



Evaluating the importance of wolverine habitat predictors using a machine learning method

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In the conterminous United States, wolverines (*Gulo gulo*) occupy semi-isolated patches of subalpine habitats at naturally low densities. Determining how to model wolverine habitat, particularly across multiple scales, can contribute greatly to wolverine conservation efforts. We used the machine-learning algorithm random forest to determine how a novel analysis approach compared to the existing literature for future wolverine conservation efforts. We also determined how well a small suite of variables explained wolverine habitat use patterns at the second- and third-order selection scale by sex. We found that the importance of habitat covariates differed slightly by sex and selection scales. Snow water equivalent, distance to high-elevation talus, and latitude-adjusted elevation were the driving selective forces for wolverines across the Greater Yellowstone Ecosystem at both selection orders but performed better at the second order. Overall, our results indicate that wolverine habitat selection is, in large part, broadly explained by high-elevation structural features, and this confirms existing data. Our results suggest that for third-order analyses, additional fine-scale habitat data are necessary.

Key words: carnivore, *Gulo gulo*, habitat predictors, metapopulation, random forest, wolverine

Wolverines (*Gulo gulo*) are the largest species of Mustelidae in North America. In the conterminous United States, the current population size is approximately 300–350 individuals on high-elevation public lands (Inman et al. 2013). There is limited information on wolverine ecology and behavior due to the effort required to study a species that occurs at naturally low densities and occupies challenging terrain. There also is still debate about what factors most strongly drive wolverine habitat use, including snow cover area and duration (Schwartz et al. 2009; Copeland et al. 2010), food abundance (COSEWIC 2014), and human land use (Laliberte and Ripple 2004; Krebs et al. 2007), although several studies have been undertaken at various scales to predict or explain wolverine habitat (Carroll et al. 2001, 2020; Aubry et al. 2007; Copeland et al. 2007).

The factors hypothesized to limit wolverine habitat use are not mutually exclusive; however, few studies have compared their relative importance across scale by sex. Undertaking analyses by sex is essential because there is evidence of

sex-specific habitat selection and dispersal in wolverines. Male home ranges are 2–4 times larger than female home ranges in the United States (Powell 1979; Magoun 1985; Dawson et al. 2010; Persson et al. 2010). Within-home-range movements and selection differ by sex, and only females select den sites. Outside of home ranges, long-distance dispersal occurs in both sexes (Vangen et al. 2001; Flagstad et al. 2004), but females often settle closer to their natal ranges than males (Moriarty et al. 2009; Inman et al. 2012; COSEWIC 2014). This suggests that sex-specific pressures affect movement and eventual home-range selection. We therefore cannot effectively examine what factors affect wolverine habitat use without considering sex-specific differences in selection.

Scale also should be considered when examining the factors hypothesized to limit wolverine habitat use because certain behaviors (e.g., territory selection, den site selection) require different resources and occur on different spatial scales. At broader landscape scales in the United States,

wolverines are associated primarily with Northwestern forested mountains (Copeland 1996) but exhibit seasonal shifts in elevation (Copeland et al. 2007; Inman et al. 2012). In Norway, female wolverines make selections at the den-site scale, home-range scale, and landscape scale based on terrain ruggedness (May et al. 2012), whereas wolverines in the United States use high latitude-adjusted elevation and cirque basins for natal dens (Copeland 1996; Inman et al. 2012). At the home-range scale, wolverines tolerate private roads, but not at the den-site selection level in Norway (May et al. 2012), and this tolerance may vary by life stage in the United States. Given the variability of selection across scales, it is essential to identify the scale at which to evaluate in habitat studies (Rather et al. 2020).

Across selection scales and sex, wolverine habitat selection analyses often rely solely on radiocollar location data. Radiocollar presence data are one of the only methods for examining the habitat associations of secretive species like wolverines but have inherent limitations and concerns, including repeated measures on individuals and high spatial autocorrelation. Ignoring spatial autocorrelation in the residuals can exacerbate errors, leading to additional interpretation bias, particularly for binary response variables like presence and availability (Dormann et al. 2007; Northrup et al. 2013). These issues commonly are overlooked in ecological habitat models and can lead to analytical and interpretational biases.

