

OCCUPANCY MODELING OF NON-NATIVE MOUNTAIN GOATS
IN THE GREATER YELLOWSTONE AREA

by

Jesse Daniel DeVoe

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ABSTRACT

Non-native species can have adverse impacts on native species; however, coexistence may be possible if their ecological niches minimally overlap. Fine spatial scale information is needed to understand these niches but can be challenging to obtain for rare, imperfectly detected species inhabiting difficult to survey landscapes. Non-native mountain goats (*Oreamnos americanus*) in the greater Yellowstone area (GYA) are such a species and have substantial potential to expand in distribution and occupy similar habitats to native Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*). To understand the niche and potential for expansion of mountain goats in the GYA, this study used a unique, fine spatial scale method to collect detection-nondetection data from two study areas with established mountain goat populations over three summer seasons (2011-2013). Relationships between scale-specific habitat covariates and mountain goat selection were evaluated using a single-species, single-season occupancy analysis to model occupancy and detection probabilities based on 505 mountain goat detections from 53,098 surveyed sampling units. Habitat selection was most strongly associated with terrain covariates, including mean slope and slope variance, at a spatial scale of 500 x 500 m, and canopy cover, heat load, and normalized difference vegetation index at a spatial scale of 100 x 100 m. These results provide new insight into multi-scale patterns of mountain goat habitat selection, as well as evidence that mean slope and slope variance are superior terrain covariates to distance to escape terrain that has dominated published mountain goat habitat models. The model predicted 10,745 km² of suitable habitat within the GYA, of which 57% is currently un-colonized. Throughout the GYA, suitable habitat appears to generally overlap extensively with areas occupied by bighorn sheep. I also estimated the GYA may have the potential to support 5,372-8,918 mountain goats when all predicted habitat is occupied, or approximately 2.5-4.2 times the most recent abundance estimate of 2,104.

INTRODUCTION

Introductions and expanding distributions of non-native species are globally common and considered to be a significant component of human-caused global environmental change (Vitousek et al. 1997). Non-native species sharing similar habitats with native species can lead to competitive exclusion if they use limited resources in the same way (Mooney and Cleland 2001, Morin 2011). However, coexistence may be possible if species can partition resources in a way that limits competition (Hutchinson 1959, MacArthur and Wilson 1967, Schoener 1974). Understanding this resource, or niche, partitioning and predicting the range expansion of non-native species is important for the development of appropriate conservation and management actions (Lodge et al. 2006, Gormley et al. 2011). However, this can be challenging when species are rare on the landscape and inhabit heterogeneous, difficult-to-survey terrain. Traditional aerial survey methods are typically applicable only at a broad spatial scale and can lead to biased interpretations of habitat selection patterns due to imperfect detection (Gu and Swihart 2004, MacKenzie 2005). The more recent development of occupancy methods has provided the ability to incorporate estimates of detection into evaluations of habitat selection for rare species (MacKenzie et al. 2005, 2006), and may also provide a means to understand selection at a fine spatial scale while effectively surveying large, heterogeneous landscapes.

The introduction and ongoing range expansion of non-native mountain goats (*Oreamnos americanus*) in the greater Yellowstone area (GYA), a 56,000 km² mountainous region representing the largest intact temperate ecosystem in the world

(Keiter and Boyce 1991), is among the leading conservation and management concerns of state and federal agencies (Schullery and Whittlesey 2001, Lemke 2004). Although agencies' specific management goals vary, the primary concern of regional biologists is the potential for non-native mountain goats to negatively impact native Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) through resource competition, behavioral displacement, and/or disease transmission (Pallister 1974, Stewart 1975, Dailey et al. 1984, Varley 1994). In western North America, bighorn sheep populations suffered catastrophic declines due to market hunting, disease die-offs, and habitat loss and degradation during European colonization (Buechner 1960, Montana Fish, Wildlife & Parks 2010). Restoration and conservation efforts over the past 80 years have been modestly successful with the GYA representing one of the largest bighorn ranges in North America, supporting 5,000 to 9,000 bighorn sheep (Garrott et al. 2012). Current conservation concerns are focused on increasing or maintaining viable bighorn sheep populations in the face of global climate change, continued habitat loss, and disease.

Although mountain goats and bighorn sheep inhabit similar steep and heterogeneous mountain terrain, their ecological niches are expected to be somewhat divergent and minimally overlapping given their shared evolutionary history and coexistence in regions where both species are native (Adams et al. 1982, Varley 1996). However, information on the fine spatial scale patterns of habitat selection is lacking due to the remote and rugged sites often occupied by these species, as well as their general rarity and imperfect detectability on the landscape. In addition, agencies in the GYA are in need of information about the extent of mountain goat range expansion to guide

management and conservation decision-making. Therefore, I used a novel field-sampling technique based on occupancy methods to assess habitat selection of mountain goats during the summer season when there may be increased use of shared forage resources. I fit suites of competing models to uncover the relative strength of association between habitat covariates and mountain goat occupancy, and extrapolated the habitat selection results based on the most supported model at the landscape level of the GYA to predict suitable summer habitat for mountain goats. Based on this prediction and recent abundance estimates of mountain goats in the colonized areas of the GYA, I estimated the abundance of mountain goats that may eventually be supported if all predicted habitat in the GYA becomes occupied.

As part of this evaluation, I sought to address two hypotheses. First, I expected that mountain goats select different habitat components at different spatial scales, as has been recognized for many species in investigations and discussions of scale-sensitive habitat selection (Johnson 1980, Wiens 1989, Hobbs 2003, Mayor et al. 2009). For example, mountain goats may select for topographic features, such as steep slopes, at a larger spatial scale than for foraging sites. However, spatially explicit habitat studies for mountain goats have not been attempted. In addition, knowledge of the spatial scale at which habitat selection occurs can improve management actions that may be effective only at certain spatial scales. Therefore, I used model selection techniques to evaluate a range of possible spatial scales for each habitat covariate, within Johnson's (1980) third-order selection, to obtain a scale-specific habitat selection model (Hobbs 2003).

