

Seasonal resource selection by introduced mountain goats in the southwest Greater Yellowstone Area

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Abstract. Mountain goats (*Oreamnos americanus*) are among the least studied North American ungulates. Aided by successful translocations from the early to mid-1900s, introduced populations have greatly expanded within non-native ranges, yet there remains a paucity of empirical studies concerning their habitat requirements and potential distributions. The lack of studies presents a formidable challenge to managers tasked with monitoring mountain goat expansion and mitigating for any potential negative impacts posed to native species and communities. We constructed summer and winter resource selection models using GPS data collected during 2011–2014 from 18 (14 female and four male) mountain goats in the Snake River Range of the southwest Greater Yellowstone Area. We used generalized linear mixed models and evaluated landscape and environmental covariates at multiple spatial grains (i.e., neighborhood analyses within 30-, 100-, 500-, and 1000-m buffers) within four related suites. The multi-grain resource selection function greatly improved model fit, indicating that mountain goat resource selection was grain dependent in both seasons. In summer, mountain goats largely selected rugged and steep areas at high elevations and avoided high solar radiation, canopy cover, and time-integrated normalized difference vegetation index (NDVI). In winter, mountain goats selected lower elevations characterized by steep and rugged slopes on warm aspects and avoided areas with high canopy cover, NDVI amplitude, and snow water equivalent. Slope was the dominant predictor of habitat use in both seasons, although mountain goats selected for steeper slopes in winter than in summer. Regional extrapolations depicted suitable mountain goat habitat in the Snake River, Teton, Gros Ventre, Wyoming, and Salt Ranges centered around steep and rugged areas. Winter range was generally characterized by the steepest slopes within a more broadly distributed and generally less steep summer range. Further research should examine the spatial and temporal overlap with native populations to further our understanding of resource selection dynamics and the potential for introduced mountain goats to alter intraguild behavioral processes of sympatric species, namely the Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*).

Key words: mountain goat; multi-grain analysis; *Oreamnos americanus*; resource selection function (RSF); Yellowstone.

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INTRODUCTION

Mountain goats (*Oreamnos americanus*), because of their propensity to inhabit rugged and remote terrain, are among the least studied North

American ungulates (Festa-Bianchet and Côté 2008). The paucity of empirical studies is most pronounced in the southern portions of their range where mountain goats are considered non-native according to reviews of archeological,

paleontological, and historical records (Laundré 1990, Schullery and Whittlesey 2001, Festa-Bianchet and Côté 2008). Mountain goats are native to northwestern North America, primarily occurring within coastal and inland mountains west of the continental divide from southern Alaska, USA, through the Yukon Territories, Alberta, and British Columbia, Canada, and into the northwestern United States (Festa-Bianchet and Côté 2008). Successful translocation efforts during the early to mid-1900s have expanded the distribution of the species with introduced populations now established in Wyoming, Colorado, Utah, South Dakota, and Nevada as well as new areas of Alaska, Alberta, Washington, Idaho, and Montana (Festa-Bianchet and Côté 2008, Flesch et al. 2016). While the majority of mountain goats occur within their native range, the general range expansion within non-native regions has highlighted the need for empirical studies that investigate their ecological roles and management concerns. Studies of introduced mountain goats in Olympic National Park, for example, documented negative impacts to fragile native alpine and subalpine communities including endemic and rare species, which prompted a large capture-relocation program in an attempt to reduce or eliminate mountain goats from the park (Houston et al. 1994). Moreover, the possibility for competition (Reed 2001) and disease transmission (Gross 2001) with native Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) is an important, but unevaluated concern throughout non-native ranges.

The Greater Yellowstone Area (GYA), one of the largest relatively intact temperate ecosystems in the world, represents a region where enhanced ecological knowledge of mountain goats within non-native ranges is needed. From an initial introduction of 170 animals to nine sites over 28 yr (1942–1970), mountain goats have expanded their distribution and grown to an estimated 1648 individuals within the GYA (Flesch et al. 2016). The northeast GYA, where introductions were first initiated and most concentrated, is nearly completely colonized by mountain goats and contains roughly 632 individuals in and adjacent to Yellowstone National Park (Flesch et al. 2016). The most recent introductions occurred in the southwestern GYA in 1969 and 1970 with the translocation of 12 individuals into the Snake River Range.

This population, currently estimated at 300 individuals (Fralick 2015, Idaho Department of Fish and Game 2015), is growing and presumably expanding northward into the Teton Range including Grand Teton National Park where 40–60 animals were estimated in 2015. Despite the continuing increase in distribution and population numbers throughout the GYA, there remains a paucity of ecological data for mountain goats, specifically concerning their spatial ecology. The lack of ecological knowledge presents a formidable challenge to managers tasked with the responsibility of monitoring mountain goat expansion and mitigating for any potential negative impacts posed to native species and communities to maintain the ecological integrity within the region.

The summer occupancy surveys conducted in the northern GYA by DeVoe et al. (2015) provided the first assessment of the terrain and environmental characteristics associated with mountain goat occupancy and the first maps of their potential distribution throughout the GYA. DeVoe et al. (2015) predicted that mountain goats in the GYA could become 2.5–4.2 times more abundant than current population estimates if range expansion continues uninhibited. Data on mountain goat winter spatial ecology in the GYA are more limited and there are no regional habitat models that predict winter habitat use. Previous work on mountain goat wintering strategies in their native ranges generally indicates that they restrict movements to smaller geographic areas and move to lower elevations to avoid deep snow (Gross 2001, Poole and Heard 2003, White 2006, Poole et al. 2009). Wintering strategies are particularly important because of the harsh environments that mountain goats inhabit and the general restriction in suitable habitats which increases the possibility for intraguild competition if multiple species (e.g., bighorn sheep) are constrained to the same limited winter range (DeVoe et al. 2015).

Our objective was to broadly describe the seasonal spatial ecology of mountain goats in the southwest GYA. Using GPS data from 18 (14 female and four male) allopatric mountain goats, we built winter and summer resource selection models to (1) further elucidate patterns in mountain goat resource selection within non-native ranges, including the terrain and environmental characteristics most strongly associated with seasonal ranges as well as the appropriate spatial

grain, and (2) provide the first spatial predictions of seasonal habitat use by mountain goats in the southwest GYA and describe their potential distribution.

METHODS

Study area

The Snake River Range spans the border between Wyoming and Idaho in the southwest GYA, with the Teton Range to the north and the Snake River and Palisades Reservoir to the south and west (Fig. 1). The rugged and steep Snake River canyon demarcates the range to the south and is frequently used by mountain goats. The Snake River Range is characterized by rugged, mountainous topography with elevations ranging from 1700 to 3000 m a.s.l. Mountain goats were first released into the Snake River Range in 1969 at Palisades Creek with an initial group of five individuals, and a secondary release of seven individuals in 1970 at Black Canyon. While the animals at Black Canyon apparently did not survive (Hayden 1984), the release at Palisades Creek was successful with a population estimate of 300 individuals (adults = 253, kids = 47) in 2014 (Fralick 2015, Idaho Department of Fish and Game 2015). Although transient bighorn sheep are occasionally observed in the Snake River Range, the mountain goat population is considered allopatric. Mountain goats are now well distributed throughout the middle and southern portions of the Snake River Range and are presumed to be expanding northward.

Animal capture and handling

From 2011 to 2014, we used a combination of ground darting and helicopter net gunning to capture mountain goats, and primarily conducted capture efforts in summer and spring months. We targeted adult females, although due to the difficulty of capturing mountain goats, mature males were also included in the sample. All captured animals were fitted with a store-on-board GPS (Telonics TGW-4400-2 and TGW-4400-3) and very high frequency (VHF; Telonics MOD 401-1) radio collars. The dual collaring method enabled us to obtain fine spatial and temporal location information for 1.5–2 yr before the GPS collar released from the animal, and an additional five years of monitoring with the VHF collar. The collars collected GPS

locations at 4- or 6-h intervals. All animals were processed at the capture location and handled according to the International Animal Care and Use Committee guidelines (Montana State University permit numbers 2011–17, 2014–32).