An alternative to logistic models is machine learning models. Some machine learning methods do not have all of the assumptions of model-based inferential methods. Machine learning methods can be used as predictive inferential methods (e.g., random forest [RF]) or inferential methods of the difference, and selection depends on the goal of the research. When compared, logistic regression and the machine-learning algorithm RF can yield substantially different results (Shoemaker et al. 2018). If researchers have the computing capacity and data requirements, machine learning tools present a reliable comparison to validate or compare with logistic regression. In addition, machine learning methods are widely underapplied in conservation when limited species data are available (Mi et al. 2017).

Here, we evaluated the relative importance of a small number of high-elevation variables or their surrogates on wolverine habitat quality by sex for 38 wolverines around the Greater Yellowstone Ecosystem (GYE). We carried out our analysis at two different spatial scales to account for scale-specific ecological processes and provide decision-makers with more information for future management (DeCesare et al. 2012; Rather et al. 2020). Based on their adaptations for cold environments along with observations of feeding resting and denning in talus, we expected distance to high-elevation talus and snow water equivalent to be important predictors of wolverine habitat (Telfer and Kelsall 1984; Copeland 1996; Copeland et al. 2010; May et al. 2012; Inman et al. 2013). In some populations, females require different habitat types and resources for offspring at various developmental stages; thus, we also expected female wolverines would have more complex habitat associations than males (Krebs et al. 2007).

MATERIALS AND METHODS

Study area.—Our study area, in the GYE, encompasses Yellowstone National Park and Grand Teton National Park. Watersheds, geologic materials, vegetation, and geomorphic and hydrologic processes define the GYE boundary (Marston and Anderson 1991). Within the GYE, elevation, fire regime, and precipitation jointly drive vegetation communities, including short-grass prairie, sagebrush communities, conifer forest, mixed forest, alpine tundra, and barren talus (Despain 1990). Across the GYE, elevation ranges from 300 to 3,300 m. Steppe habitats dominate the GYE below 1,700 m, and montane conifer forests and alpine tundra habitat dominate above 1,700 m and 2,900 m, respectively (Despain 1990). There is considerable spatial variation in precipitation patterns in the GYE (Whitlock and Bartlein 1993). This broad range of precipitation patterns, vegetation communities, and elevation supports a rich diversity of plant and wildlife species (Bailey 1930; Streubel 1989; Marston and Anderson 1991). While the GYE is one of the last intact temperate ecosystems and one of the largest wildland areas in the contiguous United States, increasing human pressures, climate change, and invasive species have significant influences (Berger 1991; Westerling et al. 2011; Hansen et al. 2016). The GYE also represents the current southern extent of the wolverine distribution.

Wolverine data.—Previous research efforts provided location data from 38 wolverines (23♀, 15♂) from the GYE (Inman et al. 2012) and followed ASM guidelines (Sikes et al. 2011). For each resident animal, we used relocations to create 95% kernel density estimates (KDEs) fit with a bivariate kernel function using a least-squares cross-validation bandwidth to avoid oversmoothing of the data (Calenge 2006). The KDEs were used to represent year-round home ranges for the second-order analysis. We included all resident animals in each of the coefficient comparison analyses.

We used both a second-order and third-order analysis scale to determine the relative importance of habitat variables or their surrogates on wolverine habitat quality by comparing “use” and “available” points. For the second-order selection scale, which characterizes individual home-range selection within the population home range, we extracted points within individual home ranges to represent used locations. Random points outside the home range represented available points. For the third-order selection scale, which characterizes individual-level selection of used areas within home ranges, we selected random unused points within the home range as available points, and telemetry locations represented used points.