Secondly, I sought to compare the performance of a predominant and well-supported habitat covariate, distance to escape terrain (DET), with new covariates capturing mean slope (SLP) and variance in slope (SLPv). DET, measuring proximity to the nearest area of a specified slope threshold (e.g., slopes $\geq 40^\circ$), has been used to capture the close association of mountain goats with steep and rough terrain, often termed “escape terrain” in reference to sites used for predator avoidance (e.g., Gross et al. 2002, Poole and Heard 2003, Shafer et al. 2012). However, the choice of a threshold value has not only been variable (ranging from 25 to 50°) and generally arbitrary, but also assumes mountain goat selection for slopes greater than that value is constant (e.g., for $\geq 25^\circ$, everything from 25 to 90° is of equal quality), even though studies have indicated greater use of intermediate slopes (Gross et al. 2002, Poole and Heard 2003). DET also assumes that selection for steep slopes is the same regardless of the variability in slope. I therefore hypothesized that SLP and SLPv would outperform DET, providing a more flexible and biologically meaningful alternative.

METHODS

Study Areas

In order to make inferences regarding potential mountain goat habitat selection at a landscape level, two study areas (Figure 1) were selected that captured a range of variation in mountainous regions of the GYA and had well-established mountain goat populations. The Gallatin Crest (GC) study area (425 km²) was located in the southern Gallatin Range of Montana and Wyoming between the Yellowstone and Gallatin Rivers, lying partially within the Gallatin National Forest and extending south into Yellowstone National Park (YNP). The North Absaroka (NA) study area (925 km²) was located in the Absaroka Range of Montana and Wyoming, lying in the northeast corner of YNP and partially in the Gallatin and Shoshone National Forests. Elevations ranged from 1,800 to 3,300 m in the GC and from 2,000 to 3,475 m in NA. Average annual precipitation was 118.8 cm in the GC (Shower Falls SNOTEL at 2,469 meters, 1981-2010 data) and 131.1 cm in the NA (Fisher Creek SNOTEL at 2,774 meters, 1981-2010 data; <http://www.wcc.nrcs.usda.gov/snow>).

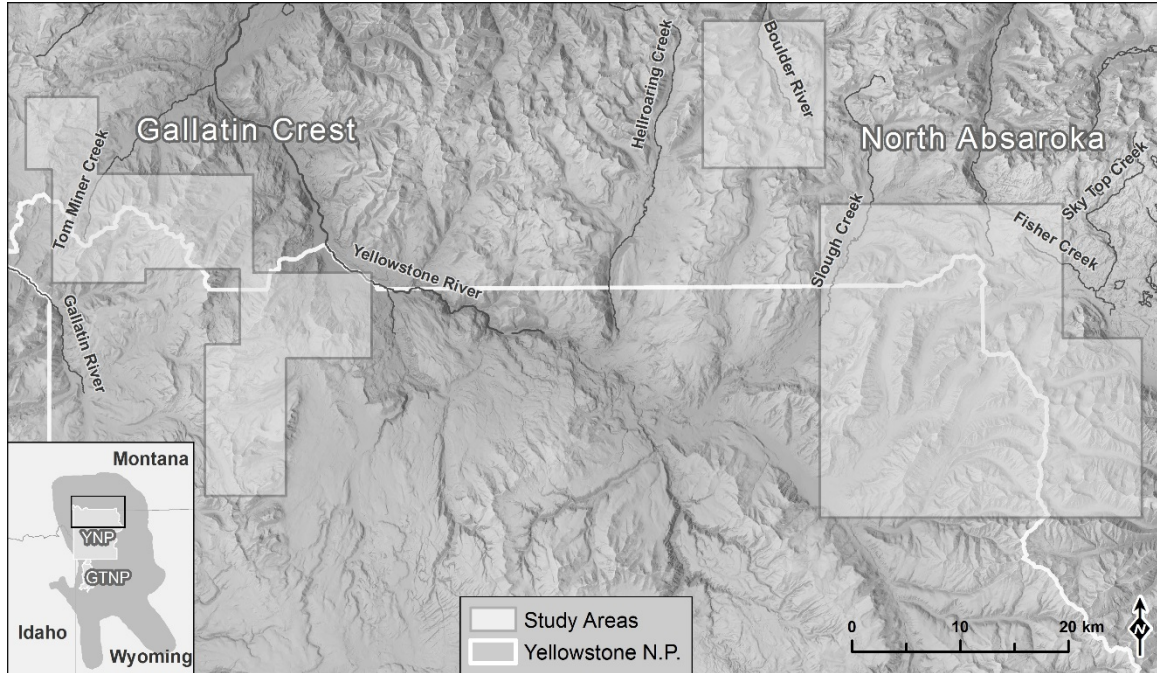


Figure 1. The Gallatin Crest and North Absaroka study areas in the northern portion of Yellowstone National Park.

Geology of both areas was dominated by Eocene volcanic parent material in the upper elevation, with intrusions and Quaternary alluvium deposits interspersed, primarily at lower elevations. Sedimentary rock also occurred in the extreme southern region of the GC (Smedes and Prostka 1972). Vegetation in both study areas was dominated by dry-mesic spruce-fir forests (including Engelmann spruce, *Picea engelmannii*, and subalpine fir, *Abies lasiocarpa*) with Douglas-fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*) forests at lower elevations. Subalpine fir and whitebark pine (*Picea albicaulis*) occurred in the subalpine (~2,400-2,900 m) giving way to turf and meadow graminoid and forb species in the alpine zone (~2,800-3,400 m).

At the time of this study, mountain goats had been present in both the GC and NA for approximately 50 years, sharing sympatric range with bighorn sheep (Varley 1996,

Lemke 2004). No mountain goat transplant history exists for these areas, suggesting the areas were colonized by dispersing individuals from releases in the 1940-50's in the Madison and Absaroka Ranges adjacent to the GC and the Beartooth Range to the northeast of the NA (Laundré 1990, McCarthy 1996, Lemke 2004).