Data censoring

There are two dominant forms of error associated with GPS collars, spatial imprecision of acquired locations and habitat- or behavior-induced fix bias (Frair et al. 2004, Hebblewhite and Haydon 2010). We screened imprecise locations from the dataset by removing GPS locations with a horizontal dilution of precision (HDOP) >10. This follows the recommendation of D'Eon and Delparte (2005), but uses HDOP rather than position dilution of precision, which does not include vertical error components and is no longer included in data files from the collar manufacturer. Measures of dilution of precision are unitless and serve as an index of precision based on satellite configuration, but are not a measure of direct spatial imprecision (Telonics 2010). As a result, we also screened locations based on the measurement of horizontal error included in Generation 4 Telonics collar data files and censored all locations with an estimated error >60 m.

Fix bias can introduce error into resource selection studies by underrepresenting habitat types or landscape characteristics that reduce the probability of a GPS unit acquiring a location (Johnson and Gillingham 2008, Frair et al. 2010). Previous work suggests that dense canopy cover and steep slopes reduce GPS collar performance by diminishing communication with orbiting satellites (D'Eon et al. 2002). Because mountain goats inhabiting inland areas predominantly occur within subalpine and alpine vegetation zones with little to no canopy cover in both summer (Gross et al. 2002, Poole and Heard 2003) and winter (Taylor and Brunt 2007, Poole et al. 2009), it is unlikely that canopy cover results in large reductions in fix success. For mountain goats, terrain (e.g., slope) is likely to have a greater impact on collar performance. However, because of the strong seasonal association with steep, alpine environments (Poole et al. 2009, DeVoe et al. 2015), it is unlikely that these habitats will be greatly underrepresented in the dataset. As a result, we did not censor individuals based on fix success, and assumed that any

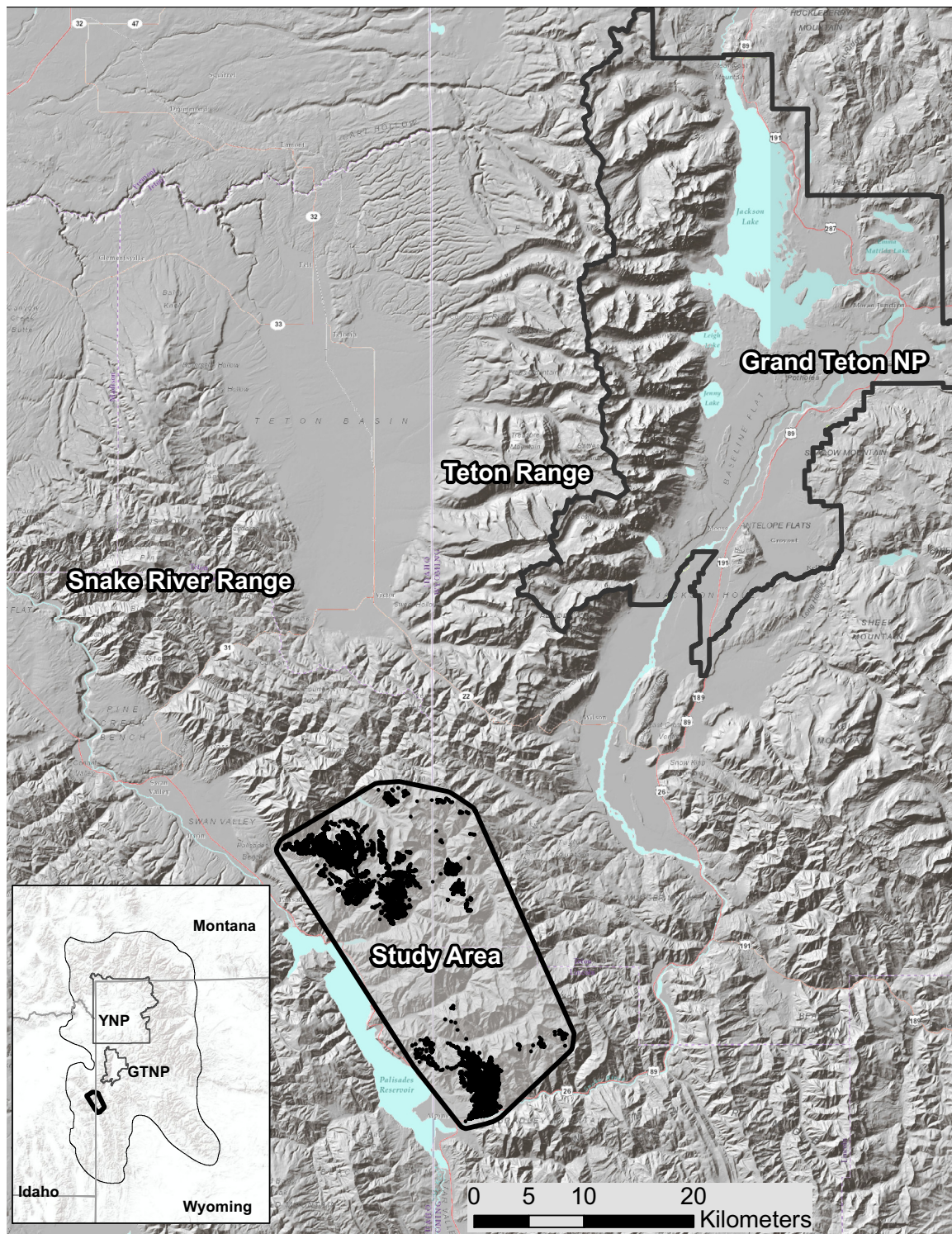


Fig. 1. GPS locations of 18 (14 female and four male) instrumented mountain goats within the Snake River Range study area spanning Idaho and Wyoming, USA, 2011–2015. The study area is contained within the Snake River Range (black polygon). The Teton Range stretches northward.

potential bias from steep slopes would not alter the fundamental conclusions regarding mountain goat seasonal resource selection.

Delineating mountain goat seasons

Mountain goat movements are difficult to delineate into seasons because of the large degree of individual variation in response to seasonal environmental conditions (Rice 2008). We applied nonlinear regression analyses of net-squared displacement (NSD; Bunnefeld et al. 2011) to delineate individuals into groups according to migration strategy and estimate migration parameters. Rather than calculating NSD from the capture location of each individual (i.e., Bunnefeld et al. 2011), we calculated NSD from a mean winter range centroid. For each individual, we calculated the centroid of the GPS locations obtained between 1 December and 31 January, which provided a location estimate of the “mean winter range” from which we measured displacement (Euclidian distance) of each GPS relocation. This approach better accommodated our seasonally staggered capture schedule and allowed us to calculate displacement from a mean winter range regardless of where or in what season an animal was captured. We then fit the equations from Bunnefeld et al. (2011) and averaged the individual start and end dates for migrants and mixed migrants to obtain an estimate of the midpoint for spring and fall migratory periods for the population. We then buffered the migratory midpoints by ± 20 d, which approximated the 90th percent quantile of the observed maximum spring and fall migration durations. This process provided estimates of spring and fall migratory periods which were removed from the dataset to build season-specific resource selection models without the associated “noise” created by migratory movements.