Ecological variables.—We used a previously determined subset of publicly available data layers in the modeling process (Carroll et al. 2020). The final variables included latitude-adjusted elevation (LAE, m), average monthly snow water equivalent (SWE, cm), distance to high-elevation talus (DHITAL, m), landform classification (LANDFORM, categorical), vegetation class (VEG, categorical), and housing density (HOUSE, houses/km²; Fig. 1; Carroll et al. 2020). We focused on a limited number of variables because a small number of high-elevation variables often predict wolverine habitat well

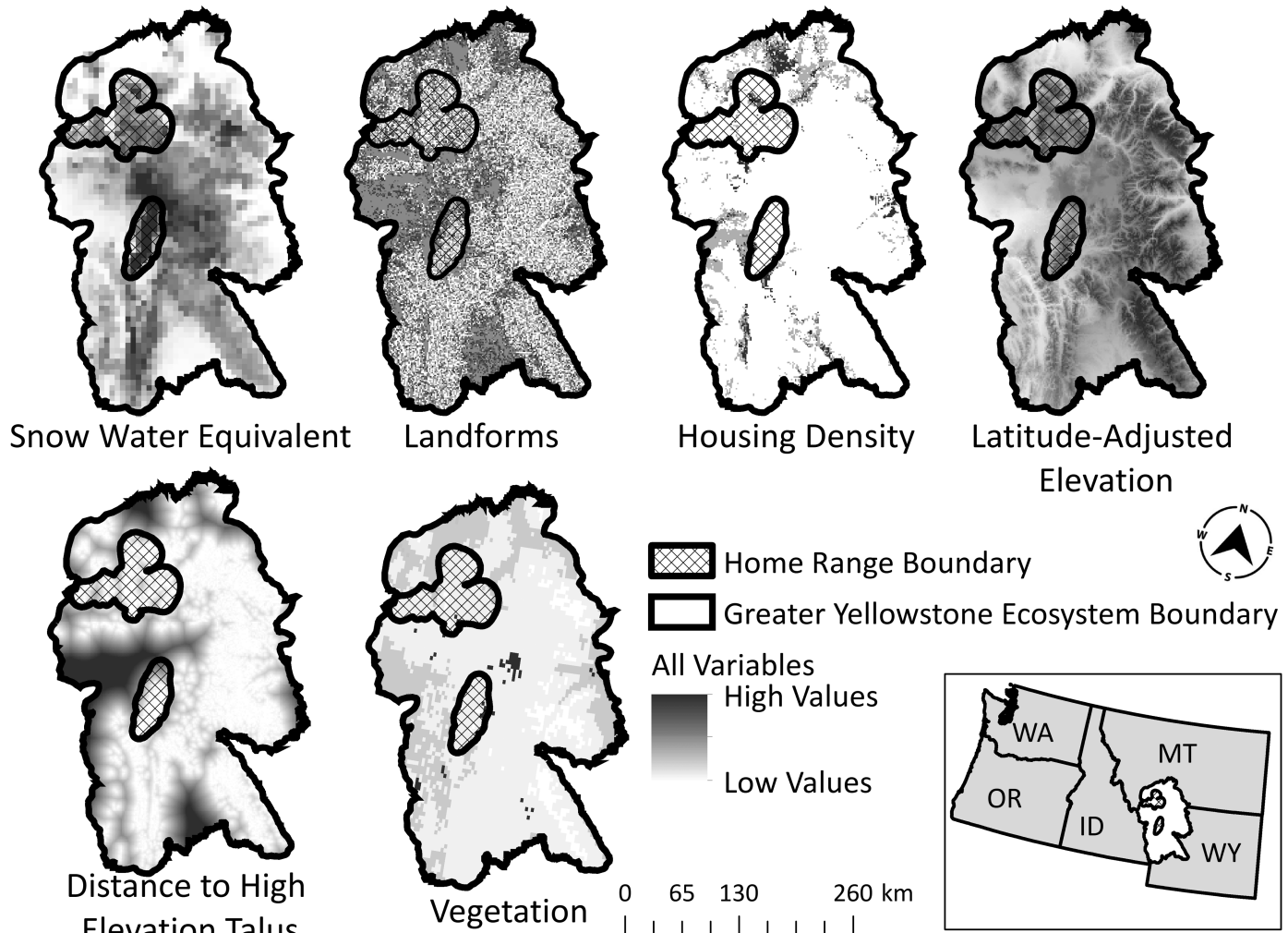


Fig. 1.—Variables used in model development for both second-order and third-order analyses. Snow water equivalent, latitude-adjusted elevation, housing, and distance to high-elevation talus are continuous. The areas with hashing represent wolverine home ranges used in the analyses.

