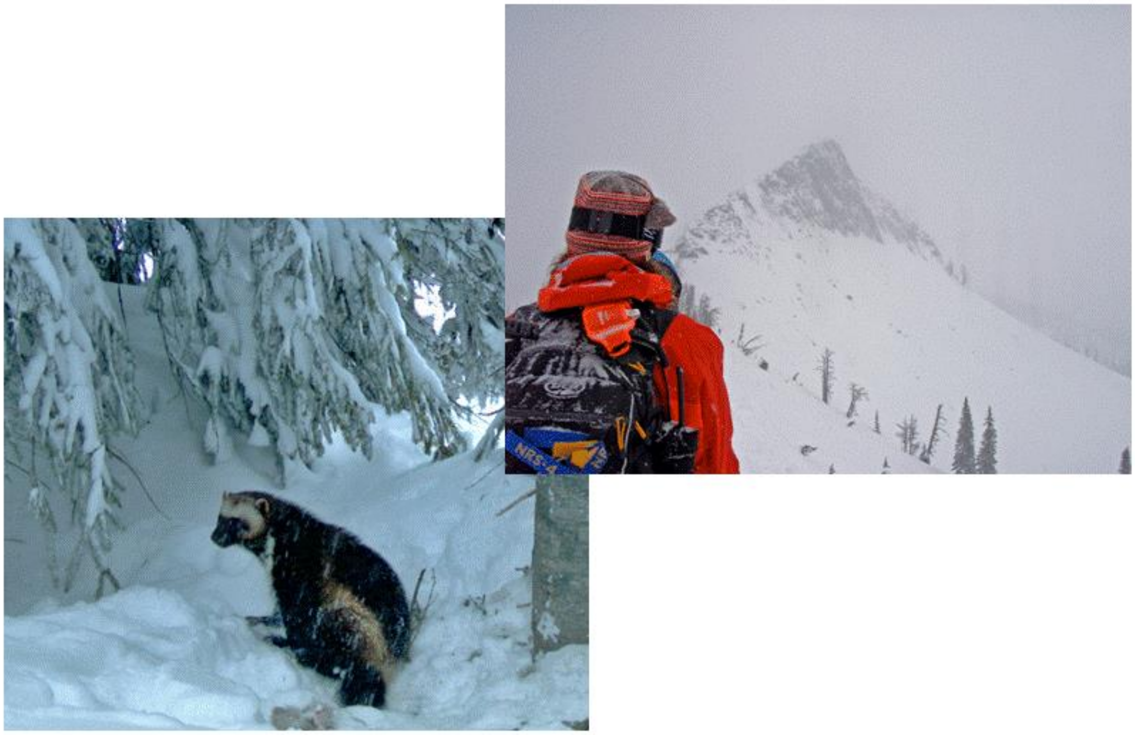
WOLVERINE – WINTER RECREATION RESEARCH PROJECT:
INVESTIGATING THE INTERACTIONS BETWEEN WOLVERINES AND WINTER RECREATION

FINAL REPORT



December 15, 2017

Heinemeyer, Kimberly S.[1], John R. Squires[2], Mark Hebblewhite[3], Julia S. Smith[1],
Joseph D. Holbrook[2], and Jeffrey P. Copeland[2,4]

[1] *Round River Conservation Studies, 104 E. Main St, Bozeman, MT 59715*
[2] *Rocky Mountain Research Station, United States Forest Service, Missoula, MT 59802*
[3] *Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, W. A. Franke College of Forestry and Conservation, University of Montana, Missoula, MT, 59812*
[4] *Current affiliation: The Wolverine Foundation, 4444 Packsaddle Rd, Tetonia, ID 83452*

WOLVERINE – WINTER RECREATION RESEARCH PROJECT:

INVESTIGATING THE INTERACTIONS BETWEEN WOLVERINES AND WINTER RECREATION

FINAL REPORT

DECEMBER 15, 2017

HEINEMEYER, KIMBERLY S.[1], JOHN R. SQUIRES[2], MARK HEBBLEWHITE[3], JULIA S. SMITH[1],
JOSEPH D. HOLBROOK[2], AND JEFFREY P. COPELAND[2,4]

WITH THE SUPPORT OF PROJECT PARTNERS AND COLLABORATORS INCLUDING:

BOISE, BRIDGER-TETON, CARIBOU-TARGHEE, PAYETTE AND SAWTOOTH NATIONAL FORESTS
IDAHO DEPARTMENT OF FISH AND GAME
LIZ CLAIBORNE ART ORTENBERG FOUNDATION
THE WOLVERINE FOUNDATION
UNIVERSITY OF MONTANA
GRAND TETON NATIONAL PARK
WYOMING DEPARTMENT OF GAME AND FISH
US FISH AND WILDLIFE SERVICE
IDAHO STATE SNOWMOBILE ASSOCIATION
BRUNDAGE MOUNTAIN RESORT
GRAND TARGHEE RESORT
JACKSON HOLE MOUNTAIN RESORT
CENTRAL IDAHO RECREATION COALITION
DEFENDERS OF WILDLIFE
THE SAWTOOTH SOCIETY
THE WINTER RECREATION COMMUNITIES OF CENTRAL IDAHO AND WESTERN YELLOWSTONE.

[1] *Round River Conservation Studies, 104 E. Main St, Bozeman, MT 59715*
[2] *Rocky Mountain Research Station, United States Forest Service, Missoula, MT 59802*
[3] *Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, Colege of Forestry and Conservation, University of Montana, Missoula, MT, 59812*
[4] *Current affiliation: The Wolverine Foundation, 4444 Packsaddle Rd, Tetonia, ID 83452*

Acknowledgements

We are grateful to our multiple partners and collaborators who have assisted the project in numerous ways. Funding, equipment and logistical support for the project has been contributed by the US Forest Service, Liz Claiborne Art Ortenberg Foundation, Round River Conservation Studies, Idaho Department of Fish and Game, The Wolverine Foundation, Wyoming Department of Game and Fish, Idaho State Snowmobile Association, Sawtooth Society, the Nez Perce Tribe and the University of Montana. Several additional organizations have supported the project through assisting with the hand out of GPS units to winter recreationists including: Brundage Mountain Resort, Jackson Hole Mountain Resort, Grand Targhee Resort, Sun Valley Heli Ski, Teton Backcountry Guides and numerous local businesses in the towns of Cascade, Driggs, Fairfield, Island Park, McCall, Stanley, Sun Valley and Victor in Idaho and Jackson, Wyoming.

The project would not have been possible without individuals within our partnering agencies who tirelessly assisted the project in numerous ways. In particular, we thank Diane Evans Mack and Rob Cavallaro (IDFG), Tammy Fletcher (Caribou-Targhee National Forest), Ana Egnew (Payette NF), Lisa Nutt and Joe Foust (Boise NF), Robin Garwood (Sawtooth NF), Gary Hanvey and Kerry Murphy (Bridger-Teton NF) and Aly Courtemanch (Wyoming Game and Fish) for diligently ensuring the success of the project. We also want to thank Mark Drew, veterinarian at IDFG for supporting safe handling of wolverines. Many additional agency personnel assisted us – we thank you for your assistance and support. A large amount of effort is invested behind the scenes in personnel, project and financial management, and we are grateful to Kathleen Wilson at Round River Conservation Studies for always cheerfully handling these often thankless but critical tasks. We thank Lucretia Olson and Dennis Sizemore for advising and commenting on earlier versions of this report.

The backbone of the research is high quality data collection under sometimes challenging conditions, and we are indebted to our hard-working field crew, many of whom worked multiple winters on the project: Blakeley Adkins, Matt Amick, Isaac Babcock, Anne Blackwood, Kristina Boyd, Grace Carpenter, Llona Ney Clausen, Drew Chambers, Chris Cole, Jeff Copeland, Jim Corbet, John Councilman, Katie Coyle, Ross Dorendorf, Danielle Fagre, Tony Folsom, Gary Gadwa, Tom Glass, Erica Goad, Sierra Groves, Jessica Haas, Dylan Hopkins, Brooklyn Hudson, Zack Huling, Lindsay Jones, Rollie Jones, Shannon Jones, Suzanne Johnston, Tyler Kaebisch, Matt Kasprzak, Chris Klingler, Kyle Krapster, Tulley Mackey, Scott Martin, Alex May, Madison McConnell, Cy McCullough, Josh Metten, Nick Miller, Ryan Mong, Celina Moreno, Katy Nelson, Zoe Nelson, Ben Rooney, Rachel Rubin, Joel Ruprecht, Toni Ruth, Kristen Sellmer, Molly Shuman-Goodier, Will Tyson, Carson White, and Jarrod Zweigart. Your commitment, professionalism and good humor made the project not only successful, but also good fun.

We thank the thousands of recreationists who agreed to carry funny little orange data loggers while out having fun and who took the time to return them to us. Your contribution provides a critical foundation to the project. Finally, we thank the wolverines who also carried funny, little data loggers for us, and who have taught us so much.

Table of Contents

Acknowledgements ____ *i*

Executive Summary ____ *iv*

Introduction ____ *1*

Methods ____ *5*

- **Study Area** ____ **5**
- **Wolverine capture and monitoring** ____ **7**
- **Resource Selection Function Analyses** ____ **8**
- **Location data and home range analyses** ____ **9**
- **Environmental variables** ____ **10**
- **Winter recreation sampling and models** ____ **10**
- **Model Selection** ____ **12**
- **Comparing potential and realized habitat quality** ____ **13**
- **Functional responses to winter recreation** ____ **14**

Results ____ *15*

- **Wolverine trapping and location data** ____ **15**
- **Recreation Monitoring** ____ **16**
- **Environment resource selection function** ____ **24**
- **Environment and winter recreation resource selection functions** ____ **26**
- **Potential and realized habitats** ____ **29**
- **Functional Responses to Winter Recreation** ____ **32**

Discussion ____ *34*

- **Wolverine habitat selection** ____ **34**
- **Influence of winter recreation on wolverine habitat selection** ____ **36**
- **Roads and linear winter access** ____ **40**
- **Cumulative impacts of climate change and winter recreation** ____ **41**

Conclusion ____ *42*

Literature Cited ____ *45*

Appendix A: Wolverine capture and monitoring* __________________________________ *50

Trapping and handling ____ 50

Aerial telemetry monitoring and identification of denning females _______________________ 51

Wolverine GPS location data and home range summary_________________________________ 52

Appendix B: Description of Environment Covariates* _______________________________ *53

Identification of environment covariates ____ 53

Spatial scaling of covariates____ 58

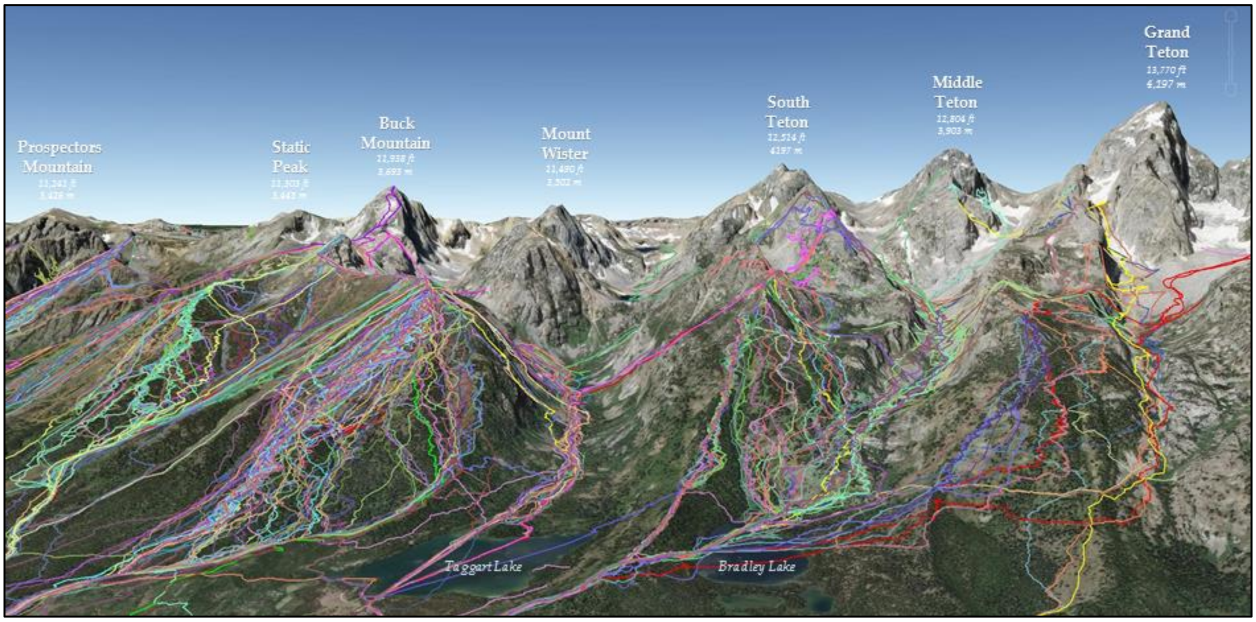
Appendix C: Winter recreation sampling and analyses* _____________________________ *59

Development of winter recreation spatially-explicit models______________________________ 59

Winter recreation aerial surveys to validate recreation maps______________________________ 61

Backcountry winter recreation types and patterns ____________________________________ 63

Appendix D: Wolverine habitat models and indirect habitat loss* ______________________ *63



Backcountry ski and snowboard Global Positions System (GPS) tracks collected during the winter of 2014 by volunteer recreationists.

Executive Summary

Outdoor recreation provides opportunities for people to connect to nature, and is a critical economic driver and part of the cultural fabric of some rural communities. Outdoor recreation is also increasingly recognized to have potentially important impacts on nature and wildlife, and we need to understand these potential effects. In recent years, technological advancements in over-snow equipment including 'powder snowmobiles' and lightweight backcountry ski gear provide opportunity for backcountry enthusiasts to access previously remote landscapes for winter recreation activities. Wolverines may be vulnerable to direct and indirect impacts of recreation during winter, as they remain active through the winter, naturally occur at low densities, have low reproductive rates, and enter reproductive dens within deep snowpack during the winter recreation season. The Rocky Mountains represent the southern extent of wolverine distribution and in this region they are limited to high elevation habitat, which overlaps the same types of mountainous terrain sought by backcountry winter recreationists.

Over 6 winters (2010 – 2015) and four study areas, we GPS collared 24 individual wolverines over 39 animal-years to collect >54,000 GPS locations, one of the largest GPS datasets collected on wolverines in the lower 48 states. These wolverines were exposed to a diversity of winter recreation activities across our study areas spanning >1.1 million ha in Idaho, Wyoming and Montana. Simultaneously, we monitored and sampled winter recreation, collecting 5,899 GPS tracks from backcountry winter recreationists representing >198,000km of recreation activity, in the most intensive and extensive backcountry winter recreation monitoring effort that we know of to date. Backcountry winter recreation information was also collected through trail use counts and aerial-based recreation surveys, and the combination of data allowed us to create maps of backcountry winter recreation portraying the extent and relative intensity of motorized recreation and non-motorized recreation within wolverine home ranges. From locations of 18 wolverines (25 animal-years, >53,000 locations), we modelled habitat selection of male and female wolverines within home ranges using resource selection functions and used remaining wolverine data to validate these models. We characterized the habitat selection responses of wolverines to varying winter recreation patterns, and assessed the potential for indirect habitat loss from avoidance of recreated areas. Replicating this across multiple study areas allowed us to evaluate functional responses of wolverines to differing levels and types of recreation, providing further insights into wolverine responses to winter recreation.

Wolverines exhibited selection for specific habitat characteristics within home ranges, with female selection differed in some important ways from males. Female wolverines, which were represented by both denning and non-denning females in our sample, selected for talus and for snowier and colder habitats when compared to males, and we suggest these may represent denning affiliations similar to those found in other studies. Both males and females selected for drainage bottoms and avoided steep slopes. Both male and female wolverines selected for fir-associated conifer forest, avoided open areas but selected for areas close to forest edges. Unlike females, males were found closer to roads than expected; these roads were primarily unmaintained, snow-covered secondary roads with little human use during winter.

Wolverines maintained multi-year home ranges within landscapes that support relatively intensive levels of winter recreation, suggesting that wolverines tolerate winter recreation at some scales. Individual wolverine exposure to winter recreation varied notably across study areas and animals, a key aspect of our study design. Variation in the spatial extent of motorized

recreation ranged from <1% to 51% within home ranges, while non-motorized recreation tended to have smaller footprint areas covering an average of <5%, and ranging from <1% to 9.3% within home ranges. Wolverines responded negatively to increasing intensity of winter recreation, with off-road or dispersed recreation eliciting a stronger response than recreation concentrated on access routes. Indirect habitat loss from winter recreation reduced the quality of 2 – 28% of available habitat within home ranges. Female wolverines exhibited strong avoidance of off-road motorized recreation and were more vulnerable to higher levels of indirect habitat loss than males who appeared to be less sensitive to disturbance. While non-motorized recreation covered a relatively small proportion of home ranges, these areas were also avoided by male and female wolverines. The avoidance of areas of linear access used by winter recreationists was not as strong as estimated for dispersed recreation and wolverines may be less sensitive to predictable patterns of human use.

The strength of wolverine negative responses to dispersed motorized and non-motorized recreation increased with increasing levels of the recreation within the home range. This functional response of wolverines to recreation intensity suggests that potentially important indirect habitat loss may occur when a notable portion of an animal's home range receives recreation use, as it is exactly those animals exposed to higher levels of recreation that are most strongly displaced from these areas. The functional response also suggests that limited exposure may mute the indirect habitat loss, and some of our animals were exposed to relatively low levels of winter recreation. Our ability to understand wolverine responses to non-motorized recreation is hindered by having few wolverines exposed to higher levels of this recreation type.

Currently, exposure to winter recreation is highly variable within home ranges and across individuals indicating further work is needed to understand population-level effects. We suggest significant habitat degradation to reproductive females during denning season should be of concern within landscapes with higher levels of winter recreation. We speculate that the potential for backcountry winter recreation to affect wolverines may increase under climate change due to reduced snow pack and snow season that may concentrate winter recreationists spatially and temporally in these high elevation habitats during a season when these species face increased energetic stressors and females enter reproductive dens. We recommend that solutions to finding a balanced approach to sustaining the diverse values of these wild landscapes requires creative approaches and collaborations between land managers, stakeholders and wildlife professionals.

Cite as: Heinemeyer, K. S., J. R. Squires, M. Hebblewhite, J. S. Smith, J. D. Holbrook, J. P. Copeland. 2017. Wolverine – Winter Recreation Research Project: Investigating the interactions between wolverines and winter recreation. Final Report, December 15, 2017. 71pp. Available at: www.roundriver.org/wolverine.

Introduction

Fostering societal appreciation for nature conservation partly relies upon individuals connecting to nature during leisure activities including participating in outdoor recreation activities. Winter snow-based recreation is an important component of the outdoor recreation industry, and includes backcountry sports in undeveloped landscapes. In recent years, technological advancements in over-snow equipment including ‘powder snowmobiles’ and lightweight backcountry ski gear provide opportunity to access previously remote landscapes. Not only are backcountry recreationists potentially important advocates for the landscapes they visit (Teisl and O'Brien 2003, Gifford and Nilsson 2014), but the winter recreation is important economically and culturally for many small communities (e.g., (Scott et al. 2008).

While maintaining societal values for nature partly depends on supporting interactions with natural landscapes, the potential impacts of this use needs to be understood (Boyle and Samson 1985, Knight and Gutzwiller 1995, Taylor and Knight 2003). There have been an increasing number of studies highlighting a diversity of recreation-based impacts on habitats and wildlife species (Steven et al. 2011, Sato et al. 2013, Larson et al. 2016, Ewacha et al. 2017). The most commonly recorded wildlife responses include both behavioral and physiological stressors on individual animals, including increased avoidance of the disturbance, elevated stress hormones and displacement from preferred areas (Harris et al. 2014, Arlettaz et al. 2015, Larson et al. 2016). Recreation that results in the avoidance of disturbed areas leads to indirect habitat loss (Patthey et al. 2008, Polfus et al. 2011, Coppes et al. 2017b). The importance of disturbance and particularly indirect habitat loss from winter recreation may be elevated if animals face increased energetic demands for thermoregulation and travel over snow while food may be less abundant or of lower quality (Telfer and Kelsall 1979, Parker et al. 1984, Neumann et al. 2009).

Habitat displacement and indirect habitat loss from winter recreation activities have been documented in a diverse array of montane and alpine species. In Europe, for example, high elevation forest grouse (*Tetrao* sp.) are negatively impacted by backcountry winter recreation including habitat displacement as well as energetic and physiological effects (Patthey et al. 2008, Braunisch et al. 2011, Arlettaz et al. 2015, Coppes et al. 2017b). Many species of large herbivore (e.g., red deer (*Cervus elaphus*), mountain caribou (*Rangifer tarandus caribou*), bighorn sheep (*Ovis canadensis*), mountain goat (*Oreamnos americanus*), and moose (*Alces alces*)) have exhibited negative physiological or behavioral responses including indirect habitat loss through avoidance associated with motorized and non-motorized winter recreation (Seip et al. 2007, Neumann et al. 2009, Courtemanch 2014, Richard and Cote 2016, Coppes et al. 2017a, Lesmerises et al. 2018). As backcountry winter recreation grows in intensity and spatial extent coupled with the potential concentration of activities due to climate change, there is a growing need to understand the potential effects on wildlife species particularly those that are sensitive, snow-associated, and occupy alpine habitats.

Large carnivores are globally threatened and declining, and have experienced negative effects of human-caused habitat fragmentation and loss throughout their range (Ripple et al. 2014). In North America, the Rocky Mountains represent a large carnivore hotspot (Noss et al. 1996, Laliberte and Ripple 2004), where some species are restricted to high elevation habitat. The wolverine (*Gulo gulo*) is limited to northern latitudes across its circumpolar distribution, is closely associated with snow and subalpine or alpine habitats throughout the winter and reproductive denning, and is a species of conservation concern. Indeed, there is high potential for overlap and interactions between wolverines and backcountry winter recreationists because they both occupy similar areas. Wolverines may be vulnerable to direct and indirect impacts of recreation during winter, as they naturally occur at low densities, have low reproductive rates, and remain active through the winter (Hash 1987). There has been no effort focused on understanding wolverine responses to winter recreation, though research suggests they are sensitive to human activities and infrastructure (May et al. 2006, Krebs et al. 2007, Stewart et al. 2016, Heim et al. 2017). Females enter reproductive dens within deep snowpack in during the winter recreation season with kits born in mid-Feb to early March and they occupy these dens through late April or mid-May (Hash 1987, Magoun and Copeland 1998). The potential impact of backcountry winter recreation to denning females is of primary concern (Carroll et al. 2001, May et al. 2006, Copeland et al. 2007, Krebs et al. 2007). In Canada, wolverine status was changed to ‘Special Concern’ in 2014 with increased winter recreation use combined with sensitivity of denning females among the considerations (www.cosewic.gc.ca). In the United States, wolverines are being considered for listing under the Endangered Species Act, with the most recent status review (Service 2013) indicating a lack of evidence to assess potential effects of winter recreation.