Defining habitat availability

We evaluated population-level resource selection (i.e., second order; Johnson 1980) and employed a used-available design where individuals were identified and contained a unique “used” set, but “availability” was measured at the population level (i.e., Design II; Manly et al. 2002). We defined the extent of availability using a buffered minimum convex polygon (MCP) and used the same extent for summer and winter seasons. The MCP encompassed the pooled GPS

locations and was buffered by the 95% step length between consecutively acquired locations (Laforge et al. 2015b). This approach allowed the extent of availability to be determined by the movement metrics of the study animals. Within the availability extent, we generated a random sample of points at a ratio of 1:10 (used:available). The 1:10 ratio ensured a sufficient sample to avoid numerical integration error and convergence issues (Northrup et al. 2013), and adequately described the distribution of each covariate within the study area (Appendix S1).

Resource covariates and spatial grain

We hypothesized the effect (Table 1; positive or negative) of each covariate on mountain goat use and evaluated these hypotheses through the model selection process. We evaluated covariates within four suites: terrain, vegetation, heat load, and snow (Table 1; DeVoe et al. 2015). The terrain suite included elevation (ELEV), slope (SLP), and three measures of ruggedness—slope variance (SLPv), calculated as the standard deviation² of SLP (DeVoe et al. 2015), the standard deviation of landscape curvature (CurvSD; Poole et al. 2009), and vector ruggedness measure (VRM), which measured the integrated variation in SLP and aspect (Sappington et al. 2007). With the exception of ELEV in winter, we predicted that all of the terrain covariates would be positively correlated with mountain goat use (Table 1). We did not include measures of distance to escape terrain (DET) in the initial model building process following recent suggestions from DeVoe et al. (2015) who concluded that the combined use of SLP and SLPv provided a more biologically meaningful understanding of mountain goat habitat. Rather, we conducted post-hoc model comparisons with DET (*Post-hoc model comparisons* section below) to further evaluate the findings of DeVoe et al. (2015).

The vegetation suite contained canopy cover (CanCov) and two competing measures of normalized difference vegetation index (NDVI), NDVI amplitude (NDVI_{Amp}; USGS EROS Center 2016) and time-integrated NDVI (NDVI_{Tin}; USGS EROS Center 2016). We included NDVI covariates as a measure of forage in both summer and winter seasons and predicted that NDVI would be positively correlated with mountain goat use. While vegetation is mostly covered by snow during the winter

Table 1. Covariate descriptions and the hypothesized relationships (summer, winter) with the relative probability of use (Pr(use)) for introduced mountain goats in the Snake River Range, Wyoming, ID, 2011–2015.

Abbreviation	Description	Form	Spatial grain†	Relationship with Pr(use)
Terrain suite				
CurvSD	Standard deviation of landscape curvature	Li, Ps	30, 100, 500, 1000	pos, pos
ELEV	Elevation (m)	Li	30	pos, neg
SLP	Slope (°)	Li, Sq	30, 100, 500, 1000	pos, pos
SLPv	Slope variance: standard deviation ² of SLP	Li, Ps	30, 100, 500, 1000	pos, pos
VRM	Vector ruggedness measure	Li, Ps	30, 100, 500, 1000	pos, pos
Vegetation suite				
CanCov	Canopy cover	Li	30, 100, 500, 1000	neg, neg
NDVI_Amp	NDVI amplitude: mean difference between max NDVI and baseline at beginning of growing season from 2011 to 2014.	Li	500, 1000	pos, pos
NDVI_Tin	Time-integrated NDVI: mean daily (interpolated) integration of NDVI above the baseline for the duration of the growing season from 2011 to 2014.	Li	500, 1000	pos, pos
Heat load suite				
AspectCos	The inverse cosine of aspect -35°	Li	30	neg, pos
Solar	Solar radiation (watt/m ²)	Li	30	neg, pos
Snow suite				
SWE	Snow water equivalent: mean December to January from 2011 to 2014.	Li	1000	na, neg
Snow	Snow depth: mean December to January from 2011 to 2014.	Li	1000	na, neg

Notes: Li, linear; Sq, quadratic; Ps, natural log/pseudothreshold. For each covariate, the functional forms and spatial grains that were evaluated are shown.

† Circular buffer in meters.

months, including NDVI as a winter covariate allowed us to evaluate whether or not the areas in which mountain goats forage in winter were associated with summer NDVI. We calculated the mean NDVI_{Amp} and NDVI_{Tin} from 2011 to 2014 to create a single measure for the duration of the study. The heat load suite contained two covariates that captured the intensity of solar radiation (RAD) on the landscape. We estimated the duration of solar RAD (Fu and Rich 1999) and aspect, which was transformed into a biologically interpretable index by taking the inverse cosine of the angle -35° (AspectCos; Cushman and Wallin 2002). This transformation changed the axis from N-S to NNE-SSW and ranges from -1 to 1 , respectively (Cushman and Wallin 2002). For both measures of heat load, we predicted that mountain goats would select for relatively warm areas in winter and relatively cool areas in summer. Lastly, we included two measures of snow accumulation, snow depth (SnowDepth; NOHRSC 2004) and snow water equivalent (SWE; NOHRSC 2004), and created a single value for each covariate by averaging the daily values from 1 December to 31 January in 2011

to 2014. We predicted that both measures would be negatively associated with mountain goat use.

In addition to including a linear term for each covariate, we evaluated a pseudothreshold (natural log) form for the three ruggedness indices and a squared term for SLP and ELEV (Table 1). We hypothesized that the pseudothreshold form, whereby the relationship with resource selection was allowed to asymptote above a given ruggedness threshold, would provide a better fit to the data (DeVoe et al. 2015). Similarly, we hypothesized the squared terms for SLP and ELEV, which allowed the relationship to peak at an optimal covariate value, would also be ranked higher than the linear forms (Gross et al. 2002, Poole et al. 2009). Evaluating additional functional forms provided more flexibility in determining the most explanatory covariates, and has been shown to improve model fit for previous mountain ungulate resource selection studies (Gross et al. 2002, Poole et al. 2009, DeVoe et al. 2015, Hoglander et al. 2015).

Recent work has highlighted the importance of evaluating covariates at multiple spatial grains,

and suggests that a multi-grain approach provides a more informative predictive model by incorporating the “space of influence” on animal decisions in regard to resource selection (Meyer and Thuiller 2006, Laforge et al. 2015b). The multi-grain approach formalizes the concept that an animal’s choice to select a given spatial location may not result solely from the attributes in the immediate vicinity (e.g., minimum resolution of the data) but may also be influenced by a broader region (e.g., the “space of influence”; Laforge et al. 2015b). Within the context of a multi-grain analysis, grain is defined as the size of an area surrounding a point (or pixel) within which ecological data are measured (Meyer and Thuiller 2006, Laforge et al. 2015b), and does not specifically refer to the minimum resolution of the data (e.g., Hobbs 2003). We evaluated covariates at four grain sizes by performing neighborhood analyses at 30-, 100-, 500-, and 1000-m circular buffers using the raster package (Hijmans et al. 2016) in program R (R Core Team 2015). Multiple grains were not evaluated below the minimum resolution of the data for any given covariate and were restricted to covariates that could be visually perceived (Table 1). Following DeVoe et al. (2015), we hypothesized that terrain covariates would be best characterized by larger spatial grains and that forage covariates would be best characterized at relatively small spatial grains. These hypotheses reflect a possible hierarchical structuring to mountain goat habitat selection whereby animals first select broadly for terrain covariates and secondarily select for vegetation covariates at smaller spatial grains (DeVoe et al. 2015).