(Aubry et al. 2007; Copeland et al. 2010; Fisher et al. 2013; Inman et al. 2013).

Variable evaluation.—Regression and classification trees (herein, tree methods) are machine learning approaches that use continuous or ordered discrete values to generate predictive or descriptive models, which are ideal for analyzing complex data (De'ath and Fabricius 2000; Loh 2011). Tree methods are incredibly flexible, can be applied to binary response data, and are easy to construct and interpret (De'ath and Fabricius 2000). We used RF on a training data set of 80% of the data for each sex and scale to evaluate each habitat predictor's relative importance. To ensure the errors stabilized, we generated aggregate output from 200 RF trees, with stabilization occurring after approximately 150 trees (Lawrence et al. 2006). We examined mtry values between 2 and 8 for each model and picked optimal mtry values based on percent variation explained in each regression. We estimated mean square error (MSE) increase and mean minimal depth from the RF and randomForestExplainer packages in the statistical software R, version 3.5.3 (Liaw and Wiener 2002; Kuhn 2008; R Core Team 2019; Paluszynska et al.

2020). We then used the remaining 20% holdback data to determine model performance on novel data.

RESULTS

There generally was agreement in the output of importance measures both from the RF and randomForestExplainer packages across sex and scale. The rank and importance of ecological variables differed slightly for males and females both at second-order and third-order analysis scales.

Second-order analyses.—Our second-order models compared locations within individual home ranges to available locations around the population range. For the second-order male model, with 200 regression trees and an mtry of 7, the percent variation explained was 81.27%, and the mean squared of the residuals was 0.04. This model correctly predicted holdback test data with 95.74% accuracy. The second-order female model had 200 trees, an mtry of 7, a percent variation explained of 83.13%, and a mean squared of the residuals of 0.03. This model predicted holdback data with 96.46% accuracy.

We examined RF percent increase of the MSE. This metric represents the increase in MSE of predictions as a result of permuting one variable. Variables with higher MSE represent more important variables in the model, and low MSE are the least important (Fig. 2). The most important variables were distance to high-elevation talus, followed by linear and quadratic snow water equivalent for both males and females. Males and females differed in their ranking for quadratic latitude-adjusted elevation, housing, and vegetation (Fig. 2).

In addition, we examined mean minimal depth among the trees in the RF (or most common first tree split) for variable importance (Fig. 3). The variables with the lowest minimal depth for males and closest to the root were distance to high-elevation talus, snow water equivalent, and quadratic snow water equivalent, respectively (Fig. 3). For females, the lowest mean minimal depth variables were distance to high-elevation talus, snow water equivalent, and quadratic distance to high-elevation talus. Values from both RF (one for each sex) on 200 trees indicated different patterns in importance and mean minimal depths for vegetation, housing density, and landform type at the second-order scale. However, both methods indicated that snow water equivalent and distance to high-elevation talus best explained observed patterns of wolverine habitat at the second order for both sexes (Figs. 2 and 3).

Third-order analyses.—Our third-order models compared telemetry locations within individual home ranges to random locations. For the third-order male model, with 200 regression trees and an mtry of 2, the percent variation explained was 20.44%, and the mean square of the residuals was 0.10. This model correctly predicted holdback test data with 86.59% accuracy, which was lower than the second-order model. The third-order model for females had 200 trees, an mtry of 7, a

percent variation explained of 35.54%, and the mean square of the residuals was 0.12. This model predicted holdback data with 81.92% accuracy. While the withheld prediction accuracy for males was better than the third-order model for females, it was much lower than either of the second-order models. Furthermore, the percent variation explained indicated poor performance for both third-order models.