Sampling Design

General mountain goat distribution data collected by management agencies during several decades of population surveys were used to delineate approximate areas within each study area for conducting occupancy surveys. Valleys and low- to mid-elevation, densely-forested slopes were excluded while all alpine and subalpine habitats and portions of forested slopes adjacent to subalpine zones were considered for sampling. All regions of each study area identified for sampling were overlaid with a 100 x 100 m grid in a Geographic Information System (GIS) to delineate contiguous occupancy sampling units (see Appendix A for grid development). Logistics and safety precluded randomized selection of sampling units. Instead, I used a systematic approach based on travel routes and groups of sampling units (viewsheds) that were visible from fixed vantage points (viewshed survey point). The travel routes (primarily along trails, drainage bottoms, and ridgelines) providing access to viewsheds were designed to accommodate 3-5 day backpacking trips and cover all accessible regions of the study areas during the summer season (June to October). The first viewshed survey point along each travel route was randomly selected within 3 km from the start, with subsequent viewshed survey points placed systematically every 3 km along the remaining travel route. A 500 m buffer around each viewshed survey point allowed observers to select a location that maximized

visibility of viewsheds that were obstructed by immediate structures such as trees or rock outcrops.

Because vast areas can be visible from viewshed survey points, observers constrained the viewshed to areas that could be surveyed in a reasonable amount of time (typically less than 2 hours) and generally within 3 km of the observers, where optical performance was reliable (e.g., to avoid distortion from heat shimmer) and detection appeared practical. Observers surveyed sampling units within the viewshed with the aid of 10X binoculars and 20-60X spotting scopes to determine if each sampling unit was occupied by a mountain goat group (at least one mountain goat). At most viewshed survey points (~86%), two observers surveyed the same viewshed independently and simultaneously. Observers situated themselves such that neither was influenced by the behavior and activities of the other, typically by placing a barrier (i.e., rock outcrop, ridge, tree, or backpack) between each other, ceasing communication, and maintaining a distance of at least 5 m to limit visual cues of detections. These concurrent surveys were used to construct the detection history (presence=1, absence=0) for each sampling unit to account for imperfect detection of mountain goat groups.

Field computer tablets displaying the grid of sampling units layered over an aerial photograph of the area to be sampled and a custom program written in ArcPad 10.2 (ESRI 2013a) allowed observers to record occupied and unoccupied sampling units using the tablet's touch screen. Any sampling unit surveyed where a group was observed within its boundaries during the period of observation was recorded as occupied and all other cells surveyed were recorded as unoccupied. Group size, initial behavior of the majority

of individuals (e.g., feeding, resting, traveling, or other), and sex and age class of individuals were recorded (Chadwick 1983, Côté and Festa-Bianchet 2003). Observers additionally recorded date, survey point ID and location, and survey start and end times. Surveys were conducted the summers of 2011- 2013 during the full range of daylight hours between the third week of June and the second week of October each season. Sampling units were often revisited during multiple backpacking trips, however, these were treated as separate sampling units for analysis. For a detailed description of the methods for data management and processing after field work, see O'Reilly (2012).

Model Development

I used single-species, single-season occupancy modeling (MacKenzie et al. 2002) in package “unmarked” of program R version 3.1.0 (Fiske and Chandler 2011, R Development Core Team 2013) to estimate occupancy (ψ) and detection (p) probabilities of sampling units by mountain goat groups. ψ was defined as the probability of a group being in a sampling unit at the time of the survey, and p was defined as the probability of detecting a group given that it was present at the time of the survey. Sixteen habitat attributes were selected based on review of published mountain goat studies and hypotheses of habitat relationships, and included in models as site covariates on ψ (see Appendix A for covariate development). To address specific hypotheses as well as to simplify otherwise large and complex model lists, I arranged covariates into four model selection suites: sloped terrain, ruggedness, forage, and heat load (Table 1; see respective descriptions in *Model Suites*). A range of possible scale-specific habitat selection was captured by considering each covariate at five spatial scales: 100 x 100 m (that of the

sampling units), 300 x 300 m, 500 x 500 m, 700 x 700 m, and 900 x 900 m. These spatial scales are referenced as 100 to 900 m (e.g., “500 m” for 500 x 500 m) and indicated by subscript (e.g., SLP₅₀₀). Additionally, linear, pseudothreshold (natural log transform; after Franklin et al. 2000), and quadratic forms were considered for each covariate in order to allow flexibility in the hypothesized relationships that may better describe the data. Each functional form was evaluated at each of the five spatial scales. No interactions were modeled due to the limited amount of detections in the dataset, and a model that held ψ constant was also included in each suite for model comparison purposes. Pairs of covariates with Pearson correlation coefficients of $|r| > 0.60$ (Appendix B) were not considered together in the same model to avoid collinearity problems and reduce the number of possible models. To aid in model convergence and covariate comparisons, all covariates considered for linear and quadratic functional forms were mean-centered and divided by their standard deviation. If necessary, covariates considered for the pseudothreshold form were adjusted slightly by addition of 0.005 to avoid values less than or equal to zero, allowing log transformation.

Table 1. Covariates considered for modeling occupancy (ψ) probability arranged in model suites to evaluate mountain goat habitat selection. Five spatial scales (100, 300, 500, 700, & 900 m) were developed for each covariate (excluding DET covariates).