Statistical framework and model selection

We identified individual mountain goats as the sample unit and accounted for the autocorrelation within individuals and unbalanced sample size among individuals by specifying a random intercept for each mountain goat using a mixed-model framework (Gillies et al. 2006, Fieberg et al. 2010). We calculated the relative probability of use using the exponential resource selection function (RSF):

$$\hat{w}(x) = \exp(\hat{\beta}_0 + \hat{\beta}_1 x_1 + \hat{\beta}_2 x_2 + \cdots + \hat{\beta}_n x_n)$$

where $\hat{\beta}_0$ is the intercept, and β' are the coefficients of the effects of the covariates, X_i , on $\hat{w}(x)$, the relative probability of use. The exponential

RSF is a relative probability function, not a true probability (i.e., RSPF; Lele and Keim 2006, Lele 2009). Following similar studies (e.g., Gillies et al. 2006, Hebblewhite and Merrill 2007, Laforge et al. 2015b), we retained the intercept term, $\hat{\beta}_0$, when generating regional predictions within the mixed-model framework. We then applied a linear stretch to rescale the predicted RSF values between 0 and 1 (Johnson et al. 2004):

$$\hat{w} = \left(\frac{w(x) - w_{\min}}{w_{\max} - w_{\min}} \right).$$

We employed a tiered approach in model selection that guided our progression from relatively simple univariate models focused on identifying the most explanatory functional form and spatial grain, to multivariate models that evaluated different covariate combinations within model suites (Franklin et al. 2000, DeVoe et al. 2015). More specifically, in tier one, we fit univariate models for each covariate for which we evaluated multiple grains and functional forms (Table 1), and selected a single grain and form for each covariate using corrected Akaike’s information criterion (AIC_c ; Burnham and Anderson 2002). Because we evaluated similar indices for some covariates (e.g., $NDVI_{Amp}$ and $NDVI_{Tin}$), we again used univariate models and AIC_c to select between similar indices in tier two. In tier three, we began multivariate model building using the covariates and the respective grains and functional forms identified in tiers one and two. Because of the strong association with steep and rugged terrain throughout their range and the predominance of terrain covariates in previous mountain goat resource selection studies (Smith 1986, Poole and Heard 2003, White 2006, Poole et al. 2009, DeVoe et al. 2015), we began by building a base terrain model which evaluated all non-collinear combinations of SLP, ELEV, CurvSD, SLPv, and VRM. Lastly, we built upon the base terrain model with an all combinations approach using the remaining covariates from the vegetation, heat load, and snow (in winter) suites. Because we were predominantly interested in marginal (population) inferences, we used conventional AIC_c throughout the model selection process as recommended by Vaida and Blanchard (2005). In all multivariate models, we excluded covariate pairings with a Pearson’s

correlation coefficient of $r > |0.6|$. We followed the same sequential, step-wise approach for summer and winter and fit mixed-effects models using the lme4 R package (Bates et al. 2015) with scaled and centered covariates.

Post-hoc model comparisons

We performed a series of post-hoc model comparisons to evaluate distance to escape (i.e., steep) terrain as an additional covariate and also evaluated the multi-grain approach. DET is often used as an explanatory covariate for mountain ungulate habitat models and resource selection studies (Gross et al. 2002, DeCesare and Pletscher 2006, Poole et al. 2009), but the choice of a threshold with which to define escape terrain is highly variable (ranging from 25° to 50°) and subjective (Gross et al. 2002, DeVoe et al. 2015). After evaluating a model set comparing measures of DET with SLP and SLPv, DeVoe et al. (2015) recommend that SLP and SLPv be used in place of DET as a more biologically informative interpretation of mountain goat habitat associations. While these efforts have helped to demonstrate the combined importance of SLP and SLPv, their model comparisons did not allow for the combined influence of DET with SLP and SLPv. Notwithstanding collinearity issues which can be problematic when characterizing landscape terrain (Fu and Rich 1999, Poole et al. 2009), we hypothesized that DET, in combination with SLP and SLPv, would improve model performance and predicted that DET would have a negative relationship with mountain goat resource selection. We evaluated this hypothesis with three measures of DET defined as slopes $\geq 40^\circ$, 45° , and 50° (DET40, DET45, and DET50, respectively), and added each to our top summer and winter model. We then evaluated the inclusion of the DET terms using AIC_c (Burnham and Anderson 2002). All DET covariates were characterized at the 30-spatial grain. DET measures with a Pearson's correlation coefficient of $r > |0.6|$ when combined with any covariate in our top a priori models were not evaluated.

We tested the multi-grain approach by fitting a new model with the same covariate structure as our top a priori model, including the potential addition of DET, but used the minimum resolution available for each covariate. For each season, we ranked the multi-grain and minimum resolution

models using AIC_c. Using the minimum resolution available for a given covariate is often the default approach for resource selection studies, but there is little biological justification for the practice (Hobbs 2003, Boyce 2006, Laforge et al. 2015b). Following Laforge et al. (2015b), the post-hoc model comparison served as an additional confirmatory test of the multi-grain approach.

Mountain goat RSF extrapolations

To meet our second research objective, we generated regional extrapolations of the top seasonal models to delineate mountain goat habitat throughout the southwest GYA. We extrapolated from the Snake River Range study area to the broader Snake River Range, and also north to the Teton Range, east to the Gros Ventre Range, and south to the Wyoming and Salt Ranges. Collectively, the five mountain ranges of the southwest GYA represent a nearly contiguous expanse of mountainous terrain. In each region, we generated predictions of the relative probability of use and discretized the RSF value of each pixel into 10 equal-area bins representing a relative habitat classification from poor to best. We also generated maps of "suitable" habitat for each region and defined suitable areas as those with an RSF value $\geq$ the lower 5% of the RSF values from used locations and quantified the amount of suitable habitat in each region (DeVoe et al. 2015).

Model validation

We used a multifaceted approach to evaluate model predictive performance. First, within the study area, we performed k -fold cross-validation where k indexed each individual rather than a random data fold (Boyce et al. 2002). Within an iterative process, we withheld the locations for each individual, 1 through k , fit an exponential RSF with the individuals that were retained, and then predicted the fitted values for the observations that were withheld. We then summed the occurrence of used locations within 10 equal-area RSF bins and evaluated the correlation between the frequency of occurrence and the relative RSF score using the Spearman's rank correlation (Boyce et al. 2002). The adjusted frequencies should be highly correlated with the relative RSF if the model performs well (Boyce et al. 2002).

Secondly, we validated the Teton Range extrapolation with an independent sample of 800 summer

and 2405 winter mountain goat GPS locations that were collected from December 2014 to March 2016. We indexed the available distribution of RSF values within the Teton Range by generating 10,000 random locations which were used to define 10 equal-area bins for each seasonal extrapolation. Following the same k -fold methods employed within the study area, we summed the frequency of occurrence within each equal-area bin using the independent sample and evaluated the predictive performance with Spearman's rank correlation (Boyce et al. 2002).

RESULTS

Data collection, censoring, and definitions

Capture efforts began in the summer of 2011 and continued to the spring of 2014, resulting in the instrumentation of 18 mountain goats (14 female and four male; Appendix S2) with GPS and VHF collar pairs. With the exception of one yearling male, all animals were classified as adults with a mean age of 4 yr (Appendix S2). Animals were monitored for an average of 514 d (range: 265–753), resulting in 38,040 GPS locations. We censored 28 locations with a HDOP >10 and 140 locations with a horizontal error >60 m. After censoring, the mean summer and winter fix success was 86% and 81%, respectively (Appendix S2). There were 15 animal-years that produced coefficient estimates for each of the Bunnefeld et al.'s (2011) movement equations. Thirteen of the 15 animal-years were classified as migrant or mixed migrant and two were classified as resident. Using the buffered midpoints from the population spring and fall migrations, we defined the summer season as 16 June to 13 October and the winter season as 22 November to 7 May (Appendix S3). After removing locations associated with migratory periods, we had 15,029 and 12,495 used locations for summer and winter, respectively. The study area MCP was buffered by 642 m, representing the 95th percent quantile of sequential step lengths and encompassed 472 km² (Fig. 1).