Understanding the responses of elusive, low-density wildlife species to relatively novel human uses such as backcountry winter recreation require committed and innovative approaches that capture the temporal and spatial variability inherent in the human use patterns and in the responses of animals to this disturbance (Tablado and Lukas 2017, Squires et al. 2018). Previous studies on the effects of winter recreation on wildlife species have been limited spatially and temporally, and most were focused within a single study area and on a single form of winter recreation (Larson et al. 2016). Over six years, we monitored the movements and habitat use of wolverines in four different study areas in the Rocky Mountains of Idaho, Wyoming and Montana. We simultaneously tracked and monitored winter recreation to characterize the spatial extent and relative intensity of activities across the landscape. We hypothesized that wolverine responses to winter recreation would be influenced by the type of winter recreation, as well as the spatial extent and intensity of the recreation. We developed resources selection analyses to both understand wolverine habitat use within home ranges and to test wolverine responses to type, spatial extent and the relative intensity of winter recreation. These analyses allowed us to evaluate the potential for indirect habitat loss due to winter recreation (Johnson et al. 2005, Polfus et al. 2011, Hebblewhite et al. 2014). While resource selection analyses provide an estimate of average responses, they tell us little about how wolverine responses may change based on the level of exposure to winter recreation (Mysterud and Ims 1998, Hebblewhite and Merrill 2008). Functional responses can include such important effects as habituation and threshold effects (Hebblewhite and Merrill 2008, Moreau et al. 2012, Holbrook et al. 2017). For example, Hebblewhite and Merrill (2008) found that wolves showed no response to humans in areas of low human activity, but as the amount of human activity increased, they displayed heighted avoidance. We tested for functional responses in habitat use of wolverines by evaluating how wolverine use of recreated areas changes with changing availability (Holbrook et al. 2017). The goals of our research were three-fold: 1) characterize fine-scale (i.e., third-order home range scale, Johnson 1980) habitat use and selection of male and female wolverines; 2) assess the importance of motorized and non-motorized winter recreation in influencing wolverine habitat use and habitat quality; and 3) test if the responses of wolverines to winter recreation were dependent upon the spatial extent and relative intensity of the recreation within individual home ranges.

Methods

To understand wolverine responses to winter recreation disturbance, we fit Global Position System (GPS) collars on wolverines to monitor movements and habitat use in mid and late winter, and concurrently sampled and monitored winter recreation. We developed wolverine resource selection functions (RSF) at the third order (within home range scale, Johnson 1980) with a use:availability design to estimate the relative probability of selection (Manly et al. 2002, Johnson et al. 2006, McDonald 2013). We developed maps of different types of winter recreation and included these as covariates in RSFs to test hypotheses concerning the effect of winter recreation on wolverine habitat selection. Based on the selected models, we evaluated indirect habitat loss from winter recreation, as measured by the loss in predicted habitat quality with the inclusion of winter recreation covariates in the RSF, with habitat quality classified by relative probability of use (i.e., Polfus et al. 2011). Finally, we tested if wolverines showed functional responses to winter recreation based on the relative intensity of winter recreation to which they were exposed. We used ArcGIS (ArcGIS Desktop: Release 10.1 – 10.5, Redlands, CA: Environmental Systems Research Institute) and R (R Core Team 2016) for data management and analyses.

Study Area

Our research included four broad study areas spanning >1.1 million ha in Idaho, Wyoming and Montana (Figure 1) which we refer to as: McCall study area (Payette NF, northern Boise NF); Sawtooth study area (including portions of the Sawtooth NF, southern Boise NF); West Yellowstone study area (including portions of the Caribou-Targhee NF, Custer-Gallatin, NF and Beaverhead-Deerlodge NF), and the Tetons study area (including portions of the Caribou-Targhee NF, Bridger-Teton NF and the Grand Teton National Park). Each study area

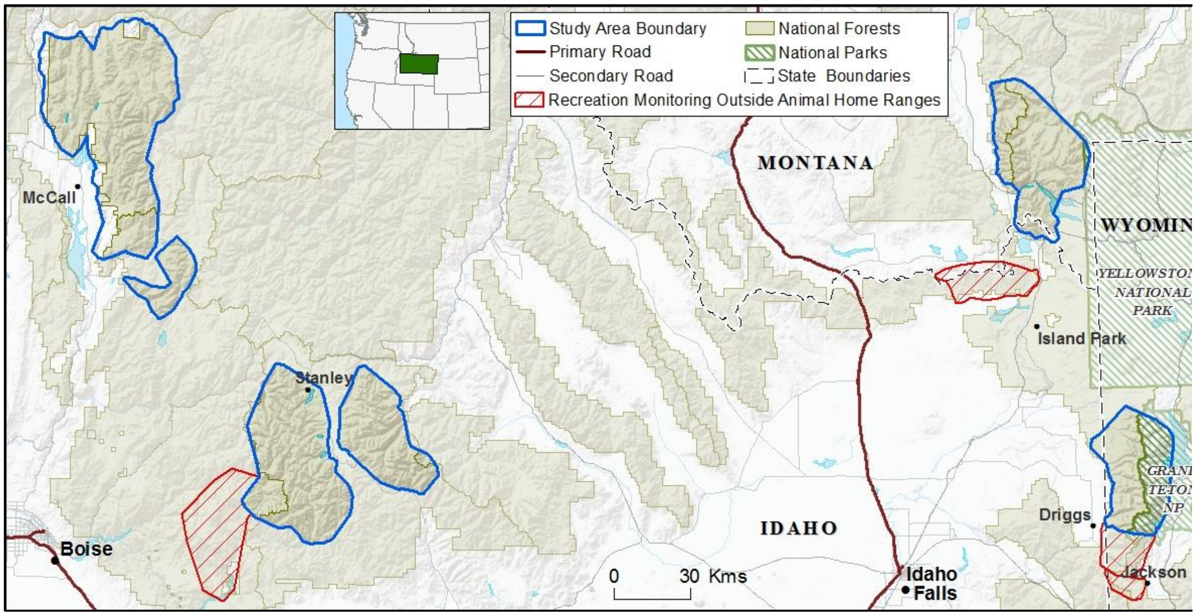


Figure 1. Four broad study areas (McCall, Sawtooth, West Yellowstone and Tetons) for examining effects of winter recreation on wolverines (*Gulo gulo*) in Idaho, Montana, and Wyoming, USA, years 2010-2015. The study area boundaries in blue identify the outer extent of wolverine home ranges monitored during the study, while the red hatched areas indicate additional areas where camera and live-trapping for wolverines occurred without the identification of wolverine presence. Winter recreation sampling occurred in all study areas.

was a popular backcountry winter recreation destination with backcountry snowmobiling, skiing or both occurring in the range of wolverines, but also large areas without intense winter human activity. Study areas were primarily National Forest System lands, but also contained a mix of other state and federal land designations. Topography was mountainous with alpine dominated by rock, ice and low-growing herbaceous vegetation, transitioning into more open conifers with open rocky or subalpine shrub, grass and herbaceous vegetation. Mid-elevation vegetation was dominated by coniferous forests, with interspersed deciduous tree and shrub communities. The lower boundaries of the study areas were defined by the lower limits of wolverine use, typically near the lower limit of forested habitats, with rare agricultural and sagebrush steppe near these margins.

Infrastructure supporting backcountry recreation varied across the study areas. All study areas maintained parking areas for backcountry access at trailheads or along plowed roads, and some study areas had a network of groomed snowmobile trails. Within wolverine home ranges, roads were almost exclusively secondary roads that were not plowed for vehicle travel though some were groomed for snowmobile use. Plowed roads occurred along the periphery or in close proximity outside of home range boundaries. All roads were snow-covered during our study, and motorized and non-motorized recreation use was allowed on the majority of roads regardless of whether they were groomed for recreation use. Winter recreation activities varied in the number of recreationists and types of recreation, and each study area had a unique combination of backcountry recreation including snowmobile, ski (including snowboards), snowmobile-accessed ski/board (hybrid), cat-ski, heli-ski and yurt-supported ski. The McCall, Sawtooth and Teton study areas also had developed ski resorts which allowed for backcountry or out-of-bounds skiing.

Wolverine capture and monitoring

Between 2010 – 2015 we captured wolverines from early January through April using modified box traps built from logs (Lofroth et al. 2008) baited with road-kill deer or trapper-caught beaver and a skunk-based lure. Each trap was equipped with a satellite-device that notified us when the trap was triggered (Vectronics trap transmitters TT2, TT3; Vetronic Aerospace GmbH, Berlin, Germany), as well as a VHF-based trap trigger (Telonics trapsite transmitters, TBT series; Telonics, Inc, Mesa, AZ, USA); traps were visited immediately if triggered, and maintained every 3 – 5 days (see Appendix A for additional details). Traps were closed late February to late March to avoid capturing a reproducing female, and re-opened in late March through April for collar removal. Wolverines were anesthetized using a 10 mg/kg ketamine hydrocholoride and 0.075 mg/kg medetomidine mixture (Fahlman et al. 2008) delivered by a jab stick. A GPS collar (either WildCellSL collar from Lotek Wireless, Newmarket, Ontario, Canada or Quantum 4000 collar from Telemetry Solutions, Concord, CA, USA) was attached and programmed to collect a location every 20 minutes on weekends (Saturday, Sunday) and mid-week (Tuesday, Wednesday), which we expected to differ in intensity of human use. Collars were modified with a cotton strip designed to rot away within 4 – 6 months if we were unable to recapture the animal. Trapping and handling procedures were approved through the University of Montana Institutional Animal Care and Use Committee (IACUC; Permit #055-10MHECS-113010) and the National Park Service IACUC under a research permit (GRTE-2015-SCI-0003). We also obtained research permits through Idaho Department of Fish and Game (IDFG) and Wyoming Game and Fish (WGF). We monitored the status of wolverines through aerial telemetry flights, including identifying potentially denning females (Appendix A).

Resource Selection Function Analyses

Resource selection functions (RSF) compare covariate characteristics at used GPS locations with random locations (putatively available) to identify covariates that are used disproportionately more (i.e., selected) or less than (i.e., avoided) available (Manly et al. 2002). We used general linear mixed-effects models with a logit link function (GLMM) and animal-year as a random effect to control for repeated sampling of individuals (Gillies et al. 2006). The mixed-effects RSF model therefore takes the form:

$$w(x) = \beta_1 x_{1ij} + \beta_2 x_{2ij} + \beta_3 x_{3ij} + \cdots + \beta_n x_{nij} + \gamma_{0j} + \varepsilon_{ij} \qquad (1)$$

where x_n are covariate values for location *i* of animal-year *j* with the fixed regression coefficient β_n; γ_{0j} is the random intercept for animal-year *j* and is ε_{ij} is the residual variance within each animal-year. Logistic regression (Hosmer et al. 2013) is used to fit the exponential approximation to an inhomogeneous spatial-point process model, but without the intercept because in used-available designs, the true amount of non-use is unknown (McDonald 2013). Thus, the resultant probability is best considered a relative probability of selection or use (Lele et al. 2013). Animal and random (available) locations were attributed with the environmental and winter recreation covariates (see below), which were then standardized to support model fitting and allow for comparisons between model coefficients (Hosmer et al. 2013).

Location data and home range analyses

We defined available habitat by estimating home range boundaries using a local convex hull (LoCoH) non-parametric kernel method (Getz et al. 2007) with a fixed 'k' number of nearest neighbors (Appendix A). We buffered calculated polygons by the sex-specific median step length (331 m for females, 441 m for males) to account for habitat immediately available to the animal. We included individual wolverine animal-years with $\geq$5 weeks of GPS monitoring in that winter in model development. Data for individuals monitored for <5 weeks, or subadults with exploratory behaviors, were withheld for model validation. Within each home range, we estimated available habitat with random locations generated at a ratio of 2:1 random:use with random locations forced to be $\geq$30m apart.

Wolverine spent time under snow and structures that resulted in low GPS fix-rates and potential behavioral or habitat-induced bias (Frair et al. 2004, Nielson et al. 2009). To account for behavior-based missed locations, we developed a modification of Knopff et al. (2009) to identify clusters of wolverine locations based on their spatial (within 25m of each other) and temporal (within 24 hours of each other) proximity. Missed locations were associated with a known cluster site if the location before or after the failed GPS attempt was within a cluster, and the cluster centroid was imputed for their location (Frair et al. 2004). Locations <100 m of an active trap site were censored given the effect of baited traps.

Environmental variables

We evaluated land cover, topographic, snow, climate and anthropogenic covariates (Appendix B) that may be important predictors of wolverine resource selection at the third-order. First, we identified the spatial scale most strongly selected by wolverines (DeCesare et al. 2012; Appendix B). Second, we screened covariates for collinearity ($|r| >= 0.6$), and the covariate with the lowest univariate AIC was retained (Hosmer et al. 2013). Finally, we evaluated covariates for potential nonlinear relationships using general additive models (Hilbe 2015) and by testing potential non-linear models, keeping the form of the covariate with the lowest AIC (Hosmer et al. 2013). This resulted in slope being included in a quadratic form.

Winter recreation sampling and models

We developed spatially-explicit maps of winter recreation by sampling backcountry recreation using three methods: GPS tracking of volunteer recreationists (*sensu* Olson et al. 2017), infra-red trail use counters, and aerial surveys. We combined spatial information from GPS tracks with the amount of recreational use from trail counters to develop maps of winter recreation intensity of all recreation combined as well as by motorized or non-motorized recreation type. We used the aerial surveys to validate recreation maps (Appendix C).

To collect GPS tracks of recreation, we sampled recreationists at known recreation access points during mid-week (Tuesday, Wednesday) and weekend (Saturday-Sunday) days from mid-January through mid-April. We sampled recreation systematically, not in proportion to recreation use at access points or across study areas. We asked recreation groups to carry one GPS unit (Qstarz International Co., Ltd., model BT-Q1300, 1 location/5 seconds, position accuracy < 10

m) per ≤ 4 people in the group, and we recorded the type of winter recreation and the group size per GPS unit. We also distributed GPS units to backcountry guide, heli-ski and cat-ski operations, with guides carrying the GPS units and recording their group size. To estimate the number of recreationists accessing each study area, we installed infra-red trail counters (Trafx Research Ltd, Canmore, Alberta, Canada) at constriction points on backcountry snowmobile and ski/snowboard access routes. If the access route was used by both out-going and incoming recreationists, the counts were divided by two to estimate the one-way traffic.

We developed maps of winter recreation, including linear travel or access routes and the relative intensity of dispersed use based on the GPS tracks. To account for differences in overall use within and between study areas, we weighted each GPS track based on the proportion of the estimated total recreation use it represented from each trailhead or access point, with total use estimated from the trail use counters associated with the access point:

$$w_i = \left({}^{Trail\ count_j} \Big/ {}_{\sum Groups_j} \right) \times \ GPS\ Group_i \tag{2}$$

where *i* = individual GPS track, *j* = trailhead (or group of clustered trailheads), *Trail count* = the estimated total recreationists accessing from trailhead$_j$, $Groups_j$ = the total number of people sampled as the sum across all groups carrying GPS units at trailhead *j*, and GPS Group$_i$ = the number of people associated with GPS track *i*.

The GPS tracks of recreationists that use motorized access (e.g., snowmobile, cat-ski, heli-ski) to undertake non-motorized activities were split into their motorized and non-motorized components. For heli-ski GPS tracks, we used only the non-motorized portions of GPS tracks and discarded the track associated with the helicopter transport. To test for wolverine responses to spatial pattern and intensity of winter recreation, we developed maps of recreation: 1) the recreation footprint as a binomial characterization of recreation extent that includes linear and dispersed recreation; 2) recreation access routes (recreated roads and groomed trails); 3) the relative intensity of all winter recreation; 4) the relative intensity of off-road or dispersed recreation (tracks >30m from a road or groomed route) for all recreation and 5) the relative intensity of motorized and non-motorized recreation separately (see details in Appendix C).

Model Selection

To test our hypotheses of wolverine responses to winter recreation, we first developed RSFs (habitat models) based on environmental covariates not including recreation, which predicts 'potential' habitat quality in the absence of receation, based on relative probability of use (Polfus et al. 2011, Trainor and Schmitz 2014). Then, we added winter recreation covariates to the potential habitat model(s) to test for responses of wolverines to different aspects of winter recreation (e.g., spatial extent, relative intensity, recreation type) and to identify the best model to predict 'realized' habitat quality accounting for effects of winter recreation on wolverine habitat selection. We followed a two-step process to identify the environmental predictors of wolverine habitat use for all animals combined (global model), for females (female model) and for males (male model). We used fixed-effect least absolute shrinkage and operator selection (LASSO) logistic regression (Tibshirani 1996, Reineking and Schröder 2006) implemented using the 'glmnet' package in R (Friedman et al. 2010) to identify the most predictive of the potential covariates (penalty strength set within one standard error of the minimum cross-validated error; Friedman et al. 2010). In the second step, we developed RSF global, female and male models using GLMM with animal-year as a random effect using the 'lme4' package in R (Bates et al. 2015). We compared the summed AIC scores of the male and female RSF models to the global RSF AIC to determine if a single global model or separate sex-based models were supported (Burnham and Anderson 1998). To include winter recreation effects, we then developed five additional RSF models that included the potential habitat RSF covariates and five winter recreation covariates from our winter recreation maps. We selected the model with the lowest ΔAIC to best represent realized wolverine habitat use in areas that also have winter recreation. For the selected models of potential habitat and realized habitat, we used 10-fold cross validation to assess the goodness of model fit (Boyce et al. 2002). We also validated the models using out-of-sample GPS location data from wolverine animal-years not used in the development of habitat models to determine how our models predicted the frequency of wolverine use (e.g., DeCesare et al. 2012, Holbrook et al. 2017).

Comparing potential and realized habitat quality

We estimated the amount of predicted change in wolverine habitat quality that may occur in the presence of winter recreation by calculating the reduction in habitat quality between the potential habitat and realized habitat models (Johnson et al. 2005, Nielsen et al. 2010, Polfus et al. 2011, Hebblewhite et al. 2014). Given we did not measure habitat use in the absence of winter recreation, we assume that the influence of winter recreation is independent of environmental variables and evaluated this assumption by comparing the standardized model selection coefficients of environment covariates between the potential and realized models (Hosmer and Lemeshow 2008). If model coefficients were 'stable' in the potential and realized models, this suggests that recreation and other covariates were not confounded, thus enabling our ability to predict additive effects of 'adding' or 'removing' recreation.

Each model was then mapped at a 30 m^2 resolution and mapped values were binned into 10 quantiles from low to high quality or relative probability of use. We classified habitat quality by classifying the top 30% of the area (bins 8 – 10) as 'high quality habitat', the next 30% (bins 5 – 7) as 'moderate quality habitat' and the lowest 40% of habitat values (bins 1 – 4) as 'low quality habitat'. We did not include areas where gaps in winter recreation monitoring information did not allow us to predict the probability of use. Indirect habitat loss was calculated as the spatially-explicit reduction in habitat class when comparing the realized habitat model to the potential habitat model (Johnson et al. 2005, Polfus et al. 2011). We summarized the amount of change across the study areas as well as area within individual home ranges. We calculated the degree of habitat degradation by the number of classes reduced, with the most severe degradation indicated by high quality habitat that is degraded by two classes to low quality habitat.

Functional responses to winter recreation

We tested if wolverines exhibited a functional response to the relative intensity of motorized and non-motorized dispersed winter recreation by evaluating how habitat use of recreated areas changes with availability of these areas. If there is no functional response, habitat use of recreation changes in proportion to availability (Holbrook et al. 2017), while deviations from proportional use indicate a functional response. We calculated habitat use and availability of the relative motorized and non-motorized recreation intensity by computing the mean recreation intensity at used and available locations for each animal-year home range. We then analyzed these data using the following model:

$$U_{R\mathrm{i}} = \beta_0 + \beta_R \left(A_{R\mathrm{i}}\right) \tag{3}$$

where R indicates the recreation type (motorized or nonmotorized); $U_{R\mathrm{i}}$ = the average recreation intensity at used locations of each animal-year i; β_0 = y-intercept, β_R = slope of the functional response; and $\mathrm{A}_{R\mathrm{i}}$ = the average recreation intensity at available locations within the home range of animal-year i. The null hypothesis is $\beta_R = 1$ (proportional use), while $\beta_R < 1$ indicates decreasing use and $\beta_R > 1$ indicates increasing use as availability increases.

Results

In this Final Report, we focus primarily on modeling and analytical results as the key final products of this multi-year research effort. We have presented field-based results throughout the life of the research effort within Annual Progress Reports including data collection efforts and data summaries, and we recommend reviewing the progress reports for these details, available at www.roundriver.org/wolverine.

Wolverine trapping and location data

We captured 24 individual wolverines over five years of live-trapping, with two years spent within most individual study areas though the McCall study area had four years of trapping efforts (Appendix A). We did not successfully identify the presence of wolverines in either the Trinity Mtns (part of the Sawtooth study area) or the Centennial Mtns (part of the West Yellowstone study area), and we did not identify or capture any female wolverines in the Tetons Mtns or any wolverines in the southern portion of the Tetons, despite ≥2 years of high effort in each area (Appendix A). We radio-collared the 24 wolverines (11 females, 13 males), and recaptured 11 of these animals for 2 – 4 years for a total of 39 animal-years. We obtained >5 weeks of data from 18 (10 females, 8 males) animals and 25 animal-years, averaging 2101 locations/animal-year between mid-Jan and end of March (see Appendix A). An additional nine animal-years (5 female animal-years with 6,841 locations and 4 male animal-years with 9,954 male locations) were used for model validation and four collared animals either slipped their collar or otherwise could not be found and no data were collected. Raw fix-rates were 75.8%, yet 78% of failed GPS attempts were associated with clustered behavior and were thus imputed. After correcting for missed locations, our corrected fix-rate was 94.7%, providing 53,301

Table 1. Summary of the male and female wolverines (*Gulo gulo*) GPS collar locations and home range estimates during winter seasons (2010-2015) in Idaho, Wyoming and Montana as part of research examining wolverine responses to winter recreation. Home range areas were estimated using a local convex hull non-parametric kernel method (Getz et al. 2007).

	Individuals	**Animal-Years**[1]	**Ave # locations ± SD**	**Location count range (min – max)**	**Ave home range (km^2) + SD**	**Min – Max of home range sizes (km^2)**
Males	8	12	2590 ± 677	806 - 3778	1273 ± 471	401 – 2158
Females	10	13	1894 ± 547	1247 - 3079	289 ± 92	126 – 420

[1] Animal-years indicates the total number of winter seasons cumulatively monitored accounting for multiple seasons of monitoring of some individual animals

locations used in the spatial modeling and >10,000 for model validation. The average size of female winter home ranges was smaller than male winter home ranges (Table 1, Appendix A).