We examined RF MSE for the third order as well. The most important variables in the MSE were snow water equivalent, distance to high-elevation talus, and quadratic snow water equivalent for males (Fig. 2). The same three variables were most important for females, with distance to high-elevation talus ranking higher both than snow water equivalent and quadratic snow water equivalent. Males and females also differed in rankings for latitude-adjusted elevation, vegetation, and landforms (Fig. 2). The variables with the lowest minimal depth for males and females were distance to high-elevation talus, snow water equivalent, and latitude-adjusted elevation, respectively (Fig. 3). Like the second-order models, values from both third-order RF models indicated distinct patterns for male and female wolverines in importance. Still, both methods indicated that distance to high-elevation talus, snow water equivalent, and latitude-adjusted elevation best explained observed patterns of wolverine habitat at the third order (Figs. 2 and 3).

DISCUSSION

Given the uncertain future of how anthropogenic change will affect wolverine habitat, examining factors that explain wolverine habitat use and drive selection using various methods is increasingly important. We found that the importance of habitat covariates differed by sex and selection scales and supported some, but not all, of or hypotheses. Although there was variation in the order of variable importance, the same suite of variables was highly ranked for both sexes. At both selection scales, distance to high-elevation talus, snow water equivalent, and latitude-adjusted elevation were ranked highest in all analyses both for male and female wolverines. Our findings therefore align with previous wolverine research efforts at various selection scales (Aubry et al. 2007; Copeland et al. 2007, 2010; Fisher et al. 2013; Inman et al. 2013).

Those previous efforts focused primarily on predictive analyses of wolverine habitat selection using parametric methods. A first-order analysis on the same data used here revealed the importance of latitude-adjusted elevation, terrain ruggedness index, April 1 snow depth, road density, interpolated human density, distance to high-elevation talus, distance to tree cover, and distance to April 1 snow > 2.5 cm for predictive modeling (Inman et al. 2013). Other efforts found late-spring snowpack and high topographic ruggedness are predictors of wolverine habitat at first- and second-order scales (Aubry et al. 2007; Copeland et al. 2010). Those studies used various data layers to identify meaningful relationships between wolverine selection and rugged terrain or snow. Their results align with our RF findings that broad-level habitat selection for wolverines can be predicted or identified using a small number of high-elevation variables.

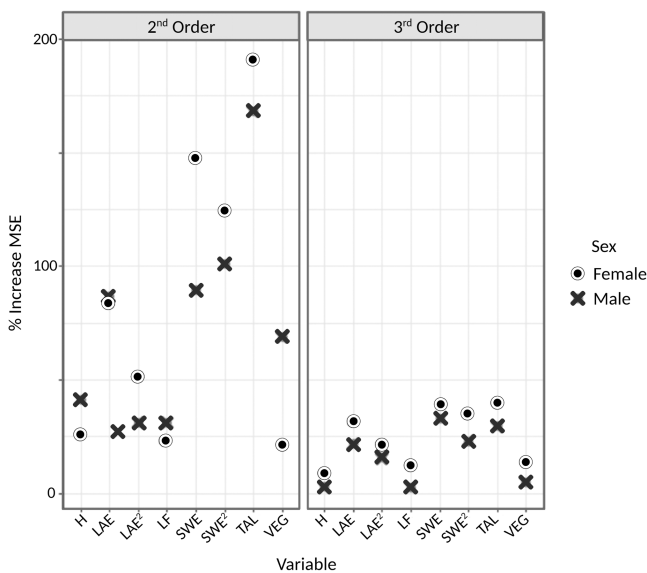


Fig. 2.—Percent mean square error (MSE) increase from the random forest. Variables with higher MSE represent more important variables in the model, and low MSE are less important. Here, SWE is snow water equivalent, LAE is latitude-adjusted elevation, TAL is distance to high-elevation talus, H is housing density, VEG is vegetation, and LF is landform type.