Model selection and validation

Our tier one results highlighted the importance of evaluating multiple spatial grains and indicated that the relationship with a given covariate can be grain dependent. For each covariate where multiple spatial grains were evaluated,

there was a clear top-ranked spatial grain and substantial differences between AIC_c scores (Appendix S4: Table S1, Figs. S1, S2). With the exception of CanCov and VRM which had opposite grain sizes in each season, the top-ranked spatial grain for a given covariate was similar for summer and winter (Appendix S4: Table S1). In contrast to our predictions, the covariates from the vegetation suite were best characterized at large spatial grains (i.e., 1000 m) in both seasons. There were mixed results within the terrain suite. In summer, CurvSD and SLP were best characterized at 500 m, SLPv at 30 m, and VRM at 1000 m. In winter, there was a general reduction in the spatial grain. Within the terrain suite, CurvSD was best characterized at 500 m, SLP at 100 m, and SLPv and VRM at 30 m. In support of our predictions, we also observed striking differences in predictive power for different functional forms (Appendix S4: Table S1, Figs. S1, S2). Within the terrain suite, the pseudothreshold form was top-ranked for all ruggedness indices, while the quadratic form was top-ranked for SLP and ELEV (Appendix S4: Table S1).

In tier two, there were substantial differences in AIC_c rankings between related indices within a suite. In summer, NDVI_{Tin} was ranked above NDVI_{Amp} (Δ AIC 16,263), and RAD was ranked above AspectCos (Δ AIC_c 314; Appendix S4: Table S2). The results were opposite in winter where NDVI_{Amp} was ranked above NDVI_{Tin} (Δ AIC_c 11,335) and AspectCos was ranked above RAD (Δ AIC 1964; Appendix S4: Table S2). In winter, SWE was ranked above SnowDepth (Δ AIC 368; Appendix S4: Table S2).

The tier three base terrain model had the same covariates and functional forms across seasons, but there were slight differences in the spatial grains (Appendix S4). The multivariate combination of SLP, SLP², SLPv^{PS}, ELEV, and ELEV² was the most supported, non-collinear terrain model for both seasons. When evaluated with the other top-ranked covariates from tiers one and two, the top-ranked summer model contained SLP₅₀₀, SLP₅₀₀², SLPv₃₀^{PS}, ELEV₃₀, ELEV₃₀², CanCov₁₀₀₀, NDVI_{Tin1000}, and RAD₃₀. The top-ranked winter model contained SLP₁₀₀, SLP₁₀₀², SLPv₃₀^{PS}, ELEV₃₀, ELEV₃₀², CanCov₃₀, NDVI_{Amp1000}, AspectCos₃₀, and SWE₁₀₀₀ (Appendix S4: Table S3).

As predicted, the post-hoc evaluations indicated that measures of DET provided additional

explanatory power above the paired combination of SLP and SLPv. When added to the previous models, DET50 and DET40 were ranked highest in summer and winter, respectively (Appendix S4: Table S4). Adding DET in winter had a greater impact on model performance than in summer (Fig. 2; Appendix S4: Table S4). The post-hoc test of multiple spatial grains further

supported the multi-grain approach (Laforge et al. 2015b). When compared to our summer and winter multi-grain models (including the respective measures of DET), models with the same structure at the minimum resolution had substantially higher AIC_c scores (summer Δ AIC: 5179; winter Δ AIC: 1651; Appendix S4: Table S5).

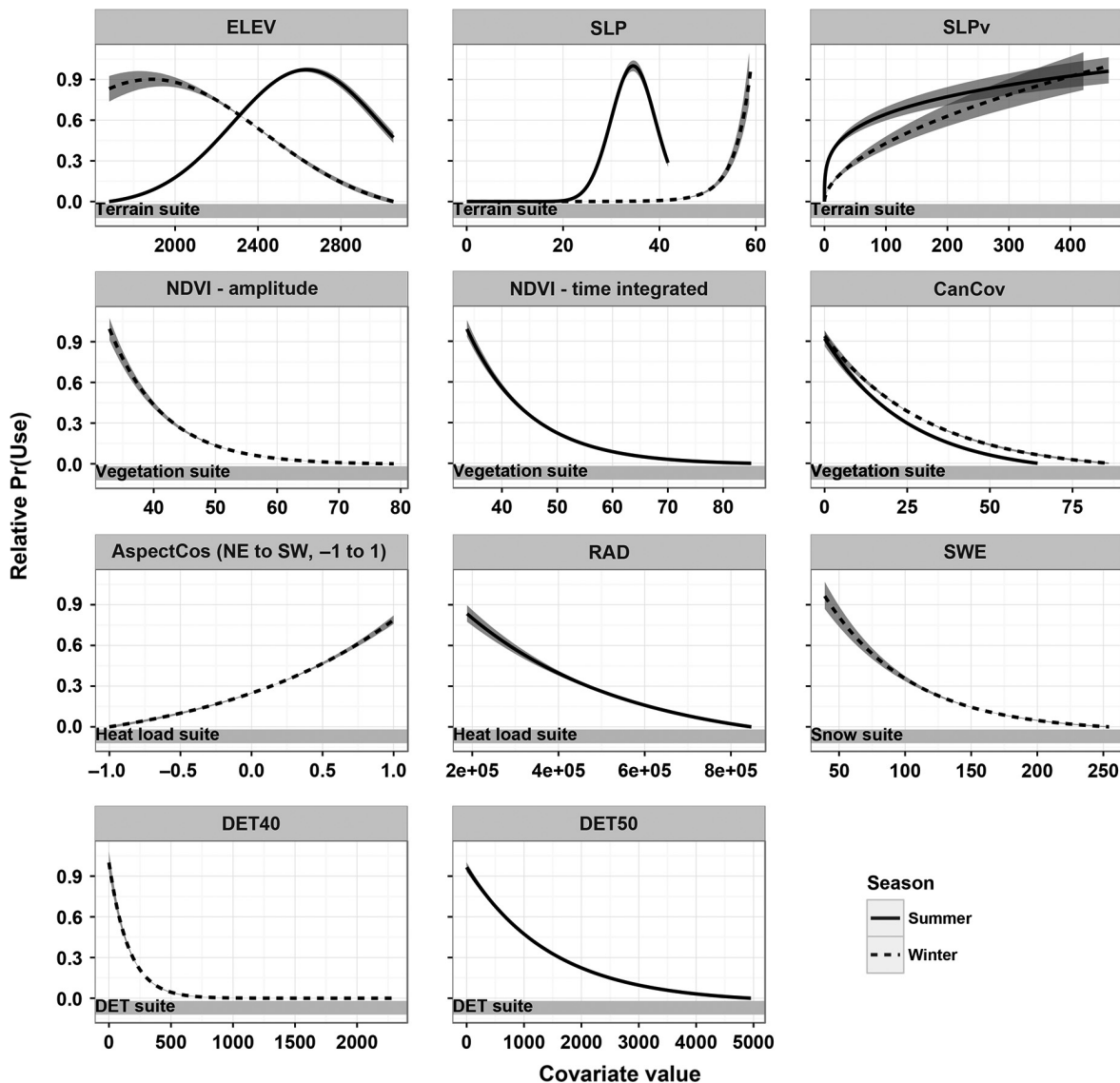


Fig. 2. Predictions of the relative probability of use for the top covariates in the final summer and winter resource selection model. Covariates are presented within suites noted at the bottom of each graph. Ninety-five percent confidence bands were generated using bootstrap techniques within the merTools R package (Knowles and Frederick 2016) and do not account for the variation associated with the random effect. Predictions were generated across the covariate range with all other covariates held at their mean value.