Abbv.	Description	Reference
<i>Sloped Terrain</i>		
SLP	slope (degrees)	
SLPv	slope variance (stdev ² of slope)	
DET25	distance (m) to $\geq 25^\circ$ slopes	Varley (1996)
DET33	distance (m) to $\geq 33^\circ$ slopes	Gross et al. (2002)
DET40	distance (m) to $\geq 40^\circ$ slopes	Poole et al. (2009), Shafer et al. (2012)
DET45	distance (m) to $\geq 45^\circ$ slopes	Poole and Heard (2003)
DET50	distance (m) to $\geq 50^\circ$ slopes	Fox et al. (1989), Smith (1994), Taylor et al. (2004)
<i>Ruggedness</i>		
RUG	ruggedness index	Poole et al. (2009)
VRM	vector ruggedness measure	Taylor et al. (2004), Sappington et al. (2007), Beus (2010)
RCK	rock land cover reclassification (proportion)	Taylor and Brunt (2007)
<i>Forage</i>		
COV	forest canopy cover (percent)	
NDVI	normalized difference vegetation index (July 2000 Landsat derivative)	
TCAP	tasseled cap wetness index (July 2000 Landsat derivative)	
MDW	meadow land cover reclassification (proportion)	
<i>Heat Load</i>		
SRI	solar radiation index (hillshade)	Ciarniello et al. (2005)
GRAD	global radiation (watt/m ²)	Fu and Rich (1999)

Although primary interest was in covariate relationships with ψ , I also modelled variation in p by including a pseudothreshold form of canopy cover measured at the scale of the sampling unit (100 m) for all models in each suite (Poole 2007, Rice et al. 2009). This form hypothesizes that increasing canopy cover decreases detection probability but at a declining rate (near-asymptotic). Post hoc, after arriving at a final inferential model for ψ , I evaluated other covariates on p including linear forms of canopy cover, as well as slope variance, ruggedness index, and vector ruggedness measure (see *Model Suites* for

covariate descriptions) to capture complex landscapes that may make detecting mountain goats difficult (Poole 2007, Rice et al. 2009). These covariates were measured at the 100 m scale and considered singly and in additive combinations of canopy cover and terrain covariates in the models. A model that held p constant was also included in the evaluation.

To avoid model convergence issues caused by low sample size, I retained detections that were made subsequent to the initial detection as groups traveled across sampling units. For models that did not initially converge or had indications of poor convergence (condition numbers $> 10^5$), several methods were attempted: 1) the number of iterations were increased (from 1,000 to 5,000 to 10,000), 2) different optimization methods (including Nelder Mead, conjugate gradient, BFGS, and L-BFGS-B) were attempted, and 3) starting values from the optimization that had the lowest negative log likelihood estimate and no apparent problems with coefficient and standard error estimates were fed into subsequent optimizations (Fiske and Chandler 2011). Convergence was indicated by no apparent problems with coefficient and standard error estimates, no improvement to the negative log likelihood with further modifications, and condition numbers $< 10^5$.

Because I suspected lack of independence of observations due to multiple detections of the same group, MacKenzie and Bailey's (2004) parametric bootstrapping technique for occupancy data was used to estimate an overdispersion parameter ($\hat{c}$). Due to the difficulty of determining a complex model from the numerous varieties and forms of covariates for estimating $\hat{c}$, a reasonable model was obtained by: 1) ranking candidate

models within each suite using Akaike's Information Criterion (AIC) and model weights, 2) including the resulting models <5 AIC units of the most-supported models in a combined model suite in all possible additive combinations (see *Combined* model suite), and 3) selecting the resulting top-ranked model. Based on the $\hat{c}$ from this model, I used quasi-likelihood (QAIC) theory to allow overdispersion in the model selection procedure and inflate the estimates of sampling variance of the parameters (White et al. 2002, MacKenzie and Bailey 2004). Within each suite and among suites, candidate models were again ranked, and models <5 QAIC units of the top models were compared in a combined model suite to identify well-supported models. From this final suite, noncompetitive models that were similar to well-supported models but containing uninformative parameters were discarded (Burnham and Anderson 2002, Arnold 2010).

Model Suites

Sloped Terrain. This suite was developed to directly test the prediction that SLP and SLPv would outperform DET covariates. I created five versions of DET based on the literature (Table 1) and compared them against SLP and SLPv. I included models with SLP alone, but never with SLPv alone because it did not make biological sense unless in combination with SLP. Models with both SLP and SLPv were considered at the same spatial scale while functional forms were allowed to vary. This suite included 66 models.

Ruggedness. This suite was developed to evaluate other terrain features based on previous mountain ungulate studies. I selected two ruggedness indices, including terrain ruggedness (RUG; Poole et al. 2009), measuring the variability in the rate of change in

slope, and vector ruggedness measure (VRM; Taylor et al. 2004, Sappington et al. 2007, Beus 2010), measuring the variation in the three-dimensional orientation of a neighborhood of elevation raster pixels. Mountain goats have also been found to be in close proximity (within ~400 m) to rock outcrops and substrates typically associated with steeper, broken terrain (Foster 1982, Haynes 1992, Taylor and Brunt 2007), therefore, a rock (RCK) covariate, measuring the proportion of land cover data reclassified to rock, was evaluated in addition to RUG and VRM. Because RUG and VRM were considered different constructs of similar landscape features, they were not evaluated additively in the same model. Additive combinations of RUG with RCK and VRM with RCK were constrained to the same functional form and spatial scale within each model to maintain a model suite of manageable size. This suite included 76 models.

Forage. Mountain goats depend on summer forage to replenish fat reserves lost during the winter period, support milk production and gestation in females, accumulate muscle mass for the rut in males, and enhance survival of offspring (Pettorelli et al. 2006, 2007, Festa-Bianchet and Côté 2008), however, the majority of published mountain goat habitat models lack evaluation of covariates describing forage. This suite was therefore developed to evaluate four potential forage covariates. Because meadows may provide forage opportunities, I created a proportion meadow (MDW) covariate from land cover reclassification of meadow, grassland, shrubland, and alpine turf. From Landsat Thematic Mapper satellite imagery taken from July 2000 scenes, I derived a normalized difference vegetation index (NDVI) covariate, a measurement that correlates strongly with aboveground net primary productivity (Kerr and Ostrovsky 2003, Pettorelli et al. 2005)