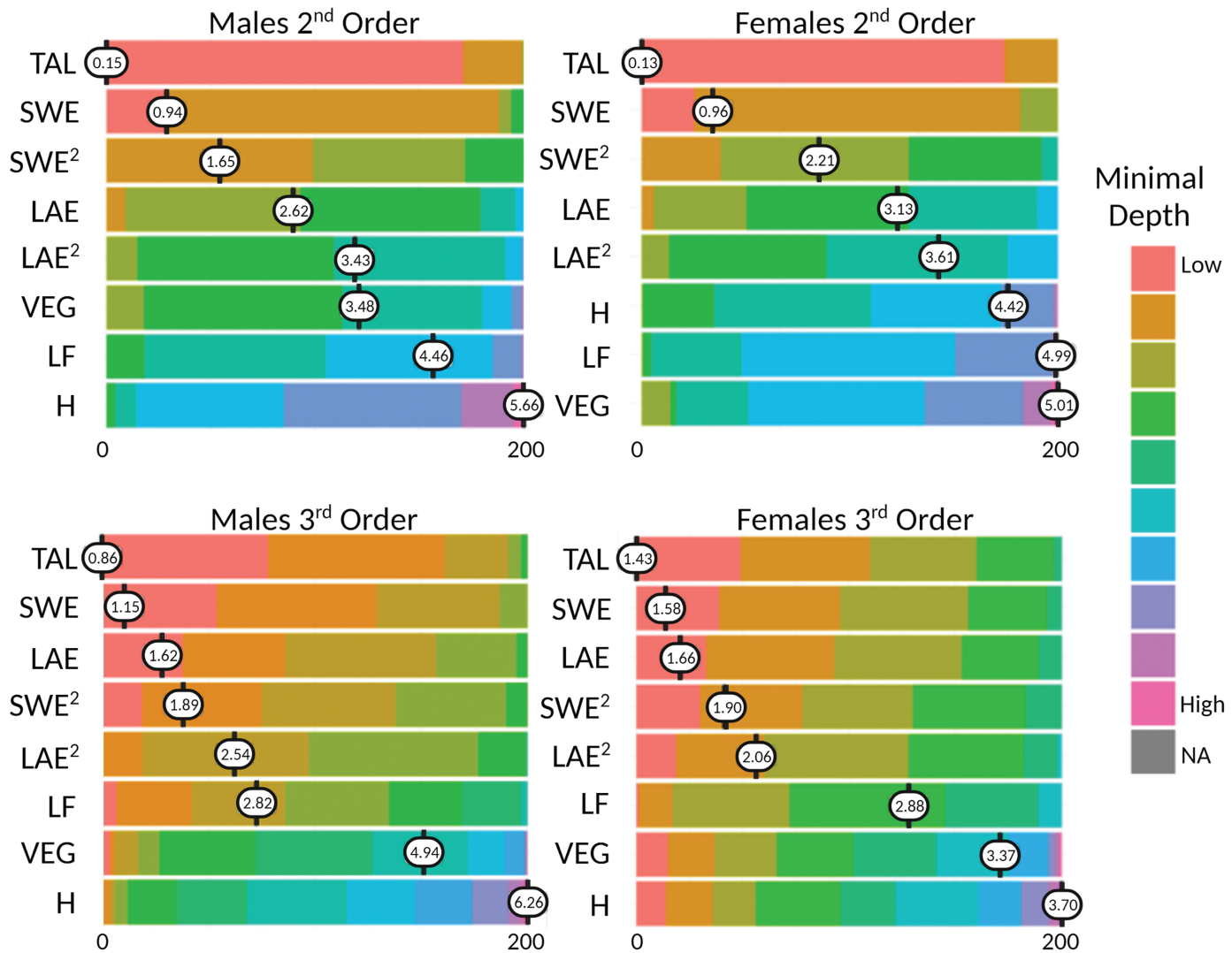


Fig. 3.—Minimal variable depth for each model. A variable's minimal depth equals the depth of the node, which splits on that variable and is the closest to the root of the tree. A low minimum depth indicates many observations are divided into groups based on this variable. The black labeled vertical bars represent the mean of the distribution (Paluszynska et al. 2020). Here, SWE is snow water equivalent, LAE is latitude-adjusted elevation, TAL is distance to high-elevation talus, H is housing density, VEG is vegetation, and LF is landform type.