Recreation Monitoring

Every study area had at least one year of GPS-based recreation tracking, infra-red trail use counts and aerial surveys, with most study areas having two years of recreation monitoring. We recorded 5,899 GPS tracks of combined length of 198,019km (Table 2). While we recorded a diversity of backcountry recreation types (Appendix C), snowmobiling was the most popular motorized backcountry recreation while skiing was the most popular non-motorized recreation. More non-motorized recreation tracks were collected (3,125) than motorized (2,956) and hybrid types of recreation were limited (237 tracks). The vast majority of non-motorized recreation tracks were collected in the Teton study area, with localized areas of non-motorized recreation in other study areas (Table 2). Snowmobile tracks were longer (average of 60km) than ski tracks (average of 10km) and snowmobile tracks constituted 82% of our total track length. Snowmobiling was a common recreation activity across all of our study areas. Heli-ski only occurred within our Sawtooth study area and cat-ski recreation was only present in the McCall

Table 2. The number (%) of motorized and non-motorized recreation GPS tracks collected in our study areas, the annual average number of recreationists sampled (carrying or in a group with a GPS), the average annual trail use counts from infra-red trail use counters, and the estimated proportion of total use that we sampled (total people represented by GPS tracks/total use).

Recreation Type	McCall	Sawtooths	West Yellowstone	Tetons
GPS tracks, motorized	1620 (93%)	755 (54%)	386 (98%)	195 (8%)
GPS tracks, non-motorized	118 (7%)	613 (46%)	9 (2%)	2385 (92%)
Ave annual number of recreationists represented by GPS tracks	4,125	2,596	1,389	3,568
Average annual recreation visits	16,173	6,149	7,215	23,387
Sampling effort	25.5%	42.2%	19.3%	15.3%

study area. We established trail use counters at 25 sites, with most sites monitored for two years. The total number of recreation visits varied considerably across our study areas, reflecting the relative popularity of each study area as a destination for recreationists traveling from other areas (Table 2). The Teton and the McCall study areas received the highest use with >23,000 and >16,000 visits annually, respectively. The proportion of recreationist sampled using GPS tracking also varied based partly on the total recreation use but also based on localized access patterns, from 42% in the Sawtooth study area to 15% in the Tetons study area (Table 2).

Winter recreation occurred in 12.5% of our study area, and the spatial extent and relative intensity of both motorized and non-motorized winter recreation varied notably within and across study areas (Table 3, Figures 2 - 5). In the McCall study area (Table 3, Figure 2), the most widespread and intense recreation occurred in the north (covering approximately 16% of the Payette NF portion of the study area), and included extensive motorized recreation adjacent to a developed ski area and backcountry cat-ski activities. The lowest overall levels of winter recreation occurred across much of our Sawtooth study area with <5% disturbance from each of motorized and non-motorized recreation activities (Table 3) though recreation did have areas of high localized intensity, and the Trinity Mtns had extensive motorized recreation covering 32% of the area (Figure 3). The Sawtooth area also included an area used for heli-ski. Relatively high levels of winter recreation levels were recorded in the West Yellowstone area (Table 3, Figure 4), with 50% of the Centennial Mtn portion of the study area within the motorized recreation footprint. One male wolverine home range extended north of our recreation monitoring area and into the southern Madison Mtns; portions of this northern area had extensive motorized recreation based on our aerial surveys resulting in a significant data gap (Figure 4). The Teton study area included a diverse array of winter recreation (Table 3, Figure 5). Motorized recreation was absent from the Grand Teton National Park, but non-motorized recreation occurred in 14% of the monitored Park area. The areas west of the Park, within the Caribou-Targhee NF support both motorized and non-motorized use including developed and out-of-bounds skiing associated with the Grand Targhee Resort. We were unable to adequately sample motorized recreation in portions of this area and based on our aerial recreation surveys (Figure 5) it is more widespread and intense than suggested by our recreation covariates. The highest overall winter recreation levels were in the southern Tetons including the Teton Pass area of the Caribou-Targhee and Bridger-Teton NFs (Table 3, Figure 5). We recorded >50% of this area with winter recreation, primarily as non-motorized winter recreation (47%), this also areas of motorized recreation as well as the developed and out-of-bounds skiing associated with the Jackson Hole Ski Resort (Figure 5).

The spatial extent and relative intensity of backcountry winter recreation also varied within and across wolverine home ranges. Motorized recreation, on average, occurred in 22% and 14% of female and male home ranges, respectively, but varied greatly from a low of <1% to a high of 50%. In general, non-motorized winter recreation has a smaller footprint in most of our study areas covering <5% of home ranges on average, and two females were not exposed to non-motorized recreation. The Tetons study area had more non-motorized recreation than other study areas (Table 3, Figure 5) and the male wolverine residing there was exposed to higher non-motorized winter recreation levels covering 10% of his home range. Average recreation intensity of motorized recreation ranged from 0.00025 – 0.422 within home ranges. Given the smaller footprint of non-motorized recreation, it is not unexpected that the maximum average non-motorized recreation intensity value is lower, with a range of values of 0.001 – 0.093 within home ranges.

Table 3. Summary of the recreation footprint by study area, broken out by Administrative area or by distinct mountain ranges (see Figures 1); the proportion of each area in the motorized recreation footprint and in the non-motorized recreation footprint are estimated by our GPS track-based recreation maps.

Study Area[1]	Study Area (km^2)	Area (%) Motorized Recreation (km^2)	Area (%) Non-motorized Recreation (km^2)
McCall			
Payette NF	2,553	419 (16%)	47 (2%)
Boise NF	620	37 (6%)	1 (<1%)
Sawtooth			
Sawtooth NF	2,776	125 (5%)	72 (3%)
Sawtooth NRA	2,142	99 (5%)	54 (3%)
Trinity Mtns (BNF)	385	124 (32%)	0
West Yellowstone			
Henry Mtns (CTFN, CGNF)	250	50 (20%)	6 (2%)
Centennial Mtns (CTFN, CGNF)	395	196 (50%)	0
Tetons			
Teton National Park	477	0	67 (14%)
Northwest Tetons (CTFN)	588	41 (7%)	37 (6%)
South Tetons/Pass (CTFN, BTNF)	240	12 (5%)	113 (47%)
Mosquito Cr (CTFN, BTNF)	92	23 (25%)	0

[1] CTFN: Caribou-Targhee NF, CGNF: Custer-Gallatin NF; BTNF: Bridger-Teton NF

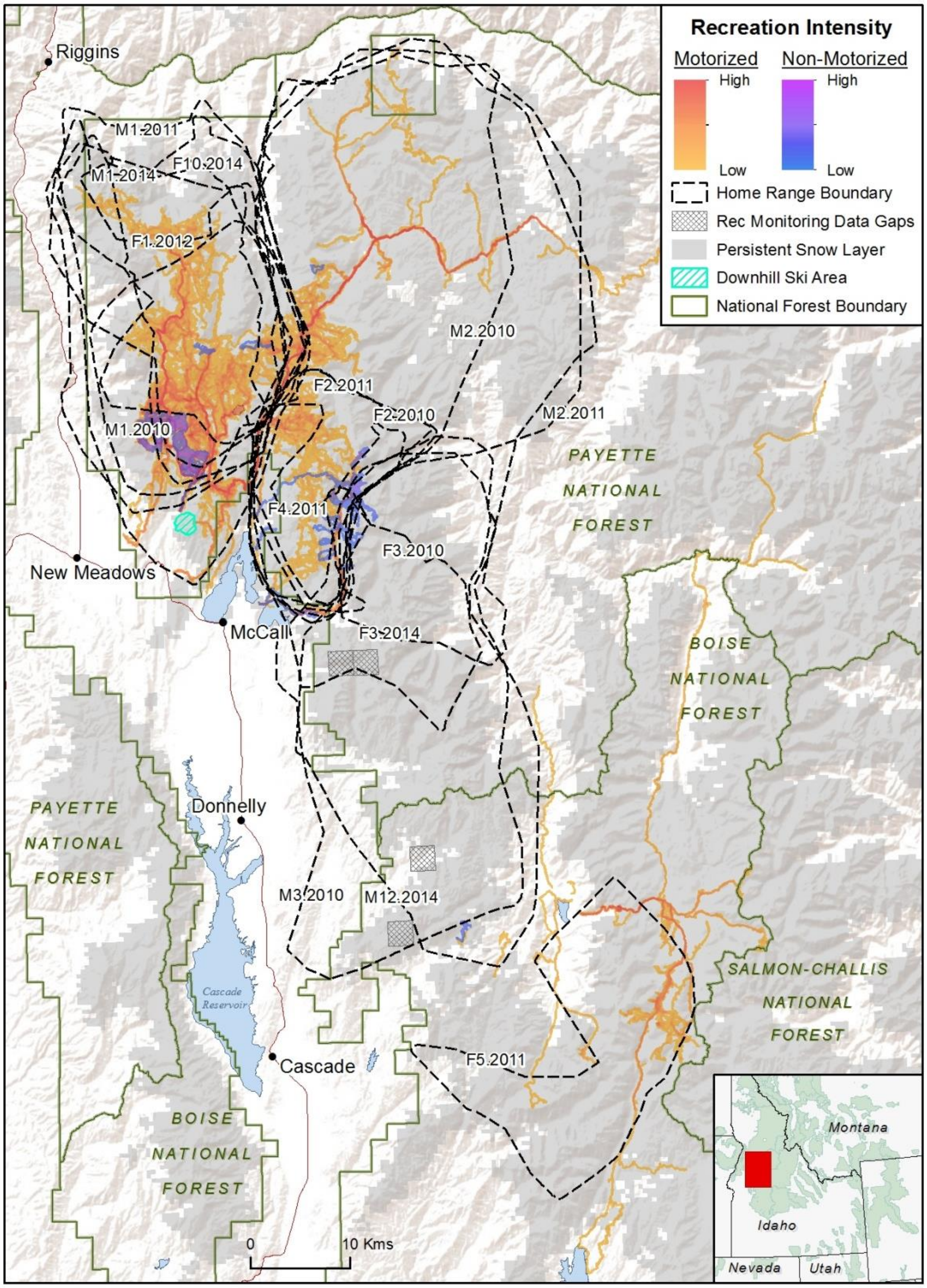


Figure 2. Map of wolverine (*Gulo gulo*) winter home ranges (2010-2014) and estimated backcountry winter recreation relative intensity in the McCall, Idaho study area as estimated based on GPS tracks collected from volunteer recreationists (2010-11) and used to develop recreation maps. Square or rectangular hatched areas indicate areas where we had gaps in GPS track sampling based on aerial recreation surveys.

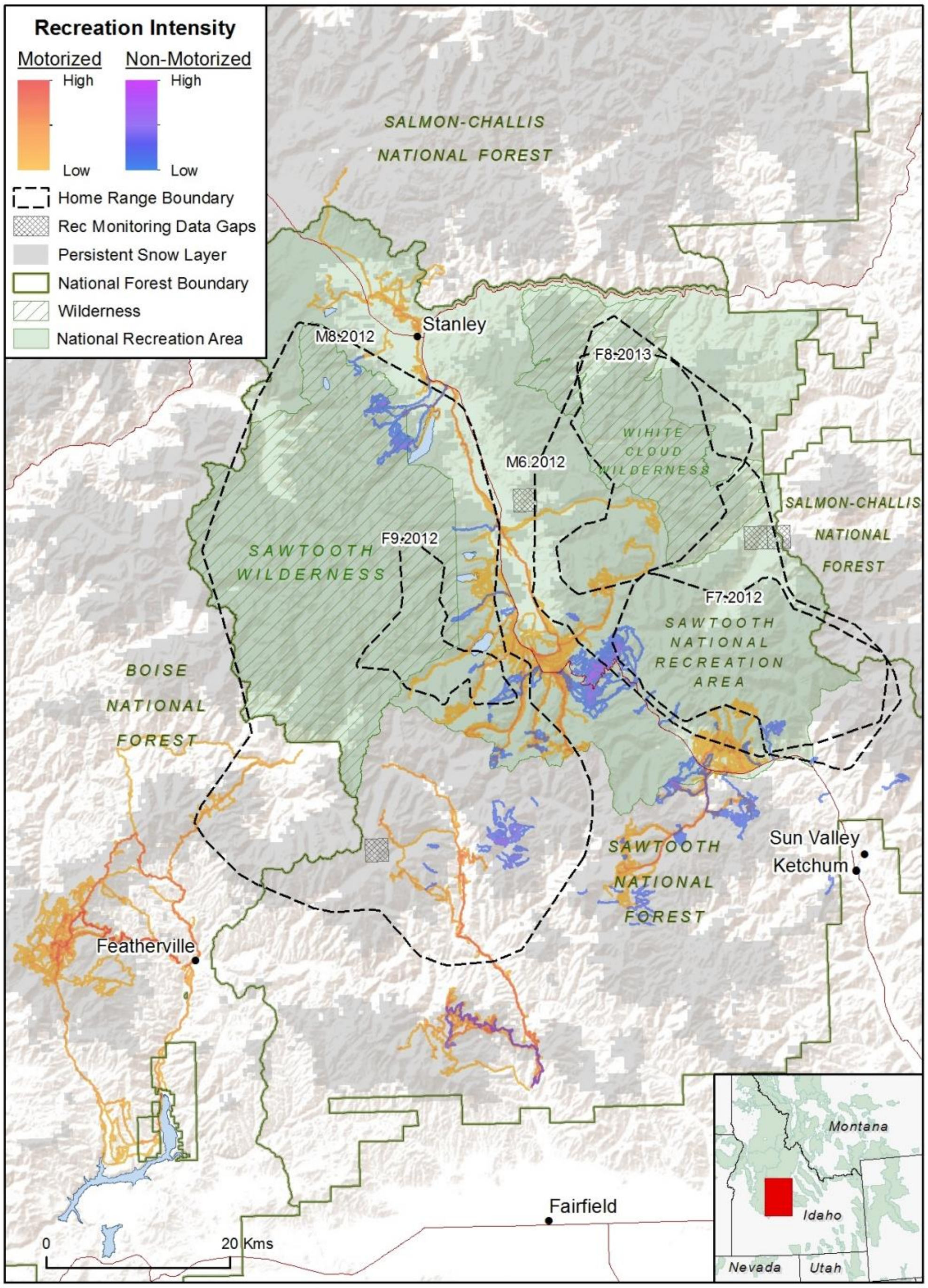


Figure 3. Map of wolverine (*Gulo gulo*) winter home ranges (2012-2013) and estimated backcountry winter recreation relative intensity in the Sawtooth study area as estimated based on GPS tracks collected from volunteer recreationists (2012-13) and used to develop recreation maps. Square or rectangular hatched areas indicate areas where we had gaps in GPS track sampling based on aerial recreation surveys.

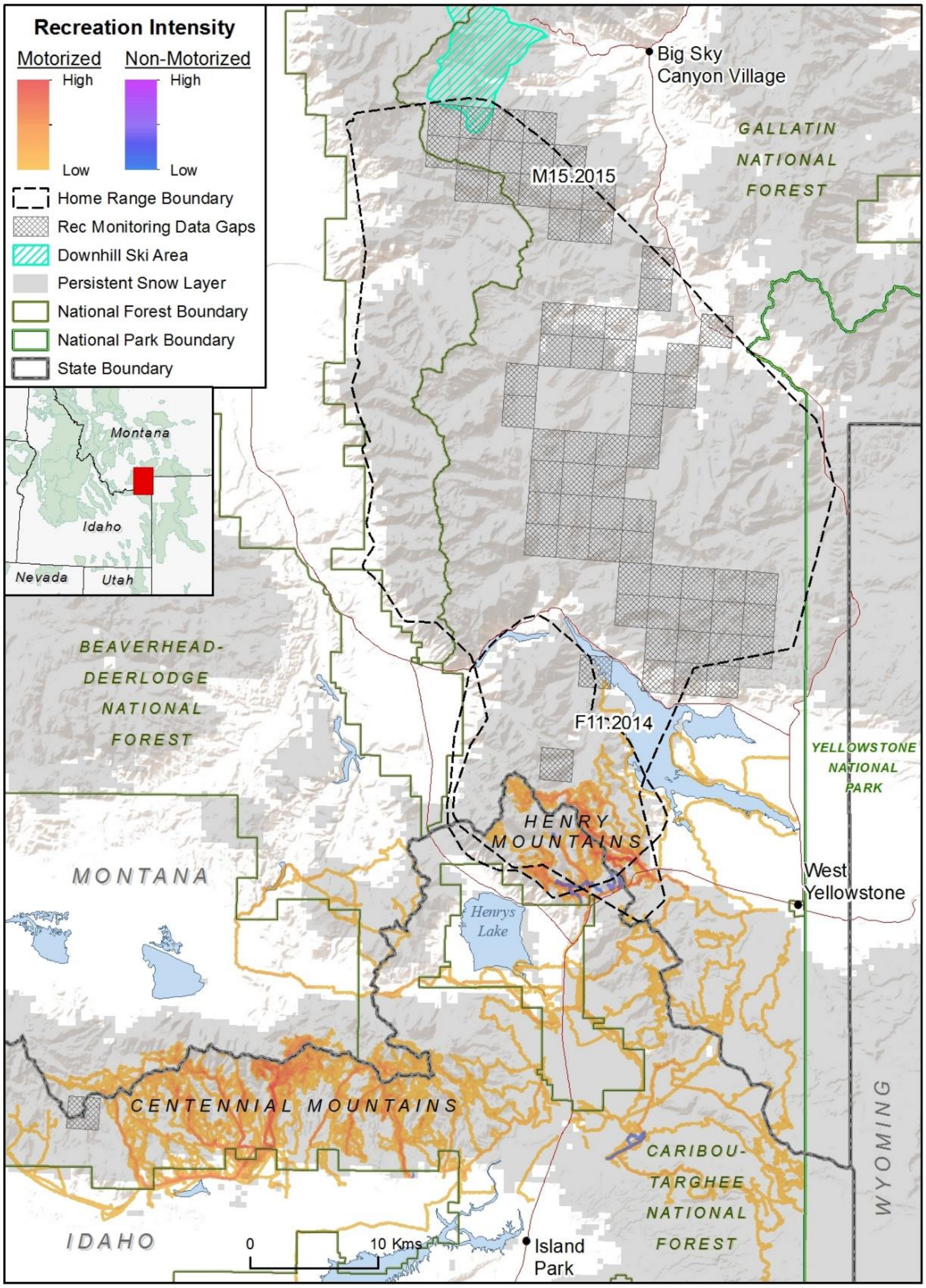


Figure 4. Map of wolverine (*Gulo gulo*) winter home ranges (2014-2015) and estimated backcountry winter recreation relative intensity in the West Yellowstone study area as estimated based on GPS tracks collected from volunteer recreationists (2014-15) and used to develop recreation maps. Square or rectangular hatched areas indicate areas where we had gaps in GPS track sampling based on aerial recreation surveys.

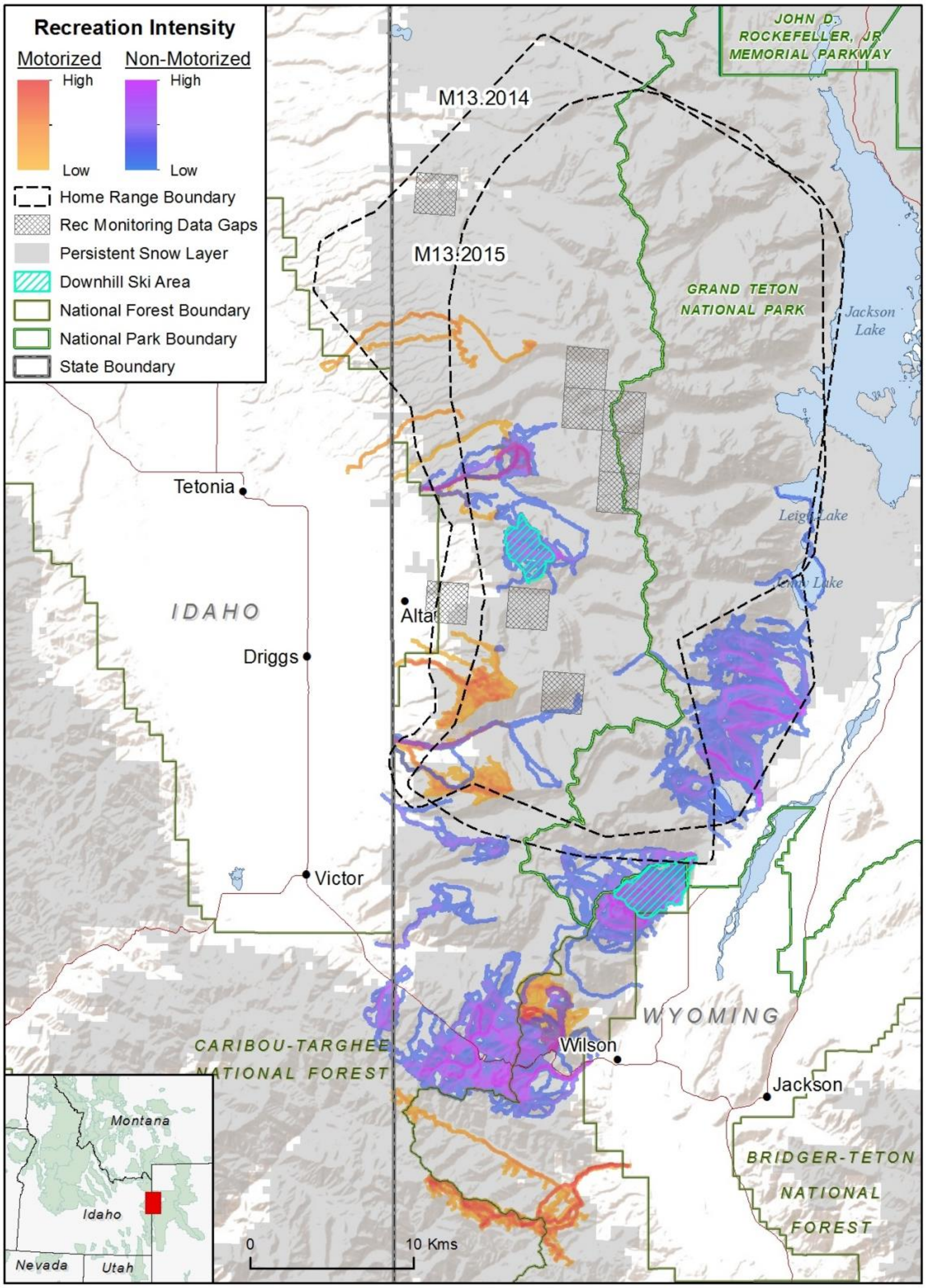


Figure 5. Map of wolverine (*Gulo gulo*) winter home ranges (2014-2015) and estimated backcountry winter recreation relative intensity in the Teton study area as estimated based on GPS tracks collected from volunteer recreationists (2014-15) and used to develop recreation maps. Square or rectangular hatched areas indicate areas where we had gaps in GPS track sampling based on aerial recreation surveys.

Environment resource selection function

The summed AIC score of the male and female environment-only models (i.e., potential habitat models) was notably lower than the AIC of the global with ΔAIC of 1,669, suggesting that resource selection by males and female differed significantly, thereby justifying separate treatment. The male wolverine model showed that resource selection was best characterized by nine environmental variables, while female wolverine habitat selection was best characterized by ten covariates. The male model uniquely included covariates for distance to roads and the proportion of lower elevation grass and shrub land cover types. Alternatively, the female model included talus, persistent spring snow cover and forest edge:area covariates, which were not identified as important predictors of male habitat use. All covariates were statistically significant (Table 4). The models shared several covariates including topographic position index, quadratic form of slope, distance to forest edge, solar insulation and the percent cover of forest, riparian and montane open cover types.