and has been used to assess impacts to juvenile survival and condition (Pettorelli et al. 2006, 2007), reproductive success (Pettorelli et al. 2006), and seasonal migration patterns (Sawyer and Kauffman 2011, Bischof et al. 2012, Lendrum et al. 2014) in ungulates. From the Landsat imagery, I also derived the tasseled cap wetness (TCAP) covariate, which correlates with vegetation biomass and soil moisture (Todd et al. 1998). Tasseled cap wetness has been evaluated in a limited number of habitat studies of other species (Carroll et al. 2001, Alexander et al. 2005), but has not been applied to mountain goats. For both NDVI and TCAP covariates, the effect of forested areas with greater than 15% canopy cover was masked out in order to capture potential foraging areas. Lastly, canopy cover has only been evaluated in studies in coastal regions during winter, with hypothesized relevance for access to understory forage and as thermal refuge from the cold (Poole and Heard 2003, Taylor et al. 2004, Turney and Roberts 2004, Taylor and Brunt 2007, Poole et al. 2009). Similarly, for interior mountainous regions during the summer, sites may be selected based on canopy cover to access forage species in the understory or in open canopy (Festa-Bianchet and Côté 2008). Therefore, the percent canopy cover (COV) covariate was developed and included as a forage covariate. Canopy cover may also limit the ability to detect predators (Festa-Bianchet and Côté 2008) or provide thermal refuge from the summer heat (see *Heat Load*; Myrsetrud and Østbye 1999).

The forage suite included all functional forms and spatial scales of COV, MDW, TCAP, and NDVI. Additive combinations of forage variables were also considered where possible (no collinearity) and biologically reasonable: COV with TCAP, COV with

NDVI, MDW with TCAP, and MDW with NDVI. These were constrained to the same functional form and spatial scale within each model to maintain a suite of manageable size. TCAP and NDVI were considered as different constructs of similar forage ideas, so were not considered in the same models. This suite included 121 models.

Heat Load. Altered behavior for regulating body temperatures has been demonstrated in daily movement patterns of Alpine ibex (Aublet et al. 2009). Similarly, mountain goats may be sensitive to temperature during the summer, preferring sites with lower heat loads (e.g., sites with persistent snowbanks or deep shade). Several studies have shown preference for certain aspects, albeit mostly during winter (Foster 1982, Varley 1996, Gross et al. 2002, Poole and Heard 2003, Taylor et al. 2004, Poole et al. 2009); however, aspect measurements are difficult to interpret in relation to thermal tolerances given the effects of topographic shading and latitude. Heat load indices calculated from elevation raster data provide a more interpretable alternative that has not been evaluated in summer habitat models. This suite was developed to evaluate two heat load covariates that take into account topographic shading effects, the solar radiation index (SRI; after Ciarniello et al. 2005) and global radiation (GRAD; Fu and Rich 1999). The calculation of GRAD also takes into account effects of latitude. These two covariates were considered different constructs of similar heat load ideas, so were not considered in the same models. This suite included 31 models.

Combined. All additive combinations of the resulting models <5 (Q)AIC units of the most-supported model and the uncombined top model from each suite were evaluated in this suite. For models combining the SLP with the RUG/RCK suite top models, only

SLP or RUG was included due to collinearity between these variables. This suite included 90 and 448 models in AIC and QAIC selection procedures, respectively.

Model Validation

From the top model in the combined suite, I used the estimated coefficients for the covariates and their respective scale-specific rasters within a GIS (see Appendix C for development methods) to map a continuous surface of predicted occupancy probabilities for the northern GYA where established populations of mountain goats and independent location data (hereafter referred to as management data) from past aerial surveys performed by management agencies exist (*unpublished data*). This assigned each raster cell an occupancy probability between 0.0 and 0.419. To validate the model, I then selected the probability value of ≥ 0.004 to represent suitable habitat based on visual examination of the predicted probabilities for the proportion of occupied to available sampling units (Appendix D, Figure D1-a). This method was used because the distribution of probabilities for both the occupied and available sampling units were highly skewed right (Appendix D, Figure D1-b & c), indicating that a small proportion of the landscape consisted of suitable habitat. I constrained the management data to the third week of June to the second week of October from 1968-2012 and to those recorded on 1:50,000 or finer scale maps, and overlaid them on the occupancy probability raster to extract values for each location. Because errors in the spatial precision of the management data are inherent due to aerial survey methodology, I calculated the distance from each management data point to the nearest cell containing suitable habitat (i.e., ≥ 0.004). I then calculated the percentage of management data that fell within 200 m,

within 100 m, and within suitable habitat, as defined by my top model and occupancy probability threshold, to indicate the prediction success of the model given the likelihood of a relatively small amount of spatial error in the management data.

GYA Habitat Suitability and Abundance Predictions

Using the same method for developing a prediction raster for the northern GYA (Appendix C), suitable habitat ($\hat{\psi} \geq 0.004$) for the entire GYA was derived, and the total area (km²) of suitable habitat was calculated. To support regional management agencies, I also estimated total area of suitable habitat for regions within the GYA at various stages of colonization, including: the northern GYA, the southern Absaroka, Teton, Gros Ventre, Wyoming, and Wind River mountain ranges, and Yellowstone (YNP) and Grand Teton (GTNP) National Parks (Appendix E, Figure E1-A). I then obtained recent estimates of abundance for two delineated areas periodically surveyed by management agencies that have well-established populations of mountain goats occurring at different densities (Appendix E, Figure E1-B; *unpublished manuscript*). These survey areas included a northern (including portions of northern and north-eastern YNP) and south-western region of the GYA, where mountain goats have been present for about 50 and 40 years, respectively. The abundance estimates from each survey area were used to calculate densities of mountain goats per km² of predicted suitable habitat. The lower density estimate from the northern and the higher density estimate from the south-western survey area were used to project a best-guess low and high (respectively) abundance of mountain goats that could potentially be supported in the GYA given colonization of all suitable habitat. I also estimated mountain goat abundances for each region.