Ecological variable evaluation.—Our RF results supported the hypothesis that distance to high-elevation talus and snow water equivalent would be the most important variables for wolverine habitat selection. Talus is an important habitat structure (Copeland 1996; May et al. 2012; Inman et al. 2013), and there is evidence that wolverines use talus and boulder fields extensively for food caching, denning, microrefugia from warm temperatures during summer, and hunting (Kortello et al. 2019; van der Veen et al. 2020). Given the broad range of physical habitat structure used for various wolverine behaviors, including reproductive behavior, the importance of talus is logical for both sexes. Based on the importance of talus, geology may be a key driver of wolverine habitat selection in their southern distribution.

We also predicted that snow water equivalent (a surrogate of snow depth that summarizes site and basin snowpack conditions) would be important, given that wolverines are highly snow- and cold-adapted. Wolverine's snow adaptations include

their foot loading, pelage characteristics, general distribution, and life strategy (Telfer and Kelsall 1984). Snow water equivalent was consistently important in our analyses across sex and scale. While there is evidence against wolverines being snow obligate (Webb et al. 2016; Aronsson and Persson 2017; Jokinen et al. 2019), snow still is an important wolverine habitat feature for a variety of reasons, including niche separation, food caching, and denning (van der Veen et al. 2020).

Latitude-adjusted elevation also ranked high in our models. Latitude-adjusted elevation likely is explanatory because it captures the general ecological characteristics where the species niche exists. This could result both from current and evolutionary needs to avoid competition with larger carnivores, which are less likely to hunt at high elevations on steep terrain. In addition, in the GYE, low elevations often are devoid of trees or rock structures used as escape cover from other large carnivores.

Scale comparisons.—Our second-order models performed roughly eight percentage points better on holdback data than

the third-order models and had much higher values for percent variance explained. These results suggest that a small number of high-elevation variables explain population-level wolverine habitat selection well and match those of the previous landscape to population-level predictive analyses that used parametric methods. While our third-order models did well predicting holdback data, the percent variance explained indicated that the variables did not perform well for within-home-range analyses. This finding suggests that unlike at broader scales, wolverine habitat selection is challenging to identify with only a small number of high-elevation variables and likely requires more nuanced analyses.

There are few third-order selection studies on wolverines in the western United States. Research on within-home-range habitat selection for wolverines located primarily in and around Idaho suggests that drainage bottom topography, avoidance of steep slopes, and proximity to forest edge are essential habitat characteristics for both sexes (Heinemeyer et al. 2019). This analysis, like ours, found sex-specific differences in selection. Using ranked standardized regression coefficients, they identified that females selected for talus and smaller forest patches with more edge, while males selected for fir-dominated forests and areas close to secondary roads (Heinemeyer et al. 2019). There also is evidence that wolverines are associated with different vegetation types and elevations seasonally, prefer northerly aspects, and avoid roads at this scale (Copeland et al. 2007). These and more nuanced variables should be considered for future RF seasonal within-home-range analyses.

Management implications.—Our RF approach confirms that a small number of high-elevation variables are important for wolverine habitat at the population level in the GYE. Our RF results further indicated that high-elevation talus or similar geological features best predicted wolverine habitat selection, which aligns with some previous research (Copeland 1996; Inman et al. 2013; van der Veen et al. 2020) but contradicts others (Copeland et al. 2007). While high-elevation features explain population-level and home-range-level wolverine habitat, within-home-range selection (third order) is more complex in the GYE. The GYE represents the southern extent of the wolverine distribution, and the long-term success of wolverines in this region, like that of many other species and natural amenities, will benefit from planning for anthropogenic changes (Hansen and Phillips 2018). However, high-elevation areas in the Rocky Mountain West generally are in public ownership and well-regulated, which bodes well for wolverine conservation efforts.

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CONFLICT OF INTEREST

The authors declare no competing interests.

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