Model coefficients were standardized, allowing for within-model comparison and ranking of β coefficients for relative importance. Both sexes showed strong selection (ranked first in β coefficient importance) for drainage or valley bottom topography (β_{female} = -0.31, SE = 0.01; β_{male} = -0.42, SE = 0.01) as indicated by the negative coefficient for TPI (Table 4), and this is combined with the avoidance of steep slopes indicated by the negative coefficient of slope^2 (β_{female} = -0.27, SE = 0.01; β_{male} = -0.17, SE = 0.01). Selection for fir-dominated forests by males (β_{male} = 0.37, SE = 0.01) ranked second in coefficient importance. While females also selected for fir dominated forests (β_{female} = 0.05, SE = 0.01), this selection coefficient ranked second to last in importance (Table 4). Both sexes show a selection for areas near forest edge (β_{female} = -

Table 4. Standardized model coefficients betas and standard errors for environment RSF models for wolverines (*Gulo gulo*) monitored in Idaho, Wyoming and Montana (2010-2015), with the random effect standard deviation also included. Blank cells indicate covariates not identified for inclusion in the specified model. Negative Beta values indicate selection for lower values of the covariate.

	Female Model			**Male Model**		
	Beta	Beta St. Error	Rank	Beta	Beta St. Error	Rank
Distance to edge	-0.21	0.01	3	-0.16	0.01	6
Distance to roads				-0.21	0.01	4
Fir forest	0.05	0.01	10	0.37	0.01	2
Foothill shrub & grass				-0.06	0.01	10
Forest edge:area	0.12	0.01	6			
Montane shrub & grass	-0.09	0.01	7	-0.06	0.01	9
Riparian	0.07	0.01	9	0.11	0.01	8
Slope	-0.02	0.01	11	0.25	0.01	3
Slope2	-0.27	0.01	2	-0.17	0.01	5
Solar insolation	-0.15	0.01	4	0.13	0.01	7
Spring snow	0.09	0.01	8			
Talus	0.13	0.01	5			
TPI	-0.31	0.01	1	-0.42	0.01	1
Intercept	0.20	0.04		0.07	0.03	
Random effect		0.13			0.11	

0.21, SE = 0.01; β_{male} = -0.16, SE = 0.01), while they avoid montane shrub and grass land cover (β_{female} = -0.09, SE = 0.01; β_{male} = -0.06, SE = 0.01), and select for riparian areas (β_{female} = 0.07, SE = 0.01; β_{male} = 0.11, SE = 0.01).

Wolverines displayed some notable differences in their resource selection patterns between sexes (Table 4). Males selected areas close to secondary roads (indicated by a negative scaled RSF coefficient: β_{male} = -0.2, SE = 0.01) and avoided (indicated by a negative coefficient) foothill open areas (β_{male} = -0.06, SE = 0.01). Alternatively, females selected for talus (β_{female} = 0.13, SE = 0.01), for higher forest patch edge:area ratios (β_{female} = 0.12, SE = 0.01) indicating smaller, more fragmented forest patches and for areas with persistent spring snow (β_{female} = 0.09,

Table 5. Resource selection function models developed for wolverines (*Gulo gulo*) monitored in Idaho, Wyoming and Montana as part of research investigating wolverine responses to winter recreation (2010-2015). Model 1 for male and female are the environment only models. Models 2-6 use the environment covariates identified in Model 1 and winter recreation covariates to test hypotheses about the responses of wolverines to different characteristics of winter recreation. Models 2 – 6 were developed separately for males and females.

Models	**Variables**	**Male ∆AIC**	**Female ∆AIC**
Model 1: Female Potential Model	TPI + slope + slope^2+ fir forest + distance to edge + talus + riparian + montane shrub & grass + solar insulation + forest edge:area + spring snow	-	537.79
Model 1: Male Potential Model	TPI + slope + slope^2+ fir forest + distance to edge + distance to roads + riparian + montane shrub & grass + foothill open + solar insulation	41.71	-
Model 2: Potential Model + Rec 1	Model 1 + winter recreation footprint	43.2	286.96
Model 3: Potential Model + Rec 2	Model 1 + distance to linear recreation + dispersed motorized footprint + dispersed non-motorized footprint	355.71	266.1
Model 4: Potential Model + Rec 3	Model 1 + relative intensity of all winter recreation	0	181.44
Model 5: Potential Model + Rec 4	Model 1 + distance to linear recreation + relative intensity dispersed recreation	283.5	60.82
Model 6: Potential Model + Rec 5	Model 1 + distance to linear recreation + relative intensity of dispersed motorized recreation + relative intensity of dispersed non-motorized recreation	249.55	0

SE = 0.01). Areas of high solar insolation were avoided by females (β_{female} = -0.15, SE = 0.01) but selected by males (β_{male} = 0.13, SE = 0.01). Cross-validation of female and male environmental models had similar Spearman rank correlations (r_s) of 0.92 and 0.91, respectively. Out-of-sample data validation similarly showed strong validation (female r_s = 0.86, male r_s = 0.95).

Environment and winter recreation resource selection functions

Of the six models developed for male wolverines (Table 5; Appendix D), Model 4 (combined recreation intensity) had the lowest ∆AIC (Appendix D) and defined our realized habitat model for male wolverines. The next ranked models were the environment-only model (Model 1) and the recreation footprint model (Model 2) with ΔAIC of 41.7 and 43.2, respectively (Table 5). There was a significant avoidance of areas with higher recreation intensity (β_{male} = -0.06, SE = 0.01) though the overall importance of this was relatively low (ranked 9 out of 12 covariates) compared to other coefficients in Model 4 (Table 6). Ten-fold cross-validation of this model showed high support for the model (r_s = 0.91), and the out-of-sample male locations also validated very well (r_s = 0.90).

The best-supported habitat model for female wolverines was Model 6 (Table 5, Appendix D), with covariates for distance to linear recreation and intensity of motorized and non-motorized recreation; all covariates were significant (p-value < 0.01). The second-ranked female model (ΔAIC = 11.8) included the distance to linear recreation and a combined relative intensity dispersed recreation (both motorized and non-motorized). Beta coefficients of Model 6 show females strongly avoided dispersed motorized winter recreation (β_{female} = -0.31, SE = 0.02) as the intensity of the recreation increased and this covariate is the second ranked covariate predicting female resource selection (Table 6). Females also strongly avoided areas of higher intensity dispersed non-motorized winter recreation (β_{female} = -0.19, SE = 0.01), with this predictor ranked fifth. Females avoided areas near recreated roads and groomed routes as indicated by the positive coefficient (β_{female} = 0.08, SE = 0.01), and this covariate ranked 10 out 14. Similar to the male model, both the cross validation and out-of-sample model validation showed strong support (rs = 0.91, rs = 0.83), respectively.

Model 6 did not provide the best overall predictor of male resource selection (Model 4 had the lowest ΔAIC) but it allowed us to compare male response to female responses (Model 6) and to evaluate the differential effects of recreation type on male wolverine responses (Table 6).

Table 6. Standardized model coefficients betas, standard errors and importance rank for male and female wolverine (*Gulo gulo*) RSF models including environment and winter recreation covariates, based on wolverine GPS collar data collected in Idaho, Wyoming and Montana (2010-2015). Female Model 6 and Male Model 4 were identified as the best models based on AIC values, while Male Model 6 provides male responses to specific recreation types. The random effect standard deviation is shown. Blank cells indicate covariates not identified for inclusion in the specified model. The ranked importance of each covariate indicated based on the absolute value of the standardized coefficient. Negative Beta values indicate selection for lower values of the covariate.

	Female Model 6			**Male Model 4**			**Male Model 6**		
	β	SE	Rank	β	SE	Rank	β	SE	Rank
Distance to edge	-0.21	0.01	4	-0.16	0.01	6	-0.16	0.01	4
Distance to roads				-0.22	0.01	4	-0.10	0.01	9
Fir forest	0.05	0.01	14	0.36	0.01	2	0.41	0.01	2
Foothill shrub & grass				-0.06	0.01	11	-0.05	0.01	11
Forest edge:area	0.12	0.01	9						
Montane shrub & grass	-0.06	0.01	13	-0.06	0.01	10	-0.04	0.01	12
Riparian	0.08	0.01	11	0.11	0.01	8	0.11	0.01	8
Slope	-0.07	0.01	12	0.25	0.01	3	0.22	0.01	3
Slope^2	-0.25	0.01	3	-0.16	0.01	5	-0.16	0.01	5
Solar insolation	-0.15	0.01	6	0.13	0.01	7	0.13	0.01	7
Spring snow	0.14	0.01	7						
Talus	0.13	0.01	8						
TPI	-0.32	0.01	1	-0.42	0.01	1	-0.41	0.01	1
Distance to recreated roads	0.08	0.01	10				0.02	0.01	13
Intensity of all recreation				-0.06	0.01	9			
Dispersed motorized recreation intensity	-0.31	0.02	2				-0.07	0.01	10
Dispersed non-motorized recreation intensity	-0.19	0.01	5				-0.15	0.02	6
Intercept	0.17	0.04		0.07	0.03		0.07	0.03	
Random effect		0.13			0.11			0.11	

All covariates in Model 6 were significant (or nearly so) in predicting male wolverine habitat use (Table 6). Similar to females, males avoided areas of higher intensity dispersed motorized recreation (β_{male} = -0.07, SE = 0.01), higher intensity non-motorized dispersed recreation (β_{male} = -0.15, SE = 0.02) and areas close to recreated roads and groomed routes (β_{male} = 0.02, SE = 0.01). But the relative importance of winter recreation to males was more muted than for females. The importance of motorized dispersed winter recreation to male wolverine resource selection ranked 10 out of 13, while avoidance of non-motorized dispersed winter recreation was similar to females at a rank of 6. Avoidance of linear recreation by male wolverines was marginally insignificant (p = 0.056) and this predictor was ranked of lowest relative importance (Table 6).

Potential and realized habitats

The selection coefficients for environmental covariates were nearly identical between the environment-only (potential) habitat model and the selected model including winter recreation (realized habitat model) for both males and females (Tables 4 and 6). This indicated that wolverine selection for these environmental characteristics were stable and relatively independent of human recreation. Across the study area, the classification of potential habitat quality resulted in the prediction of 30% high, 30% moderate, and 40% low quality habitat, with 84% of animal locations found in moderate (28%) and high (56%) quality habitats. Winter recreation resulted in indirect habitat loss of moderate and high quality wolverine habitats as measured by areas transitioning to a lower class when comparing the realized habitat map to the potential habitat map (Figures 6). On average, 14% of female habitat and 11% of male habitat was degraded to lower habitat classes across the study area; calculated as proportions of available moderate and high quality indicates loss of these higher quality habitats range from <10% to >70% within individual home ranges (Appendix D). Both the amount and severity of indirect habitat loss varies across home ranges and is related to the average relative intensity of winter recreation within home ranges (Figure 7a, Appendix D). The incremental effects of winter recreation are high across home ranges with relatively low winter recreation levels, but the rate of indirect habitat loss tend to plateau across home ranges with the highest levels of recreation use (Figure 7a). Female wolverines experienced a higher degree of degradation to high quality habitat (Figure 7b), represented by high quality habitat reduced to low quality habitat (change of 2 classes; Appendix D); an average of 9.6% of available female high quality habitat but only 0.2% of available male high quality habitat was degraded to low quality across the study area.

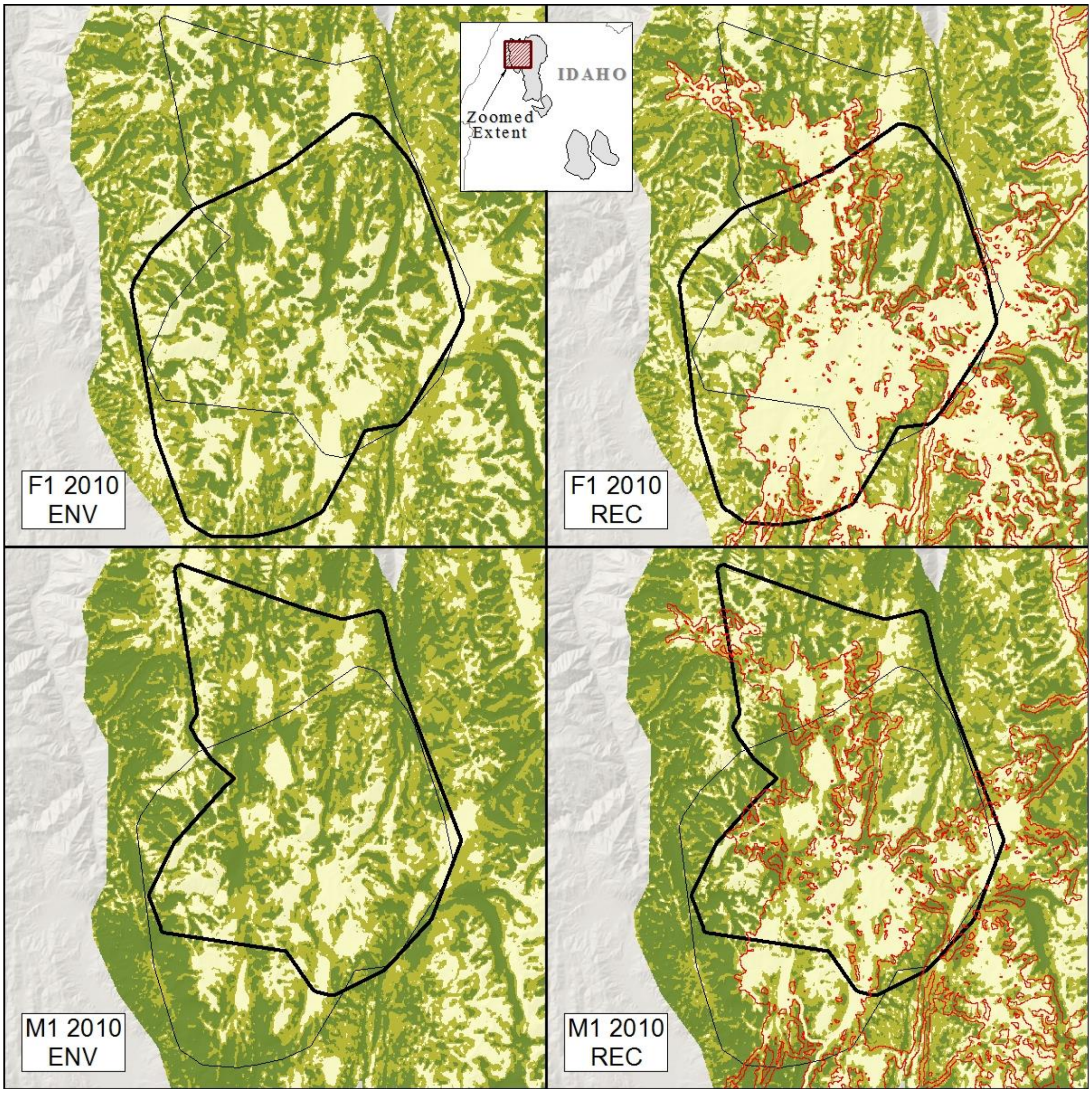


Figure 6. Example maps of potential winter wolverine (Gulo gulo) habitat predicted by the environment only model in the left-hand panels for females (top) and males (bottom) in a portion of the McCall, Idaho study area. The right-hand panel maps the realized habitat models that include winter recreation, and show the change in habitat quality. Three classes of habitat are shown: high quality in dark green, moderate quality in light green and low quality habitat in beige. The bold black lines are the home range boundaries for the animal-year indicated and the thinner black line identifying the overlapping animal of the other sex to facilitate comparing between the upper and lower panels. The red lines indicate the outline of the winter recreation footprint.

These responses translated into more pronounced indirect habitat loss for females compared to males within the same landscapes. For example, a male and female that resided in the same landscape had similar average recreation intensity within their respective home ranges of 0.37 and 0.34 and recreation footprints that covered 47% and 35% of their home ranges (Figure 6). The female experienced predicted indirect habitat losses of 36% and 38% of her high and moderate quality habitats, and 21% of the high-quality habitat was predicted to be degraded to low quality habitat. In contrast, the male experienced predicted habitat degradation to 20% of high and moderate quality habitats, with only 0.9% of high quality habitats predicted to be degraded to low quality habitat.

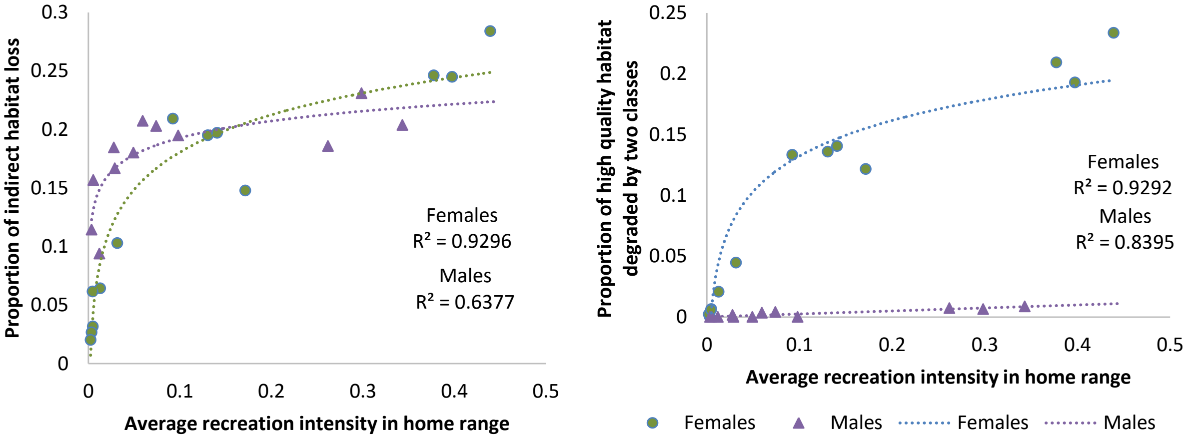


Figure 7. The percent of habitat degraded (left panel) and the severity of that degradation (right panel) across home ranges of wolverines with varying levels of winter recreation intensity. Degradation is defined by the percent of high and moderate quality habitat that degrades by at least 1 class, while severity of the degradation is measured by the proportion of the degradation that is high quality habitat dropping 2 classes to low quality habitat.

Functional Responses to Winter Recreation

The availability of motorized and non-motorized recreation as defined by the mean recreation intensity within home ranges varied notably. The mean motorized recreation intensity ranged from 0.00025 – 0.422 within home ranges. Non-motorized recreation occurred generally within smaller areas and at lower intensity, with a range of values of 0.001 – 0.093 within home ranges. Wolverines displayed negative functional responses in habitat use related to the average relative intensity of both motorized and non-motorized winter recreation (Table 7, Figure 8). Habitat use of areas with motorized recreation decreased as the availability of these areas increased within male and female home ranges, with slopes of 0.22 ($R^2 = 0.4$) and 0.38 ($R^2 = 0.72$), respectively. Similarly, both males and females showed negative functional responses to non-motorized winter recreation, even at the relatively lower average intensities this recreation occurred at. Habitat use of areas with non-motorized recreation declined as the availability of these areas increased within their home ranges, with slopes significantly <1: 0.32 ($R^2 = 0.80$) and 0.10 (R^2=0.13) for males and females, respectively. The male functional response was driven by the high average intensity of non-motorized recreation that one male experienced (2 animal-years) in the Tetons. If the Teton animal is removed, male wolverines do not show a significant functional response to non-motorized winter recreation (Table 7). Additionally, the low R^2 of the female functional response to non-motorized recreation indicates high variation and therefore a weak effect.

Table 7. Functional responses of wolverines (*Gulo gulo*) to dispersed motorized and non-motorized winter recreation measured as the proportional use of recreation intensity compared to the average recreation intensity across home ranges of individual animals. Null hypothesis is: H_0: $\beta_R = 1$, with $\beta_R < 1$ indicating increasing avoidance of recreation with increasing availability and $\beta_R > 1$ indicating increasing selection with increasing availability.

Model	**Male β_0**	**Male β_R (95% CI)**	**R^2**	**Female β_0**	**Female β_R (95% CI)**	**R^2**
Motorized	0.02	0.22 (0.05 – 0.40)	0.40	0.01	0.38 (0.24 – 0.51)	0.72
Non-motorized	0.00	0.32 (0.25 – 0.39)	0.89	0.00	0.10 (-0.05 – 0.24)	0.13
Non-motorized, removing the Teton male	0.001	0.06 (0.17 - -0.05)	0.07	-	-	-

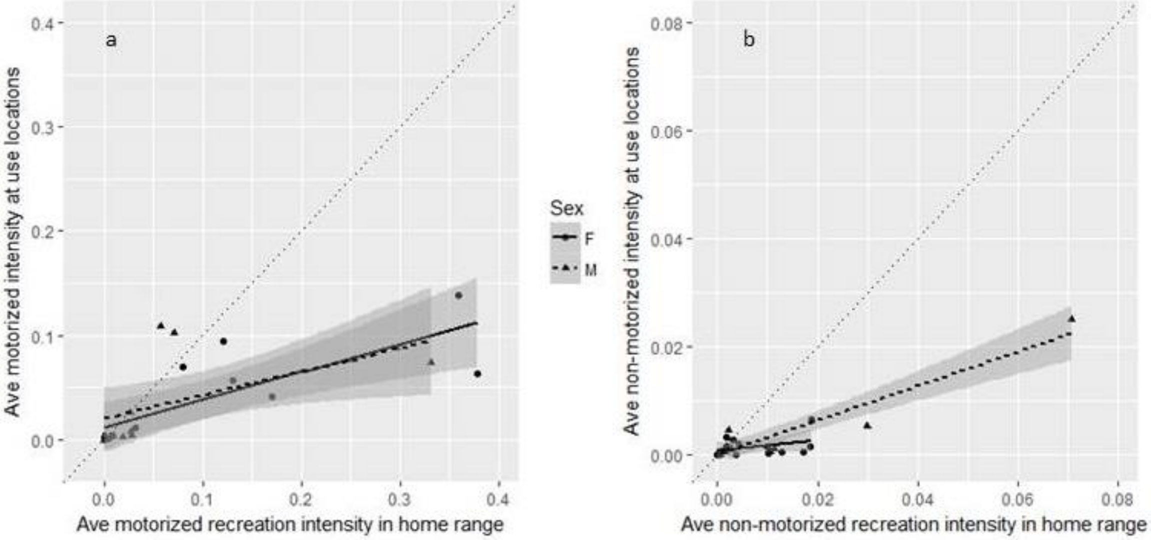


Figure 8. Functional responses of male and female wolverines (*Gulo gulo*) habitat use to the available relative intensity of (a) motorized and (b) non-motorized winter recreation in individual home ranges. The y-axis shows the average relative intensity of recreation at wolverine locations for each monitored wolverine and x-axis shows the average recreation intensity within the animal home range. The dotted 1:1 slope line indicates the null hypothesis expectation and slope if no functional response were present. Responses below the 1:1 line indicate that use is lower than expected based on availability.