RESULTS

Survey Results

From summers 2011 to 2013 (spanning the third week of June and the second week of October each season), 551 total viewshed surveys documented detection and non-detection observations for 53,098 sampling units, of which 33,152 were surveyed by double-observers. The average number of sampling units surveyed from each viewshed survey point was 77 (ranging from 3 to 312), and the average viewshed survey duration was 53 minutes (ranging from 5 to 211 minutes). A mountain goat group was detected by at least one observer in 505 sampling units (0.92 observations per viewshed survey), of which 369 were recorded by one observer only (289 in double-observer and 80 in single-observer surveys) and 136 by both observers. Observations of the same group after initial detection were recorded in 195 sampling units. Group size averaged 3 individuals (ranging from 1 to 20 individuals), with 38.8% of groups observed resting, 38.6% feeding, 21.3% traveling, and 1.3% of other behaviors.

Model Suites

The model from AIC model selection used for estimating $\hat{c}$ included SLP_{500} , SLP_{500}^2 , SLP_{V500}^{PS} , RCK_{300} , RCK_{300}^2 , COV_{100} , $NDVI_{100}$, and $GRAD_{100}$ (Appendix F, Table F1), resulting in $\hat{c} = 3.46$ from 1,200 simulations. This $\hat{c}$ supported speculation of dependence in the data from multiple observations of the same group and was therefore used to adjust AIC scores and variances of model results for all within, among, and combined suite comparisons based on QAIC scores.

Sloped Terrain

The top four models supported similar relationships, each including both SLP and SLPv, and were strongly supported (cumulative model weight = 0.96; Table 2). The best-supported model included SLP_{500}^2 and $SLPv_{500}^{ps}$. The 2nd best model was identical to the top model but included SLP^2 and $SLPv^{ps}$ at the 300 m instead of 500 m scale. The 3rd and 4th best models were identical to the top model in scale but included quadratic and linear SLPv, respectively. Other models in the suite were not well supported by the data ($\Delta QAIC \geq 5.8$), and models with any DET covariate received little support. DET40 was ranked highest, at 10.3 $\Delta QAIC$. Models containing covariates measured at scales other than 300 or 500 m received little support, with the nearest ranked model (covariates measured at the 700 m scale) at 14.6 $\Delta QAIC$. The top model's coefficient estimates indicated that ψ increased: 1) to an optimum as slopes steepen (to $\sim 38^\circ$) and then decreased with further steepening ($\hat{\beta}_{SLP_{500}} = 1.93$, SE = 0.28; $\hat{\beta}_{SLP_{500}^2} = -0.60$, SE = 0.13), and 2) as slope variance increased in a pseudothreshold relationship ($\hat{\beta}_{SLPv_{500}^{ps}} = 0.74$, SE = 0.14).

Table 2. Quasi-likelihood (QAIC) model selection results for models examining relationships of habitat covariates and occupancy probabilities of sampling units for mountain goats in the greater Yellowstone area. The top models within 5 Δ QAIC of the top-ranked model for each suite are presented. Covariate subscripts indicate spatial scale and superscripts indicate functional form (2=quadratic, ps=pseudothreshold, [none]=linear). Detection probability for each model was parameterized using COV_{100}^{ps} . Model variables are defined in “Model Development.” K = no. of parameters. Quasi-likelihood for the top model from the across-suite comparison was -859.59.

Model	K	QAIC	within suite		across suites	
			Δ QAIC	wt _i	Δ QAIC	wt _i
<i>Sloped Terrain</i>						
SLP ₅₀₀ + SLP ₅₀₀ ² + SLP _{v500} ^{ps}	7	1733.18	0.00	0.47	0	0.47
SLP ₃₀₀ + SLP ₃₀₀ ² + SLP _{v300} ^{ps}	7	1734.52	1.34	0.24	1.34	0.24
SLP ₅₀₀ + SLP ₅₀₀ ² + SLP _{v500} + SLP _{v500} ²	8	1735.59	2.41	0.14	2.41	0.14
SLP ₅₀₀ + SLP ₅₀₀ ² + SLP _{v500}	7	1736.11	2.94	0.11	2.94	0.11
<i>Ruggedness</i>						
RCK ₃₀₀ ^{ps} + RUG ₃₀₀ ^{ps}	6	1785.74	0.00	0.60	52.56	0.00
RCK ₃₀₀ + RCK ₃₀₀ ² + RUG ₃₀₀ + RUG ₃₀₀ ²	8	1787.13	1.39	0.30	53.95	0.00
RCK ₅₀₀ + RCK ₅₀₀ ² + RUG ₅₀₀ + RUG ₅₀₀ ²	8	1790.45	4.70	0.06	57.27	0.00
<i>Forage</i>						
COV ₁₀₀ + NDVI ₁₀₀	6	1852.34	0.00	0.93	119.16	0.00
<i>Heat load</i>						
GRAD ₁₀₀	5	1836.47	0.00	0.38	103.29	0.00
GRAD ₁₀₀ ^{ps}	5	1838.12	1.66	0.17	104.95	0.00
GRAD ₁₀₀ + GRAD ₁₀₀ ²	6	1838.35	1.88	0.15	105.17	0.00
GRAD ₃₀₀	5	1838.85	2.38	0.12	105.67	0.00
GRAD ₃₀₀ ^{ps}	5	1839.94	3.47	0.07	106.76	0.00
GRAD ₃₀₀ + GRAD ₃₀₀ ²	6	1840.85	4.38	0.04	107.67	0.00
GRAD ₅₀₀	5	1841.42	4.95	0.03	108.24	0.00

Ruggedness

The top three models included both RCK and RUG, with the top model including both as pseudothresholds measured at the 300 m scale, and the 2nd and 3rd best model as quadratics measured at the 300 and 500 m scale, respectively. Other models in the suite were not well supported by the data (Δ QAIC $\geq$ 6.4). Models containing covariates measured at scales other than 300 or 500 m received little support, with the nearest

ranked model (with covariates measured at the 100 m scale) at 8.2 Δ QAIC. The best ranked model with VRM had a Δ QAIC of 20.0. The top model's estimates of coefficients indicated that ψ was positively related to RCK and RUG ($\hat{\beta}_{\text{RCK}_{300}^{\text{ps}}} = 0.21$, SE = 0.06; $\hat{\beta}_{\text{RUG}_{300}^{\text{ps}}} = 1.22$, SE = 0.20), which was in accordance with expectations.