As predicted, mountain goats generally selected for relatively high elevations in summer and lower elevations in winter (Fig. 2). The quadratic form of the covariate indicated optimal summer and winter elevations of 2630 and 1888 m, respectively. In both seasons, there was a strong positive association with SLP; however, the opposite signs for SLP² resulted in strikingly different relationships (Fig. 2; Appendix S4: Table S6). In summer, the negative coefficient for SLP² resulted in a convex function with an optimal SLP angle of 35°. In contrast, the positive coefficients for both SLP and SLP² in winter indicated that the relationship with SLP increased as a positive quadratic function and that relatively steeper slopes were selected in winter than in summer (Fig. 2). In both seasons, mountain goats selected for rugged areas with high SLPv values at the minimum spatial grain (30 m). The pseudothreshold form of SLPv was stronger in summer than in winter, yet in both seasons the relationship began to asymptote as SLPv increased (Fig. 2).

Within the vegetation suite, the indices for NDVI varied among seasons. Contrary to our prediction, we found a negative relationship with NDVI_{Tin1000} in summer and NDVI_{Amp1000} in winter (Fig. 2). As expected, there were negative relationships with CanCov in both seasons. In summer, mountain goats avoided CanCov at a larger spatial grain than in winter (Fig. 2). The top-ranked covariates within the heat load suite varied between seasons, yet corroborated our predictions and indicated that mountain goats selected against heat in summer and for heat in winter. In summer, RAD₃₀ was the top-ranked index of heat load and showed a negative relationship. In winter, head load was best indexed by AspectCos₃₀ with which there was a positive relationship, indicating preference for southwest aspects (Fig. 2). Lastly, as expected, there were negative relationships with SWE in the winter snow suite and DET in both seasons (Fig. 2).

The *k*-fold evaluation methods for interpolations within the study area showed a strong correlation between area-adjusted frequencies and the relative RSF in summer ($r_s = 0.98$, $P < 0.0001$) and winter ($r_s = 1$, $P < 0.0001$; Appendix S5: Fig. S1, Appendix S6). Moreover, the extrapolations within the Teton Range were also highly correlated with the relative RSF score in both seasons

(summer: $r_s = 0.98$, $P < 0.0001$; winter: $r_s = 0.95$, $P < 0.0001$; Appendix S5: Fig. S1).

Mountain goat RSF extrapolations

Regional extrapolations highlighted the importance of high-elevation rugged terrain in summer, which served as the core mountain goat habitat throughout the southwest GYA (Fig. 3; Appendix S7). Winter extrapolations depicted broad range contraction and preference for steep areas patchily distributed across mid-elevations (Fig. 3; Appendix S7). The cutpoints used to define suitable summer and winter habitat were 0.0023 and 0.0002, respectively. Although there were distinctive summer and winter ranges delineated by ELEV, there was noticeable overlap in suitable habitat centered around steep and rugged slopes at mid-elevations (Fig. 3). In many areas, core winter habitat was defined by the steepest slopes within a more broadly distributed and generally less steep summer range (Fig. 3; Appendix S7).

In general, the proportions of suitable habitat within each mountain range were low (Table 2). The Salt and Wyoming Ranges had the smallest proportion of suitable habitat in both summer and winter, 3.4% and 0.9%, respectively. In contrast, the Snake River Range (inclusive of the study area) had the highest proportions of suitable habitat, 9.3% and 5.6% for summer and winter, respectively. On average, suitable habitat in summer was more than double that of winter.

DISCUSSION

Our results provide an empirical assessment of the landscape and environmental covariates influencing mountain goat resource selection within their non-native ranges and the first seasonal predictions of mountain goat habitat in the GYA constructed from GPS collar data. Our findings broadly corroborate with similar studies throughout the mountain goat's native range and demonstrate a strong seasonal association with rugged and steep mountain environments (Gross et al. 2002, Poole and Heard 2003, White et al. 2012, DeVoe et al. 2015, White and Gregovich 2017), yet provide new insights for introduced mountain goats that highlight seasonal differences in resource selection and the importance of spatial grain in predicting habitat selection.

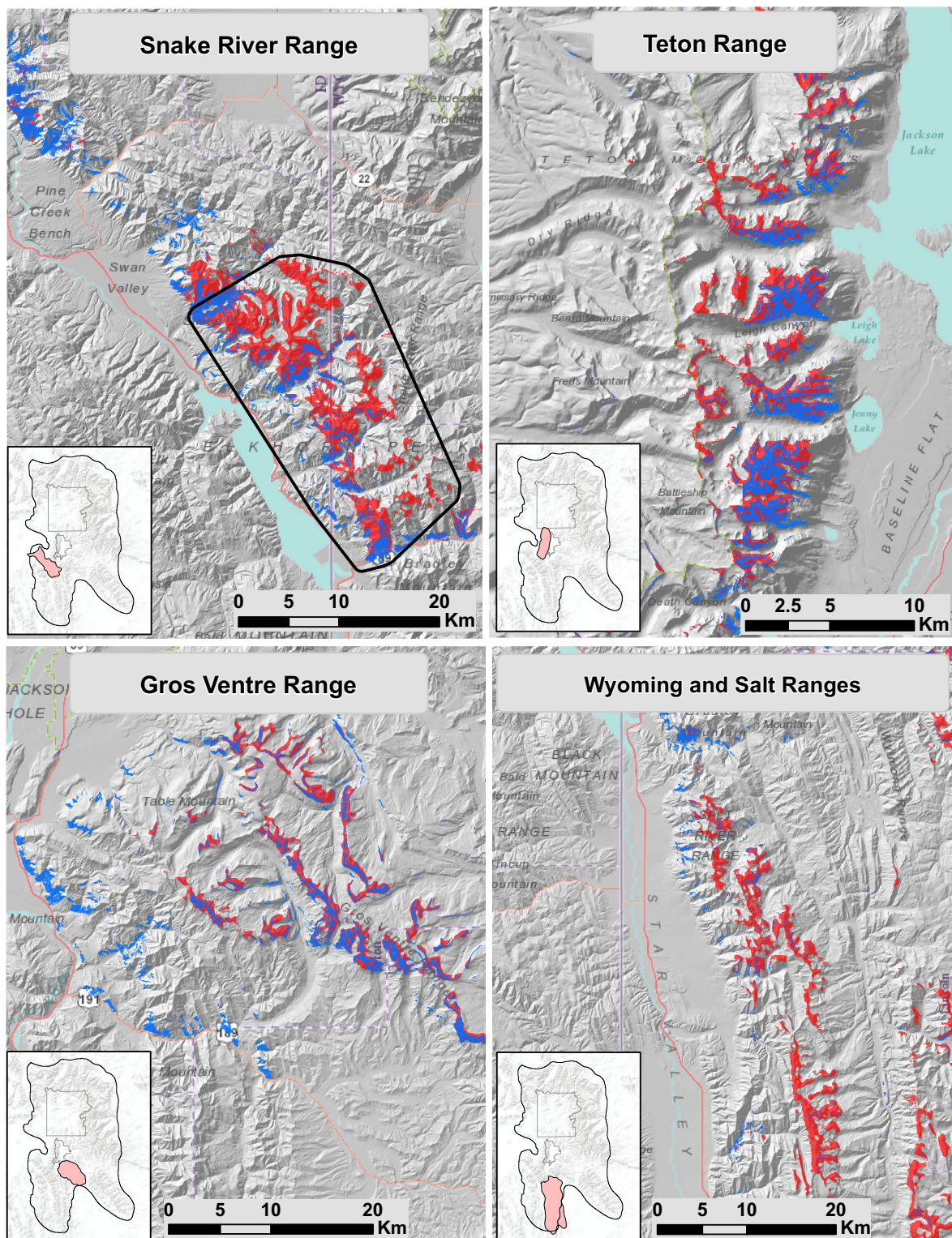


Fig. 3. Regional extrapolations of suitable mountain goat habitat within the southwest Greater Yellowstone Area. The cutpoints used to define suitable summer (red) and winter (blue) habitat were 0.0023 and 0.0002, respectively.