Discussion

We found that male and female wolverines showed some notable differences in the selection for environmental covariates, and that their selection for these covariates was independent of the potential effects of winter recreation. The RSF defining the realized habitat models that included winter recreation covariates showed that both males and females responded negatively to increasing intensity of winter recreation within home ranges. Dispersed recreation activities elicited a stronger response than recreation along roads and groomed routes, with females showing more sensitivity to disturbance than males. The functional responses to dispersed recreation, particularly to motorized dispersed recreation, suggests that avoidance results in potentially important indirect habitat loss when a significant portion of an animal's home range receives recreation use, as it is exactly those animals exposed to higher levels of recreation that are most strongly displaced from these areas. Other wolverines were exposed to winter recreation within only a relatively small portion of their large home ranges, and the functional responses also suggest that this limited exposure may mute the indirect habitat loss. The weak avoidance of areas near linear access used by winter recreationists suggests wolverines may be less sensitive to these linear disturbances.

Wolverine habitat selection

Wolverine occur at low densities in northern latitudes and generally in areas with limited human use and infrastructure, creating a multitude of logistical hurdles in conducting detailed research and monitoring of this species. Prior habitat analyses in the Rocky Mountain portion of the North American wolverine distribution have been primarily at the first or second-order landscape scales (Aubry et al. 2007, Copeland et al. 2007, Copeland et al. 2010, Fisher et al. 2013, Inman et al. 2013), identifying characteristics that predict the distribution or presence of wolverines, though Krebs et al. (2007) provides a multi-scale analyses of habitat selection. These efforts have indicated that wolverine are found at higher elevations (Copeland et al. 2007, Krebs et al. 2007, Copeland et al. 2010, Inman et al. 2013), in areas associated with late spring snowpack (Aubry et al. 2007, Copeland et al. 2010, Inman et al. 2013), alpine and subalpine habitats (Aubry et al. 2007) or with higher topographic ruggedness (Krebs et al. 2007, Fisher et al. 2013, Inman et al. 2013) compared to the broader landscape. In contrast to the broader association to more rugged terrain, our work demonstrated wolverines select less extreme topography characterized by concave or drainage bottom type topography (negative coefficient of TPI and slope covariates) and forested landscapes (similar to May et al. 2006, Copeland et al. 2007). We also found an avoidance of open alpine and subalpine areas, but that wolverines are found close to these areas as indicated by their selection for areas near forest edges. Within the winter season, wolverines use lower elevations than in the summer including subalpine and mid-elevation forest types (Copeland et al. 2007, Krebs et al. 2007), which is similar to our result of a selection for fir-associated conifer forests and riparian habitat during winter. Drainage bottom, riparian and forested edge habitats may represent good travel paths or more productive habitats (Scrafford et al. 2017) within a generally low productivity, high elevation landscape.

Prior analyses have also consistently identified the presence of spring snow as an important predictor of wolverine distribution, particularly in the southern portion of the species range in North America (Aubry et al. 2007, Copeland et al. 2010, Inman et al. 2013). We found persistent spring snow was moderately important for predicting female habitat use at the third-order of selection (importance rank of 7 out of 14 covariates). In addition, females also selected for cold areas (negative solar insulation covariate), which also would support the selection for areas with persistent snow. We expect that the selection patterns of our females reflect reproductive denning which has been linked to deep and persistent snowpack (Magoun and Copeland 1998), as 7 of 13 female animal-years represented denning females. Female reproductive dens in Idaho were also associated with high structure such as talus boulders (Magoun and Copeland 1998), which may partially explain our finding that females select for talus, but this covariate was not important for predicting male habitat use. At broader scales, talus selection by wolverines was associated with elevation (Copeland et al. 2007), but we found females selected talus at finest spatial scale tested (Appendix B) and believe this reflects selection for this land cover itself within home ranges. We found that female habitat selection is complex, including characteristics that may be linked to some of the coldest and snowiest habitats as well as characteristics that may represent some of the more productive areas. This complexity in female habitat selection was also described by Krebs et al. (2007) who proposed female selection was driven by a combination of factors including food, predator and human avoidance, while males may also be food-motivated but less risk-averse than females. Copeland et al. (2017) suggest that while food resource availability and distribution are the primary factors shaping female territories, males work toward developing a positive association with females through territory defense and male parental care.

Influence of winter recreation on wolverine habitat selection

Wolverines maintained multi-year home ranges within landscapes that support winter recreation, and some resident animals had >40% of their home range within the footprint of winter recreation suggesting that at some scales wolverines tolerate winter recreation disturbance. Exposure to winter recreation varied notably across study areas and animals despite the focus of this research on areas where backcountry winter recreation is popular. Most animals were exposed to winter recreation within a relatively limited portion of their home ranges, likely due to recreation use being linked to access such as roads and trails (Olson et al. 2017) combined with the large home ranges of wolverines. In some of the highest recreated landscapes, we did not successfully identify wolverines. Our research highlights the previously unrecognized and unrecorded spatial extent and intensity of backcountry winter recreation in remote landscapes. We expect the patterns of backcountry winter recreation across the extent of wolverine distribution in the western United States to be similar to our findings that some individual animals reside in highly disturbed winter landscapes while others are exposed to relatively low levels of winter recreation. While wolverine home ranges may be notably large, they still represent the minimum spatial requirement necessary to provide for needs of the individual as well as offspring and kin as expressed by the resource dispersion hypothesis (Macdonald and Johnson 2015, Copeland et al. 2017).

Harris et al. (2014) found that the total area disturbed by winter recreation is more important than the intensity of recreation use for northern ungulates. As measured in our study areas, these two metrics are correlated, and it would be difficult to disentangle the responses of wolverines to each independently. Still, models including relative intensity of winter recreation were selected over those models that characterized the footprint of winter recreation, and both within home range and across landscapes wolverines avoid areas with higher intensity winter recreation. The amount of indirect habitat loss is also related to the relative intensity of winter recreation within the home range. Habitat displacement and indirect habitat loss from winter recreation activities have been documented in a diverse array of montane and alpine species. High elevation forest grouse (*Tetrao* sp.) are impacted by backcountry winter recreation including habitat displacement as well as energetic and physiological effects (Patthey et al. 2008, Braunisch et al. 2011, Arlettaz et al. 2015, Coppes et al. 2017b). Endangered mountain caribou in southern British Columbia have been displaced from high quality winter habitat due to high levels of snowmobile recreation (Seip et al. 2007). In the Teton Mountains of Wyoming, backcountry ski recreation resulted in a 30% loss of high quality winter habitat to bighorn sheep (Courtemanch 2014). Mountain goats avoided otherwise high quality habitat associated with a developed ski area near Banff, Alberta (Richard and Cote 2016). The negative functional responses of wolverines to increasing intensity of winter recreation indicate that individual animals that have the most extensive portions of their home range affected by recreation are also the animals with the strongest avoidance of these areas. Alternatively, we would expect a more muted response by wolverines in areas with low levels of winter recreation as compared to the population average response. As backcountry winter recreation grows in numbers of participants as well as in localized intensity of use and overall footprint, we need to understand the potential effects on wildlife species, particularly on sensitive, special-status or rare species.

Female wolverines appeared to discriminate between different types of winter recreation with the best supported female model containing separate predictors for linear recreation travel, dispersed motorized recreation and dispersed non-motorized recreation. Females avoid all three forms of winter recreation but the relative importance of each is different. Females show a strong avoidance of areas with dispersed non-motorized recreation (importance rank of 5 of 11), though these areas are limited within home ranges (<5% of home ranges affected by non-motorized recreation on average). Motorized dispersed winter recreation is the second most important predictor of female habitat selection (topographic position is the most important), indicating that this disturbance has a strong influence on female wolverine habitat selection in areas where motorized recreation occurs. This strong avoidance combined with the potential for motorized recreation to cover larger areas may lead to important indirect habitat loss for female wolverines.

Krebs et al (2007) also found that female wolverines avoided areas of winter recreation and argued this supports the hypothesis that female habitat selection is consistent with a risk-averse pattern. In contrast to females, male wolverines do not appear as sensitive to winter recreation in general, with the winter recreation covariate of lower importance (rank of 9 of 11 standardized covariates) in predicting male wolverine habitat selection. Krebs et al (2007) also found that human disturbance was less important for males than females in that 3 of 4 top ranking male habitat models did not include human disturbance and they suggested that male wolverine were less risk-averse than female wolverine.

Despite concerted efforts to identify and trap wolverines in the Tetons, we only captured a single male, estimated age of 13 years based on prior research handling as a subadult. We recorded the highest and most extensive backcountry non-motorized winter recreation in the Teton study area and this animal was exposed to higher levels of non-motorized recreation than other wolverines in our study. He exhibited strong avoidance of non-motorized recreation, but we are cautious in our interpretation of this given our limited information on wolverines exposed to higher levels of non-motorized recreation. Still, the response of this wolverine reinforces our suggestions that the strength of avoidance exhibited by wolverines to non-motorized recreation depends on the intensity of recreation within their home ranges, similar to the functional response of wolverines to motorized recreation. As expected, the removal of the Teton animal from the functional response analysis strongly influenced our results and limited our ability to conclude a negative functional response of male wolverines to non-motorized recreation (Table 7). Thus, it would be useful to perform additional monitoring of male (and female) wolverines that are exposed to higher levels of non-motorized winter recreation such as we recorded in the Teton study area.

Roads and linear winter access

Males were found closer to roads than expected and these roads were identified as an important predictor of male habitat selection but not female selection (suggesting females do not strongly respond to the proximity of roads). In our study, these roads were snow-covered and most were not plowed or maintained for winter use. Research examining wolverine responses to human infrastructure has suggested wolverines avoid roads, roaded areas and development (May et al. 2006, Fisher et al. 2013, Inman et al. 2013, Stewart et al. 2016, Heim et al. 2017). At a landscape scale, the negative association may be partially confounded by the fact that wolverines are naturally not found in lower elevation valley habitats where human infrastructure is higher. We found that within home ranges during winter, human use of roads may be important than the existence of the road itself in determining wolverine responses. Male wolverines were found closer than expected to unused roads but both male and female wolverines avoided areas near roads and groomed routes with winter recreation use, though male avoidance was of low importance (rank 13 of 13). Recent research in northern Canada also found that both males and female wolverines avoided active winter roads, though they may select for some other types of human infrastructure associated with roads that provide potential foraging opportunities (Scrafford et al. 2017). Roads accessible by hunters in the fall may be associated with ungulate gut piles or wounding mortalities that are potential scavenging opportunities for wolverines (Mattisson et al. 2016); many of these roads are not used by people in winter and foraging opportunities may partially explain male attraction to areas close to these unused roads. While both males and females avoided areas near actively recreated roads, this avoidance was not as important as avoidance of dispersed motorized and dispersed non-motorized recreation, suggesting that spatially predictable recreation travel patterns may be perceived by wolverines as less risky. (Harris et al. 2014) also found higher disturbance to northern ungulates from recreation that is unpredictable in space or time than from road-based recreation.

Cumulative impacts of climate change and winter recreation

Both wolverines and backcountry winter recreation are expected to be affected by climate change, potentially resulting in an increased overlap between winter recreation and wolverine distribution as they both respond to declining snow extent, depth and the snow season. In the southern portion of their North American range, wolverines appear to be tightly linked to the area defined by the presence of persistent spring snow (Aubry et al. 2007, Copeland et al. 2010, Inman et al. 2013). The underlying ecological requirements that drive this close relationship may include denning requirements (Magoun and Copeland 1998, Copeland et al. 2010) and a dependence on scavenging large ungulate carcasses effectively preserved within and under the snowpack (Mattisson et al. 2016). Additional potential factors contributing to wolverine association with areas supporting persistent spring snow may include caching food under snow and associated cold micro-climates (Inman et al. 2012) and competitor or predator avoidance (Mattisson et al. 2016). Heim et al. (2017) suggested that the association of wolverines to persistent spring snow makes them vulnerable to climate changes and McKelvey et al. (2011) predicted a 67% loss of wolverine habitat in the western United States by 2059 due to loss of snowpack.

The demonstrated loss of snow pack and reduced winter length (Mote et al. 2005) will also have profound impacts for winter recreation in the future (Bowker et al. 2012, White et al. 2016, Wobus et al. 2017). While the reductions in winter length are predicted to cause a decline in per capita participation in winter recreation, human population growth counters these declines and most projections of winter recreation are stable or increasing (Bowker et al. 2012, White et al. 2016, Wobus et al. 2017). Winter recreationists will likely need to adapt when and where they recreate to adjust to shortened snow season and reduction of winter recreation areas due to snow loss (Dawson et al. 2013, Rutty et al. 2015). This would result in winter recreation becoming more concentrated and intense in space and time (Dawson et al. 2013, Rutty et al. 2015), especially during the mid to late winter period when snowpack is predicted to be the most consistent (Mote et al. 2005). This is also the time period when female wolverines are entering reproductive dens. Predictions of winter recreation distribution and intensity would likely suggest even more severe indirect habitat loss than our current assessment indicates. Thus, managers must consider growth of the recreation industry concurrent with declining ‘habitat’ for winter recreation, which will potentially exacerbate conflicts between recreation and wildlife.

Conclusion

Outdoor recreation provides avenues for people to connect with nature and is an important economic and cultural component of the small communities that serve as gateways to some of our larger natural areas. Balancing the many positive benefits of encouraging outdoor recreation with the impacts it may have on these natural systems is a growing field of study. Our research into the potential effects of winter recreation on wolverines represents information at spatial and temporal scales rarely achieved in other disturbance research. Clearly, at some point, displacement from high quality habitats would affect the reproductive and survival fitness of animals. Given the low density and fragmented nature of wolverines in the contiguous United States, impacts to the relatively few reproductive females should be minimized. We found that the effects of winter recreation on wolverine habitat are dependent upon the relative intensity of recreation and that winter recreation patterns are highly variable at the scale of wolverine home ranges. Some animals may be exposed to important levels of indirect habitat loss due to avoidance of areas with winter recreation while adjacent animals have relatively little exposure. We recommend that additional research is needed to understand winter recreation distribution and relative intensity within potential wolverine habitats across the western United States and elsewhere where backcountry winter recreation activities are popular. Approaches to documenting and monitoring the extent and relative intensity of backcountry winter recreation in an efficient and effective manner needs additional development, and we suggest approaches that combine modeling the potential for recreation (e.g. Olson et al. 2017) with field efforts to identify the realized extent of existing recreation, such as the standardized aerial surveys we undertook.

Our results suggest that winter recreation should be considered when assessing wolverine habitat suitability, cumulative effects and conservation. Our research provides land managers with a more detailed understanding of important habitat characteristics used by wolverines within home ranges and should inform management of wolverine habitats across the large landscapes they require. Further, it shows that female wolverines are sensitive to dispersed winter recreation which results in indirect habitat loss during the critical denning season. The functional responses to dispersed winter recreation provide insight into these negative effects, and suggest that lower levels of dispersed recreation will have less effect on wolverines than more widespread and intense recreation. We also found that recreation use of roads and groomed routes has low influence on male and female wolverine habitat use. Our research also shows that males are less sensitive to dispersed recreation, and therefore may be a lower management priority. While extremely challenging with a rare species residing in remote landscapes, research is needed that links population-level metrics to habitat and habitat conditions. These backcountry landscapes represent critical habitats for wolverines, important and highly valued areas for people to connect with nature, and are economic drivers for the small communities that surround them. Solutions to finding a balanced approach to sustaining the diverse values of these wild landscapes requires creative approaches and collaboration between land managers, stakeholders and wildlife professionals.

Literature Cited

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control **19**:716-723.

Arlettaz, R., S. Nusslé, M. Baltic, P. Vogel, R. Palme, S. Jenni-Eiermann, P. Patthey, and M. Genoud. 2015. Disturbance of wildlife by outdoor recreation: allostatic stress response and altered activity-energy budgets. Ecological Applications **25**:1197-1212.

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

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software **67**:1-48.

Bowker, J. M., A. E. Askew, H. K. Cordell, C. J. Betz, S. J. Zarnoch, and L. Seymour. 2012. Outdoor recreation participation in the United States - Projections to 2060. Page 42. Southern Research Station.

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

Boyle, S. A., and F. B. Samson. 1985. Effects of nonconsumptive recreation on wildlife: A review. Wildlife Society Bulletin **13**:110-116.

Braunisch, V., P. Patthey, and R. Arlettaz. 2011. Spatially explicit modeling of conflict zones between wildlife and snow sports: prioritizing areas for winter refuges. Ecological Applications:955.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: A practical information-theoretic approach. Page xx+353 *in* K. P. Burnham and D. R. Anderson, editors. Model selection and inference: A practical information-theoretic approach. Springer-Verlag New York, Inc. ; Springer-Verlag, 175 Fifth Avenue, New York, New York 10010 ; Heidelberger Platz 3, D-1000 Berlin, Germany.

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

Copeland, J. P., A. Landa, K. S. Heinemeyer, K. B. Aubry, J. van Dijk, R. May, J. Persson, J. R. Squires, and R. Yates. 2017. Social ethology of the wolverine.*in* D. W. Macdonald, C. Newman, and L. A. Harrington, editors. Biology and conservation of Musteloids. Oxford University Press.

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

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

Coppes, J., F. Burghardt, R. Hagen, R. Suchant, and V. Braunisch. 2017a. Human recreation affects spatio-temporal habitat use patterns in red deer (Cervus elaphus). PLoS ONE **12**:1-19.

Coppes, J., J. Ehrlacher, R. Suchant, and V. Braunisch. 2017b. Outdoor recreation causes effective habitat reduction in capercaillie Tetrao urogallus: a major threat for geographically restricted populations. Journal of Avian Biology.

Courtemanch, A. B. 2014. Seasonal habitat selection and impacts of backcountry recreation on a formerly migratory bighorn sheep population in northwest Wyoming, USA. University of Wyoming.

Dawson, J., D. Scott, and M. Havitz. 2013. Skier demand and behavioural adaptation to climate change in the US Northeast. Leisure/Loisir **37**:127-143.

DeCesare, N. J., M. Hebblewhite, F. Schmiegelow, D. Hervieux, G. J. McDermid, L. Neufeld, M. Bradley, J. Whittington, K. G. Smith, L. E. Morgantini, M. Wheatley, and M. Musiani. 2012. Transcending scale dependence in identifying habitat with resource selection functions. Ecological Applications **22**:1068-1083.

Ewacha, M. V. A., J. D. Roth, W. G. Anderson, D. C. Brannen, and D. L. J. Dupont. 2017. Disturbance and chronic levels of cortisol in boreal woodland caribou. The Journal of Wildlife Management **81**:1266-1275.

Fahlman, A., J. M. Arnemo, J. Persson, P. Segerstrom, and G. Nyman. 2008. Capture and medetomidine-ketamine anesthesia of free-ranging wolverines (Gulo gulo). Journal of Wildlife Diseases **44**:133-142.

Fisher, J. T., S. Bradbury, B. Anholt, L. Nolan, L. Roy, J. P. Volpe, and M. Wheatley. 2013. Wolverines (Gulo gulo luscus) on the Rocky Mountain slopes: natural heterogeneity and landscape alteration as predictors of distribution. Canadian Journal of Zoology **91**:706-716.

Frair, J. L., S. E. Nielsen, E. Merrill, R. L. Subhash, M. S. Boyce, R. H. M. Munro, G. Stenhouse, and H. Beyer. 2004. **Removing GPS collar bias in habitat selection studies**. Journal of Applied Ecology **41**:201-212.

Friedman, J., T. Hastie, and R. Tibshirani. 2010. Regularization paths for generalized linear models vai coordinate descent. Journal of Statistical Software **33**:1-22.

Getz, W. M., S. Fortmann-Roe, P. C. Cross, A. J. Lyons, S. J. Ryan, and C. C. Wilmers. 2007. LoCoH: nonparameteric kernel methods for constructing home ranges and utilization distributions. PLoS ONE **2**:e207.

Gifford, R., and A. Nilsson. 2014. Personal and social factors that influence pro-environmental concern and behaviour: A review. International Journal of Psychology **49**:141-157.

Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology **75**:887-898.

Harris, G., R. M. Nielson, T. Rinaldi, and T. Lohuis. 2014. Effects of winter recreation on northern ungulates with focus on moose (Alces alces) and snowmobiles. European Journal of Wildlife Research **60**:45-58.

Hash, H. S. 1987. Wolverine. Pages 575-585 *in* M. Novak, editor. Wild furbearer management and conservation in North America. Ontario Trappers Association.

Hebblewhite, M., and E. Merrill. 2008. Modelling wildlife-human relationships for social species with mixed-effects resource selection models. Journal of Applied Ecology **45**:834-844.

Hebblewhite, M., D. G. Miquelle, H. Robinson, D. G. Pikunov, Y. M. Dunishenko, V. V. Aramilev, I. G. Nikolaev, G. P. Salkina, I. V. Seryodkin, V. V. Gaponov, M. N. Litvinov, A. V. Kostyria, P. V. Fomenko, and A. A. Murzin. 2014. Including biotic interactions with ungulate prey and humans improves habitat conservation modeling for endangered Amur tigers in the Russian Far East. Biological Conservation **178**:50-64.

Heim, N. A., J. T. Fisher, A. P. Clevenger, J. Paczkowski, and J. Volpe. 2017. Cumulative effects of climate and landscape change drive spatial distribution of Rocky Mountain wolverine (*Gulo gulo* L.). Ecology and Evolution **7**:8903-8914.

Helzer, C. J., and D. E. Jelinski. 1999. The relative importance of patch area and perimeter-area ratio to grassland breeding birds. Ecological Applications **9**:1448-1458.

Hilbe, J. M. 2015. Practical guide to logistic regression. CRC Press, Talyor & Francis Group, Boca Raton, FL, USA.

Holbrook, J., J. R. Squires, L. Olson, N. J. DeCesare, and R. Lawrence. 2017. Understanding and predicting habitat for wildlife conservation: the case of Canada lynx at the range periphery. Ecosphere **8**:e01939.

Hosmer, D. W., S. Lemeshow, and R. X. Sturdivant. 2013. Applied logistic regression (3rd ed.). 3rd edition edition. John Wiley & Sons, Inc, Hoboken, New Jersey, USA.

Inman, R. M., B. L. Brock, K. H. Inman, S. S. Sartorius, B. C. Aber, B. Giddings, S. L. Cain, M. L. Orme, J. A. Fredrick, B. J. Oakleaf, K. L. Alt, E. Odell, and G. Chapron. 2013. Developing priorities for metapopulation conservation at the landscape scale: Wolverines in the Western United States. Biological Conservation **166**:276-286.

Inman, R. M., A. J. Magoun, J. Persson, and J. Mattisson. 2012. The wolverine's niche: linking reproductive chronology, caching, competition, and climate. Journal of Mammalogy **93**:634-644.

Johnson, C. J., M. S. Boyce, R. L. Case, H. D. Cluff, R. J. Gau, A. Gunn, and R. Mulders. 2005. Cumulativ effects of human developments on arctic wildlife. Wildlife Monographs:1-36.