Forage

Only the model including linear COV_{100} and NDVI_{100} was supported by the data. All other models in the suite were not well supported (Δ QAIC ≥ 5.6). The nearest ranked model containing covariates measured at scales other than 100 m was 9.3 QAIC worse than the top model. The nearest ranked models with TCAP and MDW were 24.9 and 25.4 Δ QAIC, respectively. The top model coefficient estimates indicated that ψ was negatively related to both COV and NDVI ($\hat{\beta}_{\text{COV}_{100}} = -0.75$, SE = 0.15; $\hat{\beta}_{\text{NDVI}_{100}} = -0.31$, SE = 0.08). This was expected for COV, but in contrast to the expected positive relationship for NDVI.

Heat Load

The seven top models included GRAD at various scales and functional forms. The top three models contained GRAD_{100} , with the top, 2nd, and 3rd ranked model in the linear, pseudothreshold, and quadratic form, respectively. The subsequent three supported models were identical but at the 300 m scale. The 7th best model included linear GRAD_{500} . Other models in the suite were not well supported (Δ QAIC ≥ 5.6), with all GRAD models outranking SRI models. The best ranked model with SRI was 17.9

ΔQAIC . The top model estimates indicated a negative relationship between ψ and GRAD_{100} ($\hat{\beta}_{\text{GRAD}_{100}} = -0.55$, $\text{SE} = 0.07$) which was in accordance with expectations.

Among Suite Comparison

The data provided clear support for models from the sloped terrain suite, with the four top models (cumulative model weight = 0.96) all being within 2.94 ΔQAIC . Top models from the ruggedness, heat load, and forage suites were ranked 58th, 118th, and 143rd, respectively, with none within 52 ΔQAIC .

Combined

After models with uninformative parameters were removed, four models within 5 QAIC units of the top model remained (Table 3). Model selection uncertainty between these remaining models was a result of covariates considered at different functional forms; hence, there was clear consistency across the models for the covariates and scales supported. There was consistent support for quadratic SLP and linear COV and NDVI, as well as for the 500 m scale for SLP and SLPv and the 100 m scale for COV, NDVI, and GRAD. The top model included pseudothreshold SLPv and linear GRAD. The 2nd and 3rd model differed only by a pseudothreshold GRAD and a linear SLPv, respectively. The remaining model differed by inclusion of both these forms. The top model was considered adequate for inference due to the general similarities, as well as the consistency in coefficient estimates (Appendix F, Table F2), among competitive models.

Table 3. Quasi-likelihood (QAIC) model selection results for combined models examining relationships of habitat covariates and occupancy probability of sampling units for mountain goats in the greater Yellowstone area (based on $\hat{c} = 3.46$). The top competitive models within 5 Δ QAIC of the top-ranked model are presented. Covariate subscripts indicate spatial scale and superscripts indicate functional form (2=quadratic, ps=pseudothreshold, [none]=linear). Detection probability was parameterized using COV^{ps}_{100} . Model variables defined in “Model Development.” ID number for comparison of model coefficient estimates in Appendix F, Table F2. K = no. of parameters. Quasi-likelihood for the top model was -848.634.

ID	Model	K	QAIC	Δ QAIC	wt _i
1	$SLP_{500} + SLP_{500}^2 + SLPv_{500}^{ps} + COV_{100} + NDVI_{100} + GRAD_{100}$	10	1717.27	0.00	0.11
2	$SLP_{500} + SLP_{500}^2 + SLPv_{500}^{ps} + COV_{100} + NDVI_{100} + GRAD_{100}^{ps}$	10	1717.58	0.31	0.09
3	$SLP_{500} + SLP_{500}^2 + SLPv_{500} + COV_{100} + NDVI_{100} + GRAD_{100}$	10	1718.93	1.66	0.05
4	$SLP_{500} + SLP_{500}^2 + SLPv_{500} + COV_{100} + NDVI_{100} + GRAD_{100}^{ps}$	10	1719.64	2.37	0.03

In the top model, coefficient estimates parameterizing ψ followed expected predictions (Appendix F, Table F2), indicating that ψ increased: 1) to a maximum at moderate levels of SLP, 2) as SLPv and NDVI increased, and 3) as COV and GRAD decreased (Figure 2). The coefficient estimate parameterizing p did not follow the expected prediction ($\hat{\beta}_{COV_{100}^{ps}} = 0.071$, 95% confidence interval = -0.12 to 0.263), indicating that p had no relationship with canopy cover. Estimates of p ranged from 0.43 to 0.52.