Table 2. Predicted estimates of suitable mountain goat habitat for four regional mountain ranges, southwest GYA.

Region	Total area (km ²)	Suitable habitat (km ²)	
		Summer	Winter
Wyoming and Salt Ranges	5100.24	173.71 (3.41)	45.84 (0.90)
Gros Ventre	2184.90	95.51 (4.37)	80.09 (3.67)
Teton Range	1444.41	70.47 (4.88)	40.98 (2.84)
Snake River Range	1804.77	167.62 (9.29)	100.33 (5.56)
Study area (buffered MCP)	472.75	142.12 (30.06)	77.41 (16.37)

Notes: Area (km²) and percentages (in parentheses) are shown for each mountain range. The cutpoints used to define suitable summer and winter habitat were 0.0023 and 0.0002, respectively.

During the summer months, mountain goats largely inhabited rugged and steep areas at high elevations and avoided high solar RAD, CanCov, and time-integrated NDVI. Slope was the most influential predictor of the relative probability of use and indicated an optimal SLP angle of 35°. The strong positive relationship with steep slopes was also evident in the inclusion of DET, which in summer was defined as SLP angles $\geq 50^\circ$. The transition to high alpine areas in summer is commonly observed in mountain ungulates and coincides with the greening of vegetation and snow melt (Varley 1994, DeCesare and Pletscher 2006, Pettorelli et al. 2007). The results from our evaluation of NSD and seasonal habitat predictions indicate that mountain goats in the southwest GYA undergo seasonal movements to relevantly high elevations in summer as snow dissipates. However, the negative relationship with NDVI was a surprising result and counter to our hypothesized relationship with the relative probability of use.

The use of NDVI as an index of forage is ubiquitous in similar research with related taxa (Pettorelli et al. 2005, 2011), but has not been included as a habitat covariate for similar studies of mountain goats on native ranges. Within non-native ranges of the GYA, DeVoe et al. (2015) reported a positive relationship between summer occupancy and NDVI. The explanation for the apparent avoidance of NDVI by mountain goats in this study is likely best interpreted through the differing sampling designs. Within an RSF context, we defined availability with random points generated within a buffered population MCP. These methods thoroughly indexed the entire study area, including high NDVI values associated with low-elevation forests. In contrast,

DeVoe et al. (2015) targeted alpine and subalpine “viewsheds,” which were largely void of low-elevation forests. Given the relatively broad characterization of available sites within the RSF context, the contrasting results with DeVoe et al. (2015) likely result from different characterizations of available (or unused) sites (Beyer et al. 2010), which resulted in a relatively broad characterization of NDVI within the RSF framework. Moreover, while we minimized the influence of CanCov on NDVI by evaluating two indices that measure change in NDVI from the first day of the growing season (USGS EROS Center 2016), NDVI values within the study area were consistently lower in the rugged and steep terrain selected by mountain goats when compared to surrounding regions. While forage is obviously an important component of mountain goat habitat, the relationship was likely masked by the dominant selection for steep and rugged slopes at the home range level, which are characteristically rocky and have relatively low NDVI values. It is possible that a third-order (i.e., within home range) analysis would show positive associations with NDVI.

Our top winter model indicates that mountain goats select lower elevations characterized by steep and rugged slopes and avoid areas with high CanCov, NDVI amplitude, and SWE. In winter, mountain goats also selected for relatively warm southwest aspects and for areas close to slopes $\geq 40^\circ$. As in summer, SLP was the most influential covariate, but with a notably different relationship with the relative probability of use. Selection for SLP in winter resulted in a positive quadratic function that was not maximized at an optimal SLP angle and indicated that mountain goats select for steeper slopes in winter than in

summer. The relative importance of steeper slopes in winter was also highlighted by the striking improvement in the top model with the post-hoc addition of DET. We suspect steeper slopes are selected in winter as a behavioral adaptation to avoid deep (or recently fallen; i.e., Richard et al. 2014) snow, which is more readily shed in steep environments, and in so doing reduces the metabolic costs associated with movement and increases access to forage. Moreover, mountain goats also selected southwest aspects in winter, which further reduces snow accumulation due to increased solar radiation.

Winter is an important season for mountain goats that can influence population dynamics through increased juvenile mortality (Côté and Festa-Bianchet 2003), reduced kid production (Adams and Bailey 1982), and possibly determine the ecological carrying capacity through decreased forage availability (Houston and Stevens 1988). Because of the critical importance of winter, there have been a number of targeted studies examining mountain goat wintering strategies and movements on native ranges, which generally indicate that mountain goats inhabit timbered, low-elevation slopes (White 2006, White et al. 2012) and show no differences in the optimal SLP angle between seasons (White et al. 2012, White and Gregovich 2017). We speculate the difference in wintering strategies between native and non-native populations is largely influenced by regional snow climates. Much of previous work regarding mountain goat movement patterns and resource selection has been conducted within maritime environments (although see Poole and Heard 2003) which are characterized by a relatively stable and dense snowpack (McClung and Schaerer 2006). In contrast, the majority of introduced mountain goats, including those in the GYA, are within a continental snowpack with dry, low-density snow that is more frequently shed from steep slopes (McClung and Schaerer 2006). Within the maritime environments, winter snow can accumulate on relatively steep slopes and thereby nullify the effect of SLP angle on snow depth that is observed in continental snow climates. In maritime snow climates, low-elevation, timbered slopes likely offer a better refuge from winter snow than do steep slopes. The wintering strategy of mountain goats in the southwest GYA is akin to other mountain ungulates in continental

regions such as the alpine ibex (*Capra ibex*), which select for steep rocky environments in the presence of high snow cover (Grignolio et al. 2004).

DeVoe et al. (2015) suggested that DET be replaced by SLP and SLPv, accurately arguing that measures of DET “constrain selection to an arbitrary threshold value and assume equal selection of slopes greater than that threshold.” Nonetheless, their approach to evaluate the paired combination of SLP and SLPv with DET assumed that all measures of DET were highly correlated with SLP, and therefore were not appropriate for inclusion in the same model (e.g., Gross et al. 2002). While we recognize the limitations of DET in the absence of SLP and SLPv, our results suggest that non-collinear measures of DET can be paired with SLP and SLPv to produce a more informative and predictive model. Our results also support the notion that limiting the interpretation of DET to a predator avoidance strategy misses the larger ecological story. Mountain goats have evolved to occupy an ecological niche largely associated with steep and rugged terrain where they have access to a unique suite of environmental resources necessary for survival and reproduction. While steep terrain can certainly provide a refuge from predators, our work broadens the interpretation of escape terrain to include other fundamental components of the mountain goat niche, for example, strongly associating with steep cliffs in winter as a snow avoidance strategy. We encourage future efforts to more broadly interpret the importance of escape terrain beyond simply predator avoidance in order to more realistically describe the mountain goats’ ecological niche.