Johnson, C. J., S. E. Nielsen, E. H. Merrill, T. L. McDonald, and M. S. Boyce. 2006. Resource selection functions based on use-availability data: Theoretical motivation and evaluation methods. Journal of Wildlife Management **70**:347-357.

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

Knight, R. L., and K. J. Gutzwiller. 1995. Wildlife and recreationist coexistence through management and research. Island Press, Covelo, California.

Knopff, K. H., A. A. Knopff, M. B. Warren, and M. S. Boyce. 2009. Evaluating Global Positioning System Telemetry Techniques for Estimating Cougar Predation Parameters. Journal of Wildlife Management **73**:586-597.

Krebs, J., E. C. Lofroth, and I. Parfitt. 2007. Multiscale Habitat Use by Wolverines in British Columbia, Canada. Journal of Wildlife Management **71**:2180.

Laliberte, A. S., and W. J. Ripple. 2004. Range contractions of North American carnivores and ungulates. Bioscience **54**:123-138.

Larson, C. L., S. E. Reed, A. M. Merenlender, and K. R. Crooks. 2016. Effects of Recreation on Animals Revealed as Widespread through a Global Systematic Review. PLoS ONE **11**:e0167259.

Lele, S. R., E. H. Merrill, J. Keim, and M. S. Boyce. 2013. Selection, use, choice, and occupancy: clarifying concepts in resource selection studies. J Anim Ecol **82**:1183-1191.

Lesmerises, F., F. Déry, C. J. Johnson, and M.-H. St-Laurent. 2018. Spatiotemporal response of mountain caribou to the intensity of backcountry skiing. Biological Conservation **217**:149-156.

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

Macdonald, D. W., and D. D. P. Johnson. 2015. Patchwork planet: the resource dispersion hypothesis, society, and the ecology of life. Journal of Zoology **295**:75-107.

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

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analyses for field studies, second ed. Kluwer Academic Publishers, Dordrecht, Netherlands.

Mattisson, J., G. R. Rauset, J. Odden, H. Andren, J. D. C. Linnel, and J. Persson. 2016. Predation or scavening? Prey body condition influences decision-making in a facultative predator, the wolverine. Ecosphere **7**:1-14.

May, R., A. Landa, J. Van Dijk, J. D. C. Linnell, and R. Andersen. 2006. Impact of infrastructure on habitat selection of wolverines *Gulo gulo*. Wildlife Biology **12**:285-295.

McDonald, T. L. 2013. The point process use-availability or presence-only likelihood and comments on analysis. J Anim Ecol **82**:1174-1182.

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

Moreau, G., D. Fortin, S. Couturier, and T. Duchesne. 2012. Multi-level functional responses for wildlife conservation: the case of threatened caribou in managed boreal forests. Journal of Applied Ecology **49**:611-620.

Mote, P. W., A. F. Hamlet, M. P. Clark, and D. P. Lettenmaier. 2005. Declining mountain snowpack in western North America. Bulletin of the American Meteorological Society **86**:39-49.

Mysterud, A., and R. A. Ims. 1998. Functional responses in habitat use: Availability influences relative use in trade-off situations. Ecology **79**:1435-1441.

Neumann, W., G. Ericsson, and H. Dettki. 2009. Does off-trail backcountry skiing disturb moose? European Journal of Wildlife Research **56**:513-518.

Nielsen, S. E., G. J. McDermid, G. B. Stenhouse, and M. S. Boyce. 2010. Dynamic wildlife habitat models: seasonal foods and mortality risk predict occupancy-abundance and habitat selection in grizzly bears. Biological Conservation **143**:1623-1634.

Nielson, R., B. F. J. Manley, L. L. McDonald, H. Sawyer, and T. L. McDonald. 2009. **Estimating habitat selection when GPS fix success is less than 100%**. Ecology **90**:2956-2962.

Noss, R. F., H. B. Quigley, M. G. Hornocker, T. Merrill, and P. C. Paquet. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. Conservation Biology **10**:949-963.

Olson, L. E., J. R. Squires, E. K. Roberts, A. D. Miller, J. S. Ivan, and M. Hebblewhite. 2017. Modeling large-scale winter recreation terrain selection with implications for recreation management and wildlife. Applied Geography **86**:66-91.

Parker, K. L., C. T. Robbins, and T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elf. Journal of Wildlife Management **48**:474-488.

Patthey, P., S. Wirthner, N. Signorell, and R. Arlettaz. 2008. Impact of outdoor winter sports on the abundance of a key indicator species of alpine ecosystems. Journal of Applied Ecology **45**:1704-1711.

Polfus, J. L., M. Hebblewhite, and K. Heinemeyer. 2011. Identifying indirect habitat loss and avoidance of human infrastructure by northern mountain woodland caribou. Biological Conservation **144**:2637-2646.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reineking, B., and B. Schröder. 2006. Constrain to perform: Regularization of habitat models. Ecological Modelling **193**:675-690.

Richard, J. D., and S. D. Cote. 2016. Space use analyses suggest avoidance of a ski area by mountain goats. Journal of Wildlife Management **80**:387-395.

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

Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, M. Letnik, M. P. Nelson, O. J. Schmitz, D. W. Smith, A. D. Wallach, and A. J. Wirsing. 2014. Status and ecological effects of the world's largest carnivores. Science **343**:123-148.

Rutty, M., D. Scott, P. Johnson, E. Jover, M. Pons, and R. Steiger. 2015. Behavioural adaptation of skiers to climatic variability and change in Ontario, Canada. Journal of Outdoor Recreation and Tourism **11**:13-21.

Sato, C. F., J. T. Wood, and D. B. Lindenmayer. 2013. The effects of winter recreation on alpine and subalpine fauna: a systematic review and meta-analysis. PLoS ONE **8**:e64282.

Scott, D., J. Dawson, and B. Jones. 2008. Climate change vulnerability of the US Northeast winter recreation– tourism sector. Mitigation and Adaptation Strategies for Global Change **13**:577-596.

Scrafford, M. A., T. Avgar, B. Abercrombie, J. Tigner, and M. S. Boyce. 2017. Wolverine habitat selection in response to anthropogenic disturbance in the western Canadian boreal forest. Forest Ecology and Management **395**:27-36.

Seip, D. R., C. J. Johnson, and G. S. Watts. 2007. Displacement of mountain caribou from winter habitat by snowmobiles. Journal of Wildlife Management **71**:1539-1544.

Service, F. a. W. 2013. Proposed rule: Endangeed and threatened wildlife and plants; threatened status for the distinct population segment of the North American wolverine occurring in the contiguous United States. Pages 7863-7890 *in* I. Fish and Wildlife Service, editor. 78 FR 7863. Federal Register: The daily journal of the United States Government.

Smith, J. S., and K. Heinemeyer. 2016. Modeling talus habitat using NAIP imagery and topographic features in portions of Idaho, Montana and Wyoming. Round River Conservation Studies, Bozeman, MT.

Squires, J. R., K. Heinemeyer, and M. Hebblewhite. 2018. A study of shared winter habitats: tracking forest carnivores and backcountry recreationists. The Wildlife Professional **In Press**.

Steven, R., C. Pickering, and J. Guy Castley. 2011. A review of the impacts of nature based recreation on birds. Journal of Environmental Management **92**:2287-2294.

Stewart, F. E. C., N. A. Heim, A. P. Clevenger, J. Paczkowski, J. P. Volpe, and J. T. Fisher. 2016. Wolverine behavior varies spatially with anthropogenic footprint: implications for conservation and inferences about declines. Ecology & Evolution (20457758) **6**:1493-1503.

Tablado, Z., and J. Lukas. 2017. Determinants of uncertainty in wildlife responses to human disturbance. Biol Rev Camb Philos Soc **92**:216-233.

Taylor, A. R., and R. L. Knight. 2003. Wildlife responses to recreation and associated visitor perceptions. Ecological Applications **13**:951-963.

Teisl, M. F., and K. O'Brien. 2003. Who cares and who acts? Outdoor Recreationists exhibit different levels of enviornmental concern and behavior. Environment and Behavior **35**:506-522.

Telfer, E. S., and J. P. Kelsall. 1979. Studies of morphological parameters affecting ungulate locomotion in snow. Can. J. Zool. **57**:2153-2159.

Tibshirani, R. 1996. Regression Shrinkage and Selection via the Lasso. Journal of the Royal Statistical Society. Series B (Methodological) **58**:267-288.

Trainor, A. M., and O. J. Schmitz. 2014. Infusing considerations of trophic dependencies into species distribution modelling. Ecology Letters **17**:1507-1517.

Weiss, A. D. 2001. Topographic positions and landform analyses. Poster Presentation. ESRI User Conference, San Diego, California, USA.

White, E. M., J. M. Bowker, A. E. Askew, L. L. Langner, J. R. Arnold, and D. B. K. English. 2016. **Federal Outdoor Recreation Trends: Effects on Economic Opportunities**. Pages 1-56 General Technical Report. Pacific Northwest Research Station

Wobus, C., E. E. Small, H. Hosterman, D. Mills, J. Stein, M. Rissing, R. Jones, M. Duckworth, R. Hall, M. Kolian, J. Creason, and J. Martinich. 2017. Projected climate change impacts on skiing and snowmobiling: A case study of the United States. Global Environmental Change **45**:1-14.

Appendix A: Wolverine capture and monitoring

This appendix provides additional details about the collection and processing of wolverine location information.

Trapping and handling

We attempted to confirm the presence of wolverines within each of our study areas through pre-baiting with remote cameras using road-killed deer or elk and a skunk-based lure. In study areas where we successfully identified and captured wolverines, we live-trapped, collared and monitored wolverines for a minimum of two years. In the Centennial Mtns, we live-trapped and/or camera trapped for 3 years (2014-2016) without evidence of wolverine presence; in the Trinity Mtns (2012-2015), we or the USFS collaborators camera trapped for three years without evidence of wolverine presence. In the Teton Mtns, we live-trapped and camera trapped for 3 years (2014-2016) and only captured one male wolverine estimated to be 13 years old based on prior research handling when he was estimated to be a subadult.

We built log-based box traps on-site using existing downed logs or cutting trees if permitted within the specific study area. In the West Yellowstone and Teton study areas, we refurbished log traps built by the Wildlife Conservation Society personnel for an earlier research effort, and in the Grand Teton National Park we either also refurbished existing traps or brought in lumber to build traps (Lofroth et al. 2008) that were removed at the end of the trapping season. New trap locations across all study areas was based primarily on evidence of wolverine presence, including prior remote camera surveys done as part of our preparations or by prior survey effort. Nearly all traps required snowmobiles to access, except in the Tetons where ski or snowshoe-based access was used for traps with the Grand Teton National Park. We attempted to pre-bait all trap sites using road-killed deer by mid-December depending upon access, and opened traps in early January. In the first year (2010), traps were remotely monitored 2-3 times/daily using VHF based trap transmitters (Telonics trapsite transmitters, TBT series; Telonics, Inc, Mesa, AZ, USA), and starting the second year (2011) all traps were equipped with the satellite-based trap transmitters (Vectronics trap transmitters TT2, TT3; Vetronic Aerospace GmbH, Berlin, Germany) that notified us immediately when a trap door closed. We limited visits to traps primarily to daylight hours for safety except during the recapture efforts in late March-April when we checked traps when they closed regardless of time to minimize the capture time of any lactating female. If any new or unidentified wolverine was captured during the recapture period, we collected a hair and/or saliva sample and released it, and only anesthetized animals to remove collars.

Aerial telemetry monitoring and identification of denning females

We flew telemetry flights intermittently throughout the duration of the winter season to confirm the functioning collars and presence of collared animals. Starting in mid-February, we increased our aerial monitoring of collared females to every 2-3 days to identify localized behavior and potential reproductive dens. The Telemetry Solution collars (Quantum 4000 collar from Telemetry Solutions, Concord, CA, USA) provided the ability to remotely download data through a UHF connection, which we used to confirm localized behaviors. We continued to monitor potentially denning females primarily from the air but occasionally it was also possible to use a near-by ridge or other discreet ground-based location to confirm continued occupancy for dens. Confirmation of denning was both through the intensive GPS location monitoring as well as identification of swollen teats and milk in females recaptured for collar removal (Table

A1.1). Field crews also visited den sites after abandonment in the following summer to document latrines, prey remains and characteristics of the den site itself.

Wolverine GPS location data and home range summary

Table A. 1. Summary of wolverine location data including assessed denning status, start and end dates for GPS monitoring, the k parameter used in the LoCoH home range estimate and the area of the resulting home ranges.

Animal-year	Study Area	GPS N	Denning Status	Start Date	End Date	LoCoH k	Km^2	Mi^2
F11.2014	Henry Mtns	2067	Not denning	1/19/2014	4/9/2014	46	250	96
M15.2015	Henry Mtns	2881	Male	1/25/2015	5/5/2015	71	1485	573
F1.2010	McCall	1247	Denning	1/30/2010	3/31/2010	62	397	153
F1.2012	McCall	1757	Not denning	1/15/2012	3/10/2012	82	336	130
F10.2014	McCall	3079	Denning	1/14/2014	4/19/2014	93	420	162
F2.2010	McCall	1844	Denning	1/30/2010	3/21/2010	64	228	88
F2.2011	McCall	2632	Not denning	1/25/2011	4/10/2011	92	248	96
F3.2010	McCall	1372	Denning	2/20/2010	4/3/2010	44	239	92
F3.2014	McCall	2496	Not denning	1/4/2014	3/24/2014	148	281	108
F4.2011	McCall	1386	Not denning	1/22/2011	3/16/2011	102	153	59
F5.2011	McCall	1677	Denning	1/30/2011	4/2/2011	96	377	146
M1.2010	McCall	806	Male	2/2/2010	3/10/2010	32	401	155
M1.2011	McCall	1974	Male	1/18/2011	3/15/2011	77	779	301
M1.2014	McCall	2947	Male	1/25/2014	4/13/2014	104	791	306
M12.2014	McCall	3778	Male	1/11/2014	5/27/2014	121	2158	833
M2.2010	McCall	2648	Male	2/5/2010	4/20/2010	64	994	384
M2.2011	McCall	2059	Male	2/10/2011	4/3/2011	56	1334	515
M3.2010	McCall	1340	Male	2/11/2010	4/26/2010	44	934	361
F7.2012	Stanley	1489	Not denning	2/5/2012	3/12/2012	89	375	145
F8.2013	Stanley	1943	Denning	2/2/2013	3/31/2013	80	328	126
F9.2012	Stanley	1627	Denning	2/10/2012	4/26/2012	86	126	49
M6.2012	Stanley	1896	Male	1/17/2012	3/11/2012	107	1087	420
M8.2012	Stanley	2618	Male	1/17/2012	3/24/2012	107	1988	767
M13.2014	Tetons	2766	Male	2/22/2014	7/18/2014	147	1094	422
M13.2015	Tetons	2972	Male	1/14/2015	4/3/2015	159	867	335

Appendix B: Description of Environment Covariates

This appendix provides additional detailed descriptions of the environment covariates acquired or developed to support the spatial analyses

Identification of environment covariates

Table B. 1. Environmental and winter recreation covariates identified for consideration in the wolverine winter resource selection function (RSF) models to understand wolverine responses to winter recreation in Idaho, Wyoming and Montana, 2010-2015. The native resolution indicated the finest resolution spatial information available, while the selected resolution is based on analyses following DeCesare et al. (2012). We provide information regarding the source of the data or derivation methods, and if and why the covariate was removed from the analyses.

Covariate	Native scale	Selected Scale (m)	Source	Description
Environment covariates				
Elevation	30	30	USGS National Elevation data	Collinear with multiple other covariates, removed
Slope	30	500	Derived from USGS National Elevation data	Slope (degrees), input as quadratic (Slope + Slope^2)
Aspect	30	Variable	Derived from USGS National Elevation data	Assessed categorical; high AIC relative to solar insolation, removed
Terrain ruggedness	30	100	Riley et al. (1999)	Topographic complexity; collinear with slope, removed
Topographic position index (TPI)	30	300	Weiss (2001)	Measure of landscape concavity or convexity
Solar Insolation	30	50	ESRI Area Solar Radiation tool	Index of solar insolation
Edge:area forest patch ratio	30	1000	Helzer and Jelinski (1999), using 30m resampled talus-forest cover classification of 2015 NAIP Imagery	Calculated as the length of edge/area of forest areas
Distance to forest edge	Vector	N/A	Derived from 30 m resampled talus-forest cover classification of 2015 NAIP Imagery	2D distance to forest edge, both from inside and outside the forest
Spring snow model	500	1000	MODIS Snow Cover Daily L3 Global 500m Grid, created based on methods of Copeland et al. 2010	Calculated persistent snow layer for 2009-2015
Riparian	30	100	Derived from USGS LANDFIRE Existing Vegetation Type layer. (2013, June). Available: http://landfire.cr.usgs.gov/viewer/	Mesic forested and non-forested types associated with waterways (Appendix B)
Montane Shrub-Grass	30	300	Derived from USGS LANDFIRE EVT Class v1.3,	Percent mid- to upper elevation shrub and grass types (Appendix B)
Foothill Shrub-Grass	30	30	Derived from USGS LANDFIRE EVT v1.3	Percent shrub or grass in lower elevation types (Appendix B)

Covariate	Native scale	Selected Scale (m)	Source	Description
Montane-Alpine Sparse	30	300	Derived from USGS LANDFIRE EVT v1.3	Percent sparse vegetation in upper elevation areas (Appendix B)
Fir forest	30	500	Derived from USGS LANDFIRE EVT v1.3	Percent Douglas fir, subalpine fir and associated fir forest types (Appendix B)
Ponderosa pine	30	2000	Derived from USGS LANDFIRE EVT v1.3	Not significant in univariate logistic regression
Lodgepole pine	30	3000		Not selected in LASSO
Talus	1	30	1 m classification of 2015 NAIP Imagery, mapped outputs use 30-m resampled	Percent talus cover
Winter recreation covariates				
Dist. to recreated roads	Vector	N/A	Derived from USFS & USGS roads and recreation tracks	Secondary roads and groomed routes with GPS tracks traveling parallel
Dist. to non-recreated secondary roads	Vector	N/A	Derived from USFS & USGS roads and recreation tracks	Secondary roads without GPS tracks traveling parallel
All winter recreation intensity layer	30	125	See methods and Appendix C	Linear and off-road winter recreation weighted track density
Winter recreation footprint	125	-	See methods and Appendix C	Transformed intensity values>0 to ‘1’ to create binomial layer
Motorized winter recreation intensity layer	30	125	See methods and Appendix C	Motorized off-road winter recreation weighted track density
Non-motorized winter recreation intensity layer	30	125	See methods and Appendix C	Non-motorized off-road winter recreation weighted track density

Additional details of the covariates are provided below.

Topographic covariates. We used 30m digital elevation models (DEMs) from the National Elevation dataset from the USGS for elevation, slope and aspect. In addition, we also calculated the terrain roughness (TRI), topographic position index (TPI), vector ruggedness measure (VRM), and solar insolation. The TPI (Weiss 2001) looks at the position of a pixel relative to the surrounding pixels in a given neighborhood size in an attempt to classify the landscape into slope position and landform categories. The calculation produces either positive (higher positions, i.e. ridges) or negative (lower positions, i.e. valleys) values as its output. The size of the neighborhood that best captures TPI depends on the landscape, for this analysis we generated it at the same spatial scales as for other covariates (30, 50, 100, 150, 300, 500, 700, 1000, 2000, 3000m radii) and classified rasters according to the recommendations of Weiss (2001). The TRI (Riley 1999) measures local variations about a central pixel in a 3-pixel neighborhood (8 surrounding neighborhoods) using the minimum and maximum values of the local neighborhood. We calculated solar insulation from the DEM, which aims to identify areas with less sun exposure where snow may be more likely to accumulate. Solar radiation was calculated separately for each band of latitude in the study area using ERSI's Area Solar Radiation tool. The output rasters were mosaicked together with a mean operator to provide wall-to-wall coverage.

Persistent Spring Snow. Spatially-explicit data summarizing persistent spring snow was created for the years 2009-2015 by following the same methods as Copeland et al (2010). MODIS data were projected and downloaded from the 'reverb.echo' NASA web portal and assimilated according to the steps outlined by Copeland et al (2010) and detailed by Copeland (pers. comm. 2015). This resulted in a 500 m resolution raster with values of 0-7, representing the number of years that pixel was consistently snow covered from April 24 – May 15 of each year. Additional snow data was downloaded from the SNOWDAS dataset for January – April of each year of the study. Daily variables at 1 km were compiled and mosaicked together to produce continuous rasters of the minimum, maximum, mean, range, and standard deviation of the following variables: depth (m), snow water equivalent (SWE, m), snow melt runoff at the base of the snow pack (m), and solid precipitation (kg/m^2).

Roads and groomed winter recreation routes. The best available road, trail and groomed routes data were collected from each of the seven National Forests (Boise, Bridger-Teton, Caribou-Targhee, Gallatin, Payette, Sawtooth, Beaverhead-Deer Lodge NFs) and from Grand Teton National Park. Gaps in the data were filled in with USGS Transport data. Euclidean distance was calculated to all roads, major roads (either delineated in the attributes of the assimilated data or designated by local knowledge), and winter routes or groomed routes. Winter routes were rarely designated in the attributes of the USFS-supplied spatial data, and we digitized these from the USFS Winter Recreation Maps, available for all Forests.

Land cover. We used LANDFIRE data downloaded from USGS, and developed a simplified land cover classification based on the National Vegetation Classification System Physiognomic Class (EVT_CLASS), as summarized in Table B.1. An additional land cover model specific to talus and rock habitats was produced at 1m resolution to more accurately identify talus land cover. This model predicts talus habitats at 67% accuracy, and combined talus/rock habitats at 87% accuracy. This classification also provided a higher resolution classification for conifer forests, and we used this resampled to 30m to calculate distance to forest edge as a covariate in the analyses. We also used this forest cover data to generate forest edge:area as the length of edge/forest area at the suite of spatial scales other covariates were assessed at (30, 50, 100, 150, 300, 500, 700, 1000, 2000, 3000m). See details of the land cover classification in Smith and Heinemeyer (2016).

Table B. 1. Land cover groupings were developed based on LANDFIRE National Vegetation Classification System Physiognomic Class, reducing 68 unique cover types to six broad classes for purposes of habitat modeling.

EVT Class (LANDFIRE, June 2013)	Land cover type
Northern Rocky Mountain Subalpine Woodland and Parkland	Fir Mixed Forest
Rocky Mountain Subalpine Dry-Mesic Spruce-Fir Forest and Woodland	Fir Mixed Forest
Rocky Mountain Subalpine Mesic-Wet Spruce-Fir Forest and Woodland	Fir Mixed Forest
Dry-mesic Montane Douglas-fir Forest	Fir Mixed Forest
Inter-Mountain Basins Aspen-Mixed Conifer Forest and Woodland	Fir Mixed Forest
Mesic Montane Douglas-fir Forest	Fir Mixed Forest
Middle Rocky Mountain Montane Douglas-fir Forest and Woodland	Fir Mixed Forest
Northern Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest	Fir Mixed Forest
Northern Rocky Mountain Mesic Montane Mixed Conifer Forest	Fir Mixed Forest
Rocky Mountain Aspen Forest and Woodland	Fir Mixed Forest
Subalpine Douglas-fir Forest	Fir Mixed Forest
Subalpine Western Larch Forest	Fir Mixed Forest
Xeric Montane Douglas-fir Forest	Fir Mixed Forest
Artemisia tridentata ssp. vaseyana Shrubland Alliance	Foothill Shrub and Grass
Columbia Plateau Low Sagebrush Steppe	Foothill Shrub and Grass
Inter-Mountain Basins Big Sagebrush Steppe	Foothill Shrub and Grass
Introduced Upland Vegetation-Perennial Grassland and Forbland	Foothill Shrub and Grass
Northern Rocky Mountain Lower Montane-Foothill-Valley Grassland	Foothill Shrub and Grass
Rocky Mountain Lodgepole Pine Forest	Lodgepole Pine
Rocky Mountain Poor-Site Lodgepole Pine Forest	Lodgepole Pine
Inter-Mountain Basins Montane Sagebrush Steppe	Montane Shrub and Grass
Northern Rocky Mountain Montane-Foothill Deciduous Shrubland	Montane Shrub and Grass
Northern Rocky Mountain Subalpine-Upper Montane Grassland	Montane Shrub and Grass
Northern Rocky Mountain Subalpine Deciduous Shrubland	Montane Shrub and Grass
Rocky Mountain Subalpine-Montane Mesic Meadow	Montane Shrub and Grass
Inter-Mountain Basins Sparsely Vegetated Systems	Montane-Alpine Sparse
Rocky Mountain Alpine Dwarf-Shrubland	Montane-Alpine Sparse
Rocky Mountain Alpine Turf	Montane-Alpine Sparse
Rocky Mountain Alpine/Montane Sparsely Vegetated Systems	Montane-Alpine Sparse
Barren	Other
Columbia Basin Foothill and Canyon Dry Grassland	Other
Columbia Basin Palouse Prairie	Other
Columbia Plateau Steppe and Grassland	Other
Developed-Low Intensity	Other
Developed-Medium Intensity	Other
Developed-Roads	Other
Dry-mesic Montane Western Larch Forest	Other
Great Basin Xeric Mixed Sagebrush Shrubland	Other

EVT Class (LANDFIRE, June 2013)	Land cover type
Inter-Mountain Basins Big Sagebrush Shrubland	Other
Inter-Mountain Basins Mixed Salt Desert Scrub	Other
Inter-Mountain Basins Semi-Desert Shrub-Steppe	Other
Introduced Upland Vegetation-Annual Grassland	Other
Mesic Montane Western Larch Forest	Other
Northern Rocky Mountain Avalanche Chute Shrubland	Other
Open Water	Other
Rocky Mountain Foothill Limber Pine-Juniper Woodland	Other
Snow-Ice	Other
Western Cool Temperate Close Grown Crop	Other
Western Cool Temperate Developed Ruderal Evergreen Forest	Other
Western Cool Temperate Developed Ruderal Grassland	Other
Western Cool Temperate Developed Ruderal Shrubland	Other
Western Cool Temperate Pasture and Hayland	Other
Western Cool Temperate Undeveloped Ruderal Grassland	Other
Western Cool Temperate Undeveloped Ruderal Shrubland	Other
Western Cool Temperate Urban Deciduous Forest	Other
Western Cool Temperate Urban Evergreen Forest	Other
Western Cool Temperate Urban Herbaceous	Other
Western Cool Temperate Urban Mixed Forest	Other
Western Cool Temperate Urban Shrubland	Other
Northern Rocky Mountain Ponderosa Pine Woodland and Savanna	Ponderosa Pine
Inter-Mountain Basins Montane Riparian Forest and Woodland	Riparian
Northern Rocky Mountain Conifer Swamp	Riparian
Rocky Mountain Montane Riparian Forest and Woodland	Riparian
Rocky Mountain Montane Riparian Shrubland	Riparian
Rocky Mountain Subalpine/Upper Montane Riparian Forest and Woodland	Riparian
Rocky Mountain Subalpine/Upper Montane Riparian Shrubland	Riparian
Rocky Mountain Wetland-Herbaceous	Riparian

Spatial scaling of covariates

We generated each covariate at multiple spatial scales to identify the scale most strongly selected by wolverines. We used moving windows in ArcGIS at 8 radii (50, 100, 200, 500, 700, 1000, 2000, 3000m), with the finest resolution determined by the native resolution of the covariate data. For categorical variables such as the land cover classification, we calculated the percentage of that class at each window radii. Animal and available locations were attributed with the scaled covariates, and univariate logistic regressions were fit at spatial resolution with the scale having lowest Akaike Information Criteria (AIC; Akaike 1974) selected for further analyses. Wolverines most strongly selected environmental covariates at broadly differing scales ranging from coarser resolutions of 1000 m for forest edge:area ratio to fine-scale selection at our original 30m scale for other covariates such as talus cover (Table B.1).

Appendix C: Winter recreation sampling and analyses

This Appendix provides additional information on winter recreation mapping, on winter recreation aerial surveys, and winter recreation map validation using the aerial recreation surveys.

Development of winter recreation spatially-explicit models

We used the weighted GPS tracks collected from volunteer recreationists to develop spatially-explicit models and map representing winter recreation within our study areas. These spatial depictions include identification of the network of roads and groomed routes used by recreationists within the study area to access backcountry areas (linear recreation), and estimating the relative intensity as the weighted track density of all recreation (road and dispersed combined), motorized dispersed recreation and non-motorized dispersed recreation. We also developed a simple footprint depiction of winter recreation. These models were used as covariates in the development of wolverine RSF models.

Linear recreation. We used the vector-based recreation track data to identify roads or groomed routes that had recreation tracks traveling within 30m classified as a 'linear recreation route'. Recreation GPS tracks simply crossing an otherwise unused road were ignored in these classifications, and secondary roads without documented winter recreation travel were classified as such. In areas with multiple years of GPS recreation track information, we combined years to identify recreation routes. We calculated the straight-line distance to the linear recreation as a potential predictor of wolverine habitat use in our analyses.

Relative intensity of recreation. We developed spatial layers depicting the relative intensity of recreation use calculated as the weighted density of recreation tracks:

Recreation Intensity = $\sum_i^N (w_i \ l_i \ )/Area$

where l_i is the length of each GPS track within the selected Area, generated through moving window analyses in ArcGIS, and w_i is defined in equation (1). For areas with multiple years of GPS data, we generated annual recreation intensity layers and averaged the weighted density across years.

We generated recreation intensity grids for all recreation tracks, as well as separate intensity layers for off-road or dispersed motorized recreation and for dispersed non-motorized recreation. For the motorized and non-motorized spatial layers, the proportion of GPS units handed out to each recreation type was used to estimate the proportion of total use representing that recreation type in the *w* calculations.

To determine the most appropriate scale to depict the recreation intensity layers, we generated each recreation layer at multiple moving windows from 50-5000m (DeCesare et al. 2012). Animal and available locations were attributed with the scaled covariates, and univariate logistic regressions were fit at spatial resolution with the scale having lowest Akaike Information Criteria (AIC; Akaike 1974) selected for further analyses. The relative intensity scores averaged a moving window radii of 125m had the lowest AIC for all recreation combined, motorized dispersed recreation and non-motorized dispersed recreation, and we used this spatial scale for all subsequent analyses.

Recreation footprint. The spatial extent or footprint of recreation was estimated from the scaled recreation intensity layers for all recreation combined by converting any relative intensity score > 0 to a '1' to create a binomial predictor.

Winter recreation aerial surveys to validate recreation maps

We validated our winter recreation models using aerial surveys that independently documented winter recreation type, extent and relative intensity within our study areas. Aerial surveys in fixed-wing aircraft were completed 1-4 times in each study area each year. Visually evaluating recreation levels or intensity during aerial surveys is challenging to standardize across observers, study areas and time, so we used a presence-absence survey approach to avoid observer bias. The area was systematically flown along transects spaced 2 km apart. Sequential 20-second presence-absence observations were recorded by two observers with each observer recording from one side of the plane, with presence, type (snowmobile, ski, both) and spatial pattern (linear, dispersed, both) recorded for each sample. The 20-sec interval allowed for a new field of view between samples. Transects formed the boundaries of 1 km^2 grid cells, and scores for each survey grid quadrat (500m^2) were calculated as the total number of positives/total samples taken. Aerial survey information was used in-season to identify gaps in GPS sampling such as trailhead access points not being sampled, allowing us to adjust GPS distributions to ensure comprehensive sampling. It was also used to validate and identify any spatial gaps in recreation covariates developed for analyses, and identify changes in recreation distribution in years following the collection of the GPS-based recreation data.

The aerial recreation survey data were used to validate the GPS-based recreation maps. The GPS track-based recreation footprint was compared to aerial survey cells scoring positive for winter recreation and percent overlap was calculated. We also generated an all-track recreation intensity layer at 500m^2 resolution to match the resolution of the aerial surveys and used binned values to compute the correlation with the coarser resolution scores of the aerial surveys. At the level of individual aerial survey grid cells, we identified 'gaps' in our ground-based recreation monitoring data, as indicated by the absence of GPS track information where aerial surveys indicated consistent or wide-spread use. We undertook additional validation of the recreation layers when using them in analyses of animals monitored in years subsequent to the recreation GPS tracking data collection. In these instances, we used aerial survey data collected concurrent with animal monitoring to identify potential spatial shifts in winter recreation compared to the GPS track-based layers. Animal and random locations falling in aerial grid cells in areas of notable mismatch between aerial survey and the recreation covariate layers were not included in further analyses. The maps of RSF models including winter recreation relative intensity covariates are not extrapolated into these areas of data gaps.

We completed 9 aerial recreation surveys. The correlation between the aerial survey scores and the recreation intensity layer classes was 0.80, suggesting high concurrence in the relative intensity of recreation as estimated between the two independent methods. The footprints were also very similar, with the aerial recreation surveys suggesting a larger footprint in 13% of the area, while the recreation intensity layer suggested a larger recreation footprint in 15% of the area. Animal and random locations falling within gaps in our recreation intensity models were removed from further analyses, including one female animal-year and 232 animal locations and 1875 random locations across nine additional animal-years.

Backcountry winter recreation types and patterns

Table C. 1. Summary the types of backcountry winter recreation monitored through volunteer recreationists carrying GPS units in Idaho, Wyoming and Montana (2010-2015) as part of the research examining wolverine responses to winter recreation. Each type of recreation was subsequently classified as motorized, non-motorized while recreationists partaking in both motorized and non-motorized activities (e.g., using a snowmobile to access areas for skiing) were identified and their tracks split into the component types.

Recreation Type	No. of tracks	Total km	Avg km	Classified
Snowmobile	2772	161,699	60.42	Motorized
ATV	2	75	37.50	Motorized
Motorbike	1	16	16.41	Motorized
Snowbike	1	6	6.38	Non-motorized
Ski	2485	24814	9.99	Non-motorized
Snowboard	377	3919	10.40	Non-motorized
Snowshoe	24	148	6.15	Non-motorized
Snowmobile –ski/snowboard	139	4351	31.30	Split
Cat-Ski	45	2432	54.05	Split
Heli-Ski	53	559	10.54	Non-motorized portion only
Total	**5899[1]**	**178438**	**32.57**	

[1] This is the raw track count; the snowmobile-ski/snowboard tracks were split into their component motorized and non-motorized sections.

Appendix D: Wolverine habitat models and indirect habitat loss

This Appendix provides additional details on indirect habitat loss calculated for individual wolverines. It also displays small format maps of the RSF wolverine habitat models developed using environmental and winter recreation covariates to predict relative wolverine probability of use based on GPS monitoring of wolverines 2010-2015 across four study areas in Idaho, Wyoming and Montana (Figures D.1 – D.4). Large format maps of the final RSF habitat models are available at www.roundriver.org/wolverine

Table D.1. Indirect habitat loss calculated[1] from winter recreation within individual wolverine (*Gulo gulo*) home ranges based on spatially-explicit transitions to lower habitat classes when comparing potential and realized habitat models developed for wolverines monitored 2010-2015 across study area in Idaho, Wyoming and Montana (see Figures 2-5).

	Overall Degraded	**Moderate to Low**	**High to Moderate**	**High to Low**
F1_2010	28.4%	44.5%	19.9%	23.4%
F1_2012	24.6%	38.4%	15.4%	20.9%
F10_2014	24.5%	37.6%	15.1%	19.3%
F11_2014	14.8%	24.9%	12.1%	12.2%
F2_2010	19.5%	29.7%	15.7%	13.6%
F2_2011	19.7%	28.3%	17.2%	14.1%
F3_2010	6.4%	5.4%	9.1%	2.1%
F3_2014	3.2%	2.8%	5.5%	0.6%
F4_2011	20.9%	28.3%	23.4%	13.3%
F5_2011	10.3%	10.7%	15.1%	4.5%
F7_2017	2.7%	4.0%	6.0%	0.0%
F8_2103	2.0%	2.5%	4.5%	0.2%
F9_2012	6.2%	7.2%	10.8%	0.6%
Female Average	14.1%	20.3%	13.1%	9.6%
M1_2010	16.2%	21.6%	24.1%	0.7%
M1_2011	14.3%	18.1%	18.2%	0.7%
M1_2014	16.1%	19.6%	20.1%	0.9%
M12_2014	12.3%	18.4%	18.3%	0.2%
M13_2014	9.3%	19.4%	19.5%	0.0%
M13_2015	7.7%	19.4%	16.4%	0.0%
M15_2015	11.2%	16.1%	17.2%	0.0%
M2_2010	14.3%	19.9%	20.3%	0.4%
M2_2011	13.8%	21.1%	20.1%	0.3%
M2_2012	5.5%	11.3%	11.6%	0.0%
M3_2010	11.2%	14.5%	16.6%	0.0%
M6_2012	4.8%	9.9%	8.9%	0.0%
M8_2012	5.5%	11.3%	11.6%	0.0%
Male Average	10.9%	17.0%	17.2%	0.2%

[1] Calculations: 'overall degradation' = ha degraded/total ha; 'moderate to low' = moderate degraded/total moderate available, 'high to moderate' = high degraded to moderate/high available; 'high to low' = high degraded to low/high available

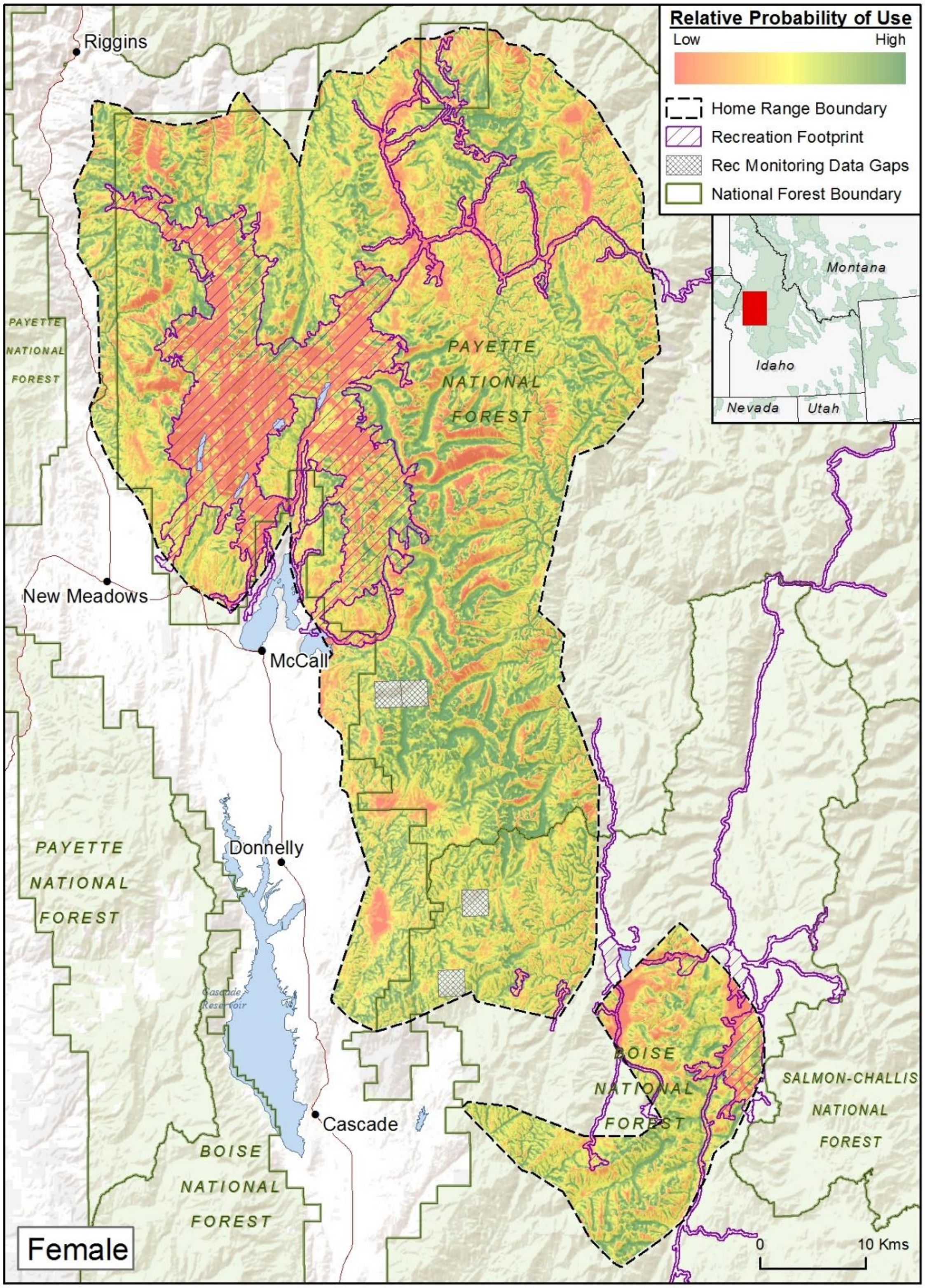


Figure D.1. Resource selection function habitat model for female wolverines (*Gulo gulo*) in the McCall study area, including environmental and winter recreation covariates to predict relative probability of use based on GPS locations of wolverines monitored 2010-2015.

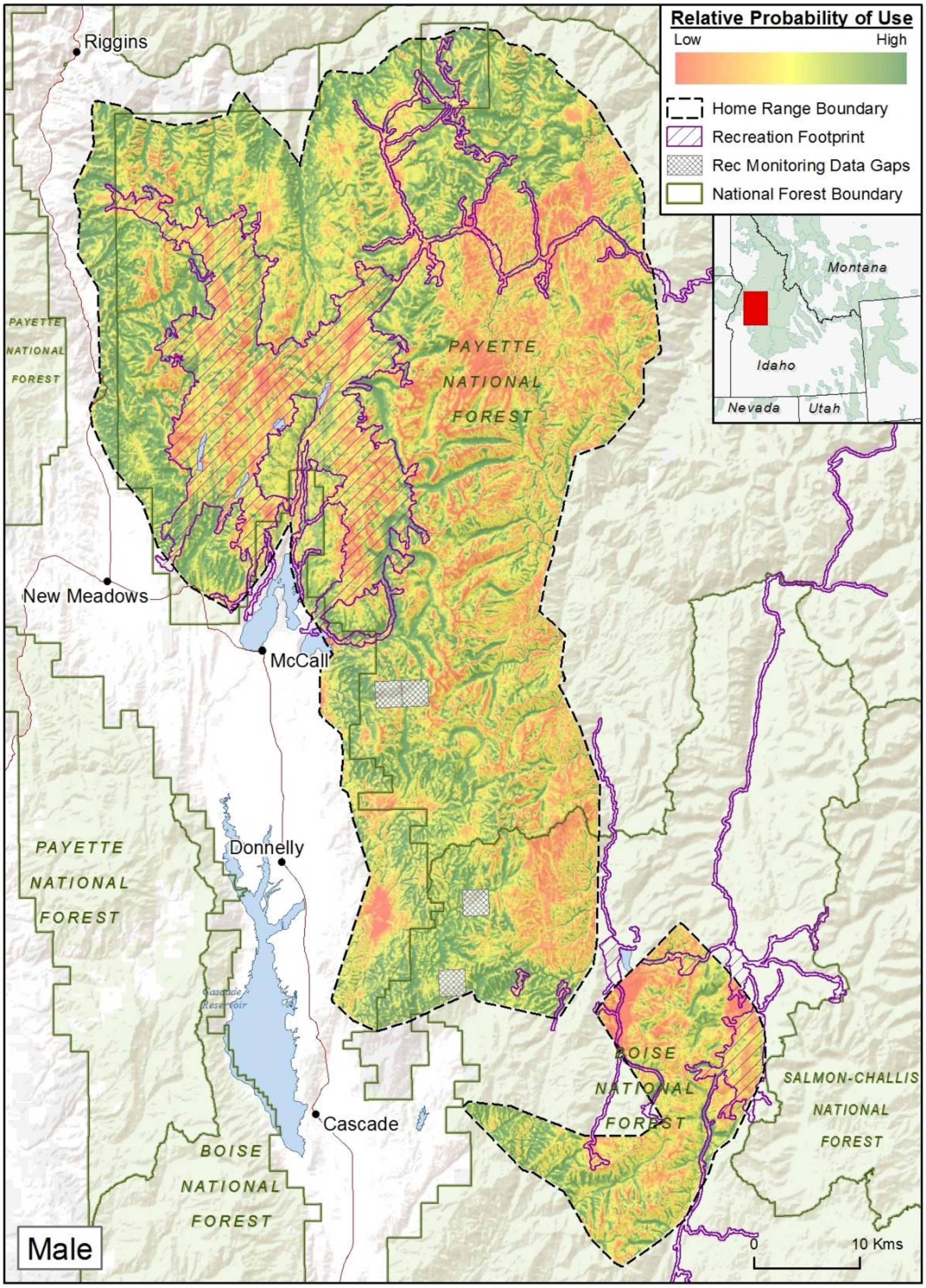


Figure D.2. Resource selection function habitat model for male wolverines (*Gulo gulo*) in the McCall study area, including environmental and winter recreation covariates to predict relative probability of use based on GPS locations of wolverines monitored 2010-2015.