The striking differences in AIC_c ranking between multiple spatial grains of the same covariate (univariate tier one models), as well as the post-hoc comparison of our top models with the minimum resolution models, provide additional support for the multi-grain RSF (MRSF; Laforge et al. 2015b) and demonstrate that mountain goat resource selection can be grain dependent. Heterogeneity and fragmentation are important determinants when relating animal resource selection to scalar processes such as a MRSF (Boyce et al. 2003, Laforge et al. 2015b), which is therefore dependent on the conditions within the study area. While our top seasonal models were greatly improved by evaluating

multiple spatial grains, there is likely a tradeoff in broad utility as models incorporate additional study area-dependent covariates, which may result in a predictive cost when extrapolated to new areas. While there was some corroboration with DeVoe et al. (2015), for example, the importance of SLP at 500 m, comparisons between studies in the southern and northern extremes of the GYA should be conducted with caution. DeVoe et al. (2015) suggested a hierarchical structuring to mountain goat habitat selection whereby animals first select for terrain covariates at broad grains and secondarily select for vegetation covariates at smaller spatial grains. In contrast to DeVoe et al. (2015), our results did not depict a clear distinction in the top-ranked grain sizes among the covariate suites. Our results for winter indicate a general reduction in the spatial grain and suggest mountain goats perceive landscape attributes at smaller spatial grains in winter than in summer. The smaller grain sizes in winter likely reflect the observed range contraction and reduced mobility. Additional studies over broad distributions will help to highlight conclusions regarding the importance of spatial grain in predicting animal resource selection. Nonetheless, the MRSF is an important methodological step in resource selection studies that can significantly improve model fit and biological interpretation (Hobbs 2003, Boyce 2006, Laforge et al. 2015a, b, Northrup et al. 2016), although we encourage additional work that explores the potential predictive cost when predicting disjunct regions.

Although the expansion of mountain goats throughout the GYA has been relatively slow, their distribution has been steadily increasing since the initial introduction (Lemke 2004, Flesch et al. 2016). As mountain goats continue to expand throughout the GYA, so too does the concern that competition and disease transfer could negatively impact native bighorn sheep on sympatric ranges (Gross 2001). Moreover, it has been hypothesized that sympatric populations on shared winter ranges are particularly vulnerable to competition due to the general restriction in suitable habitats and observed range contractions of both species (Poole and Heard 2003, DeVoe et al. 2015, Poole et al. 2016).

Within the Teton Range, our spatial predictions of suitable habitat were largely centered along the rugged and steep core of GTNP and

comprised 4.9% and 2.8% of the study area in summer and winter, respectively. These areas have also been the first to be colonized by emigrating mountain goats (S. Dewey, *unpublished data*), and are generally sparsely inhabited by native bighorn sheep, which largely occur in the northern and southern regions (Whitfield 1983, Courtemanch 2014; S. Dewey, *unpublished data*). While the seasonal ranges of mountain goats and bighorn sheep in GTNP are mostly non-overlapping at present (Courtemanch 2014; S. Dewey, *unpublished data*), it is unclear whether the observed spatial separation results from behavioral differences in resource selection influenced by intraguild competition, or because of the nascent stages of mountain goat colonization. If mountain goat numbers continue to increase within GTNP, it is reasonable to expect their distribution to expand into additional suitable areas throughout the Teton Range and increase their spatial overlap with native bighorn sheep. While sporadic sightings of single or small groups of mountain goats have been documented in GTNP since the late 1970s, 2008 marked the beginning of a steady population increase and year-round residence. Since 2008, mountain goat population estimates have increased to 20–40 individuals in 2014 and 40–60 individuals in 2015 (S. Dewey, *unpublished data*), prompting park managers to begin drafting a Mountain Goat Management Plan Environmental Assessment (<http://parkplanning.nps.gov/mountaingoat>). Within the Tetons specifically, DeVoe et al. (2015) suggested that mountain goat numbers could ultimately range from 248 to 411 individuals.

Our seasonal resource selection models indicate that the Gros Ventre Range has ample suitable habitat for mountain goats, although they are currently not present. Summer range in the Gros Ventre largely consists of the high-elevation steep slopes which generally trend from northwest to southeast, while winter range was restricted to the steepest slopes at mid-elevations as well as lower elevations in the western portion of the range. Given the nearly 40 yr it has taken mountain goats to expand to the contiguous Teton Range, it is unlikely that the potential colonization of the Gros Ventre will be a rapid event. Nonetheless, although the Gros Ventre Range is relatively isolated from current mountain goat populations in the Snake River and Teton

Ranges, dispersing individuals have been documented crossing large swaths of unsuitable habitat when colonizing new areas that exceed the geographic distance between the Gros Ventre Range and current mountain goat populations (Festa-Bianchet and Côté 2008). Moreover, as population densities continue to grow, it is likely that dispersal rates will increase (Williams 1999), thus further increasing the likelihood of colonization of unoccupied ranges. Bighorn sheep in the Gros Ventre Range remain allopatric and are currently estimated at 425 individuals that are widely distributed throughout the range (Wyoming Game and Fish Department 2015).

Interestingly, the Wyoming and Salt Ranges currently do not have resident mountain goat populations, yet are immediately south of the Snake River Range. The absence of mountain goats in the Wyoming and Salt Ranges is surprising given the close proximity to a robust source population, and is possibly explained by the joint barrier posed by Hwy 89 and the Snake River, and/or the largely disconnected seasonal ranges (Fig. 3). While our models indicate 173 km² of suitable summer habitat, winter habitat is noticeably sparse and relatively distant from summer ranges. Both the amount and lack of continuity between suitable summer and winter habitats may limit the southern expansion into the Wyoming and Salt Ranges, especially considering the relatively short seasonal migrations we observed (Appendix S3). Currently, the Wyoming and Salt Ranges are mostly void of bighorn sheep.

Using similar methods to define a “suitable” habitat cutoff, our summer model produced smaller estimates of the amount of suitable habitat in each region when compared to DeVoe et al. (2015). For example, DeVoe et al. (2015) estimated 495 km² of suitable summer habitat in the Teton Range compared to an estimate of 70 km² in this study. In addition, DeVoe et al. (2015) estimated 350 km² of suitable summer habitat in the Gros Ventre Range compared to our estimate of 95 km². It is likely that the variation in results stems from the interaction between regional differences between the two study areas and methodological differences in the modeling techniques. While we recognize the important contributions of DeVoe et al. (2015) in generating the first predictions of mountain goat habitat throughout the entire GYA, this study provides revised estimates for the

southwest GYA from a local study area. We encourage additional local studies as data become available and the continued refinement and strengthening of mountain goat resource selection models and projected densities within the GYA.

While there are a number of theoretical and speculative hypothesis regarding the ecological relationships of sympatric mountain goats and bighorn sheep (Adams et al. 1982), there have been few empirical studies (although see Laundré 1994 and Varley 1994), and no study using GPS-collared animals. Our seasonal resource selection models indicate that as mountain goats continue to expand, so too will their spatial overlap with native bighorn sheep. In the face of continued range expansion, there is a pressing need to empirically examine the spatial and temporal overlap and develop comparative studies to further our understanding of resource selection dynamics and the potential for introduced mountain goats to alter bighorn sheep behavioral processes. Moreover, additional studies examining fine-scale temporal overlap are needed to understand the potential of mountain goats to serve as an additional vector of deleterious respiratory pathogens. The GYA presents a unique opportunity to examine the ecological relationships of sympatric and allopatric mountain ungulates, and we encourage additional studies within the region.

Throughout the GYA, there are a diverse array of land and wildlife management agencies with varying objectives and mandates. The National Park Service, for example, is mandated to manage for native species and has taken steps to largely remove introduced mountain goats in other regions such as Olympic National Park (Houston et al. 1994). In contrast, mountain goats have expanded their range in Yellowstone National Park without substantial documented impacts to native vegetation communities (Aho 2012). Grand Teton National Park is currently developing a mountain goat management plan which will evaluate and rank multiple management options (S. Dewey, *personal communication*). As mountain goats continue to expand, federal and state agencies will be faced with additional decisions regarding the expansion of this introduced species. Our work has provided novel results regarding the seasonal resource selection of introduced mountain goats and developed applicable tools to help predict and anticipate the

continued range expansion of introduced populations throughout the region.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1769/full>