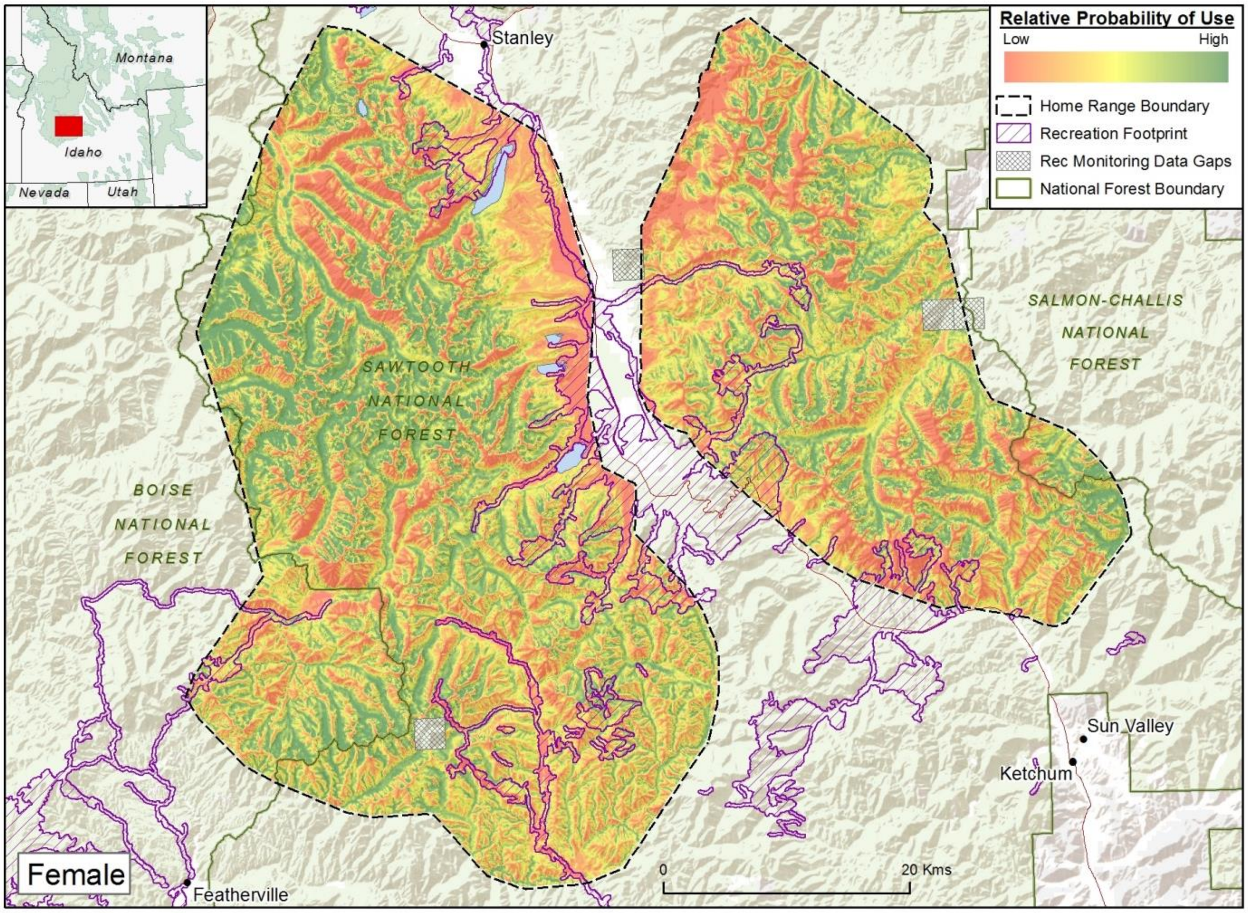


Figure D.3. Resource selection function habitat model for female wolverines (*Gulo gulo*) in the Sawtooth study area, including environmental and winter recreation covariates to predict relative probability of use based on GPS locations of wolverines monitored 2010-2015.

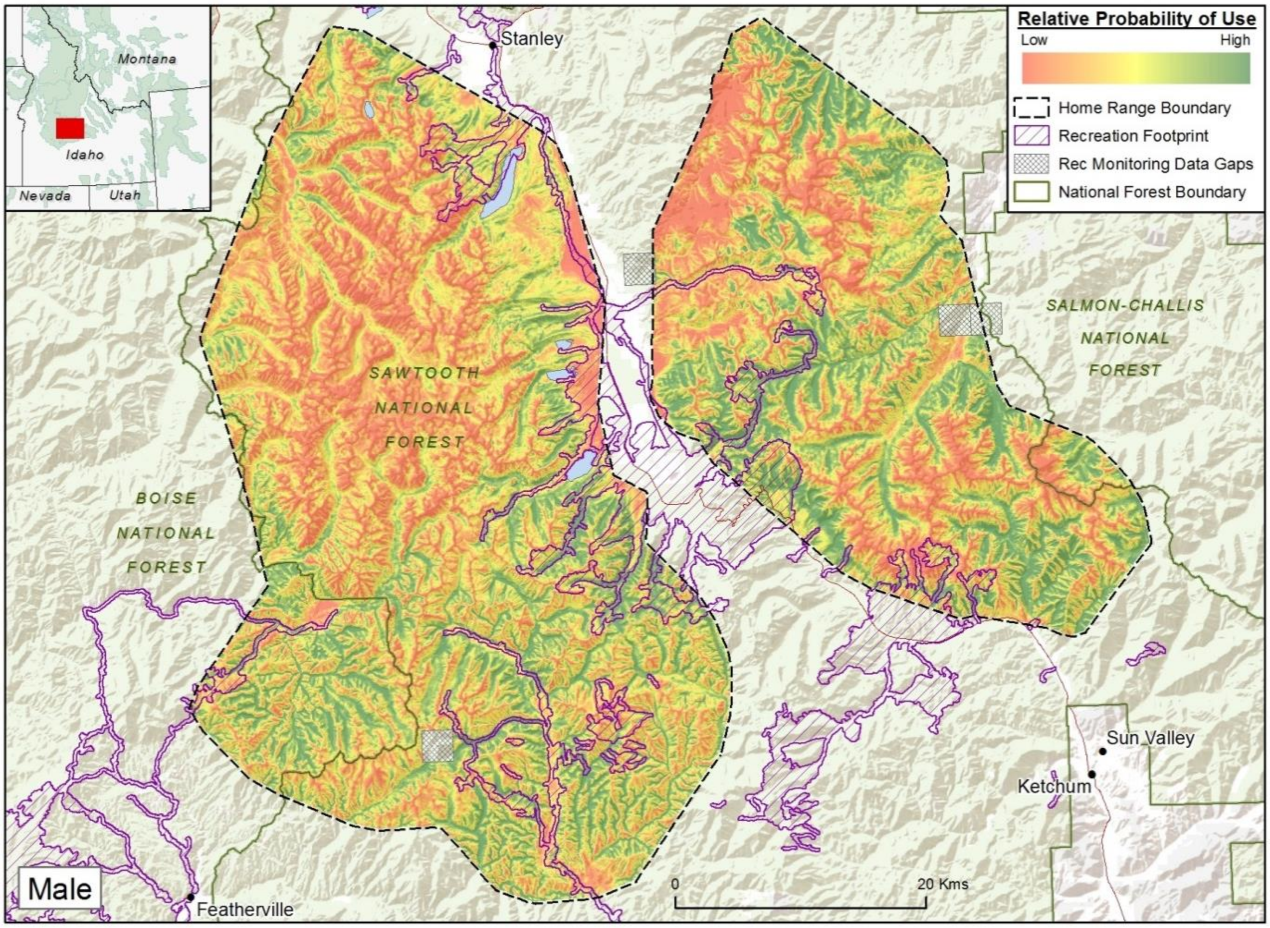


Figure D.4. Resource selection function habitat model for male wolverines (*Gulo gulo*) in the Sawtooth study area, including environmental and winter recreation covariates to predict relative probability of use based on GPS locations of wolverines monitored 2010-2015.

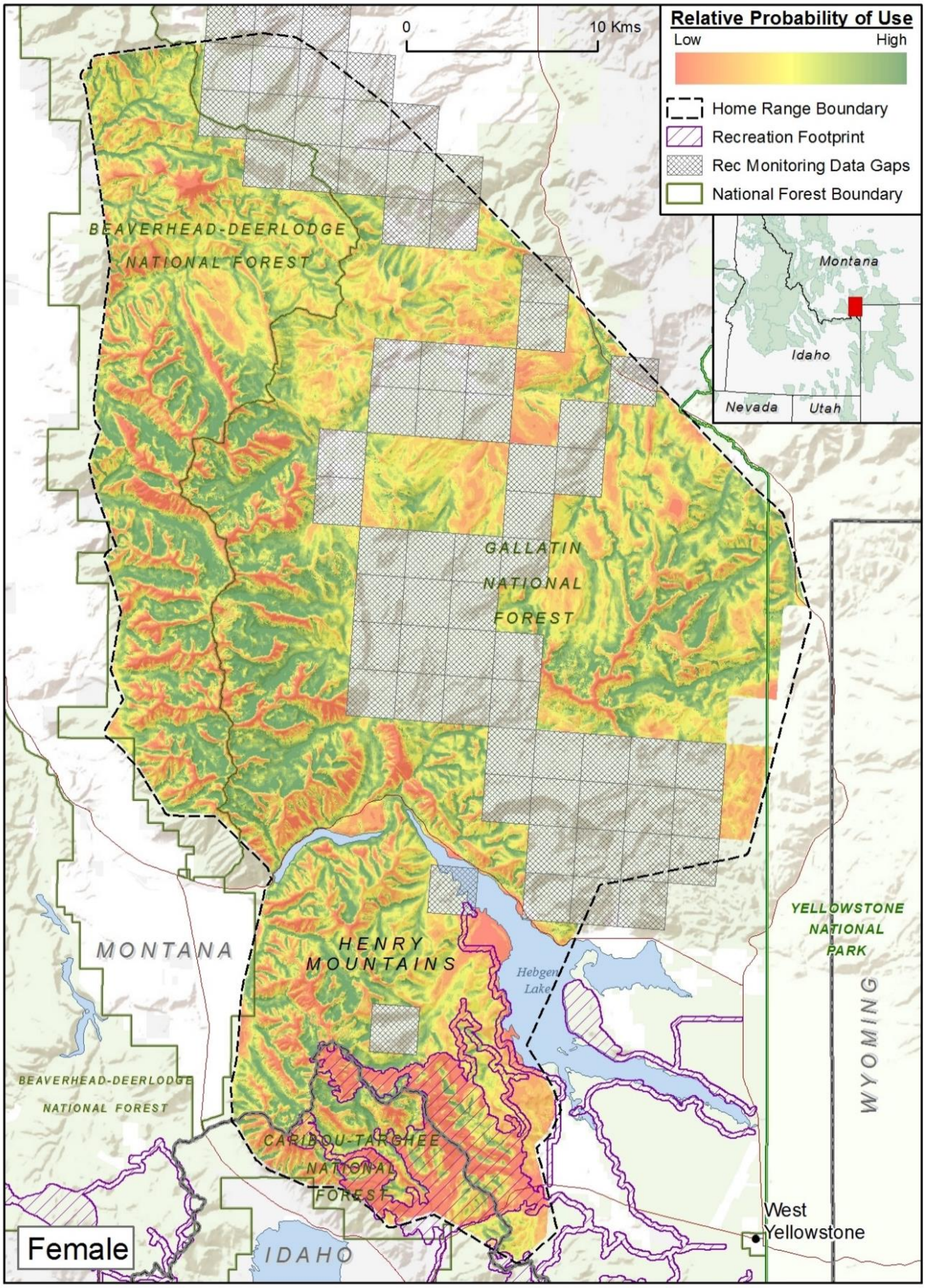


Figure D.5. Resource selection function habitat model for female wolverines (*Gulo gulo*) in the West Yellowstone study area, including environmental and winter recreation covariates to predict relative probability of use based on GPS locations of wolverines monitored 2010-2015.

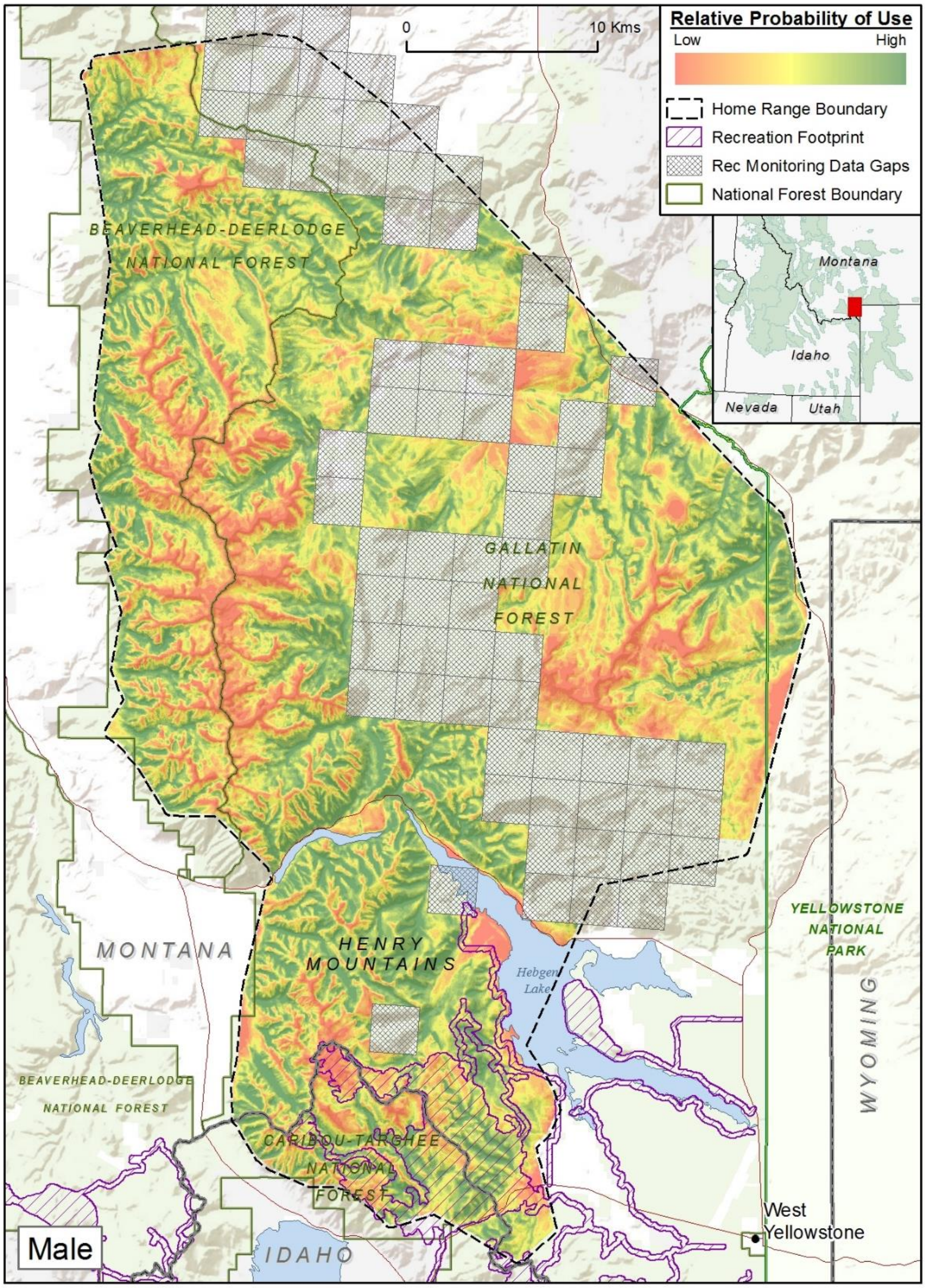


Figure D.6. Resource selection function habitat model for male wolverines (*Gulo gulo*) in the West Yellowstone study area, including environmental and winter recreation covariates to predict relative probability of use based on GPS locations of wolverines monitored 2010-2015.

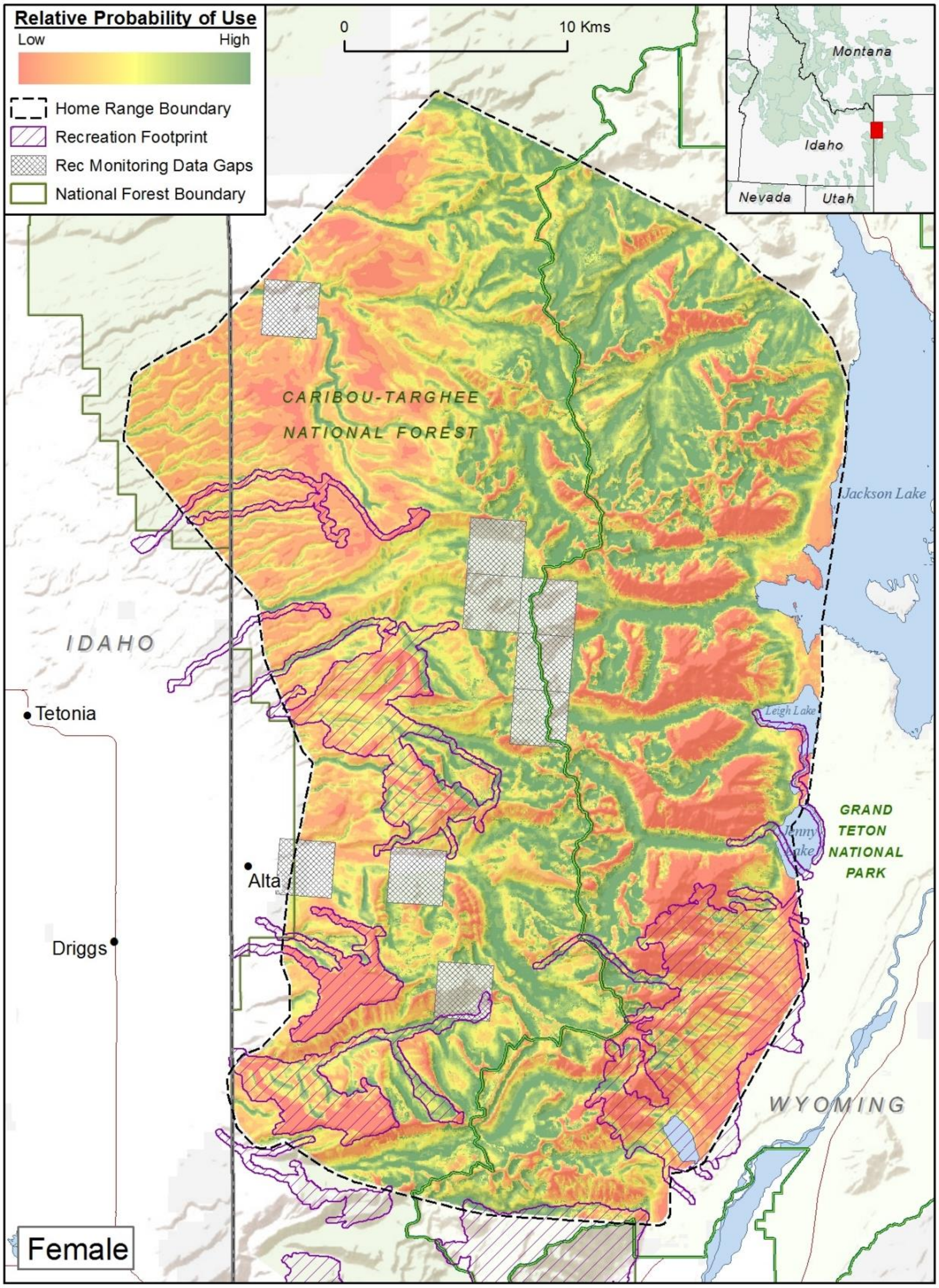


Figure D.7. Resource selection function habitat model for female wolverines (*Gulo gulo*) in the Teton study area, including environmental and winter recreation covariates to predict relative probability of use based on GPS locations of wolverines monitored 2010-2015.

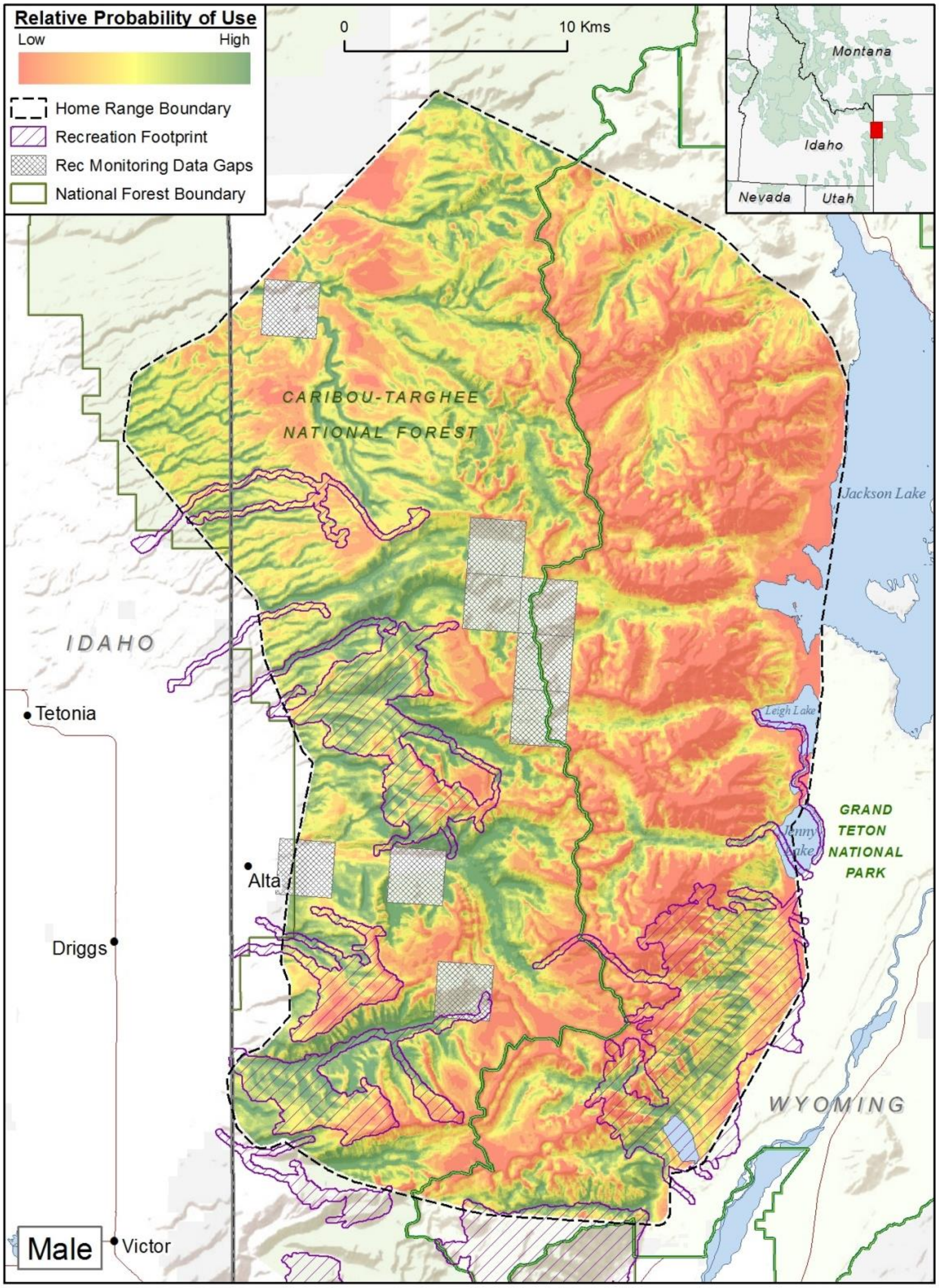


Figure D.8. Resource selection function habitat model for male wolverines (*Gulo gulo*) in the Teton study area, including environmental and winter recreation covariates to predict relative probability of use based on GPS locations of wolverines monitored 2010-2015.