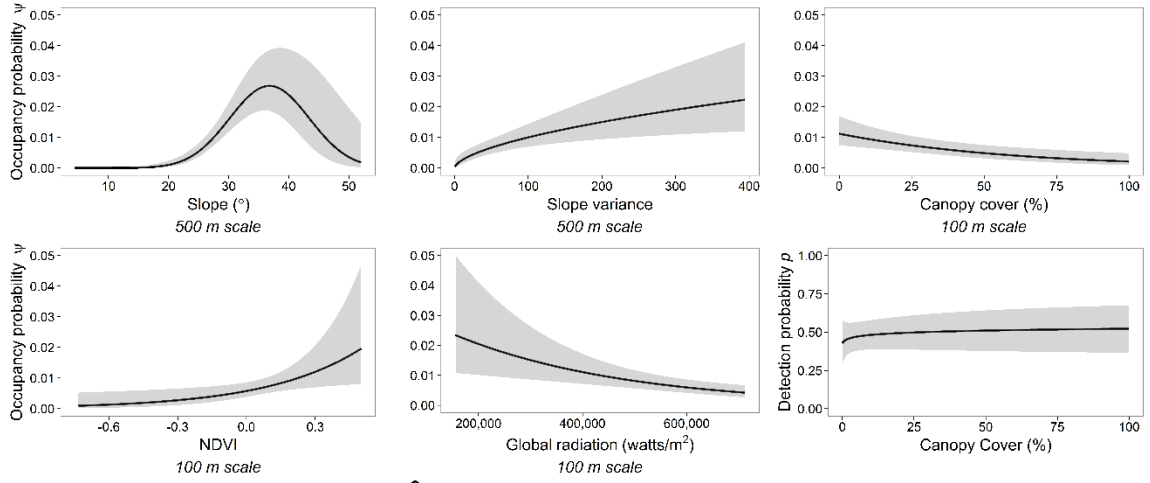


Figure 2. Predicted occupancy $\hat{\psi}$ and detection $\hat{p}$ probabilities of sampling units with 95% confidence intervals for each covariate in the inferential model for habitat selection of mountain goats in the greater Yellowstone (each respective plot holding all other covariates constant at their mean value).

The post hoc evaluation of additional covariates on p resulted in substantial model selection uncertainty, with all models within 3.5 QAIC units of the most supported, intercept-only model (Appendix F, Table F3). This model estimated p at 0.47 ($\hat{\beta}_0 = -0.10$, SE = 0.19).

Model Validation

Of 1,575 records in the management data, 93.1% (n=1,467) were within 200 m of areas identified as suitable habitat ($\hat{\psi} \geq 0.004$), 87.4% (n=1,377) were within 100 m of areas identified as suitable habitat, and 76.1% (n=1,199) were within areas identified as suitable habitat (e.g., Figure 3). These values indicated that the majority of location data were in close proximity to predicted suitable habitat.

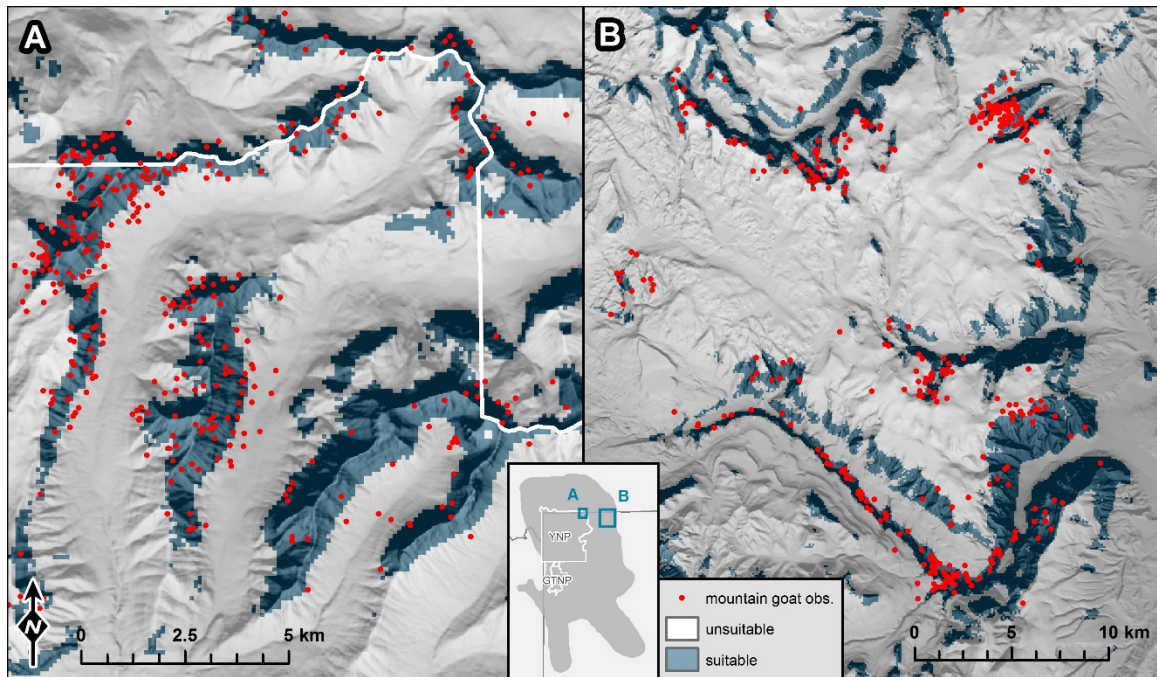


Figure 3. Predicted suitable summer habitat of mountain goats overlaid by validation data of mountain goat locations collected by management agency personnel for example areas in the northern GYA, including (A) a portion of the North Absaroka study area and (B) the Clark's Fork of the Yellowstone River. Note different map scales.

GYA Habitat Suitability and Abundance Predictions

The extent of the GYA in consideration (58,994 km²) was estimated to contain 10,745 km² of predicted suitable habitat (Table 4 & Figure 4). The northern GYA survey region had an estimated mountain goat density of 0.5/km² based on approximately 2,328 km² of suitable habitat and 1,154 estimated individuals. The southwestern GYA survey region had an estimated mountain goat density of 0.83/km² based on approximately 381 km² of suitable habitat and 316 estimated individuals. From these densities, I estimated the GYA may support 5,372-8,918 mountain goats given colonization of all predicted suitable habitat. See Table 4 for region-specific estimates.

Table 4. Colonization status, total area of delineated region, estimated area of predicted suitable habitat, and estimated abundance of mountain goats for various regions of the GYA (refer to Appendix E, Figure E1).

Region	Description	Status	Area (km ²)		Abundance	
			Total	Suitable	Min	Max
1	Northern GYA	colonized	18,507	4,236	2,118	3,517
2	South Absaroka Range	colonizing	10,558	2,789	1,395	2,315
3	Teton Range	colonizing	1,345	495	248	411
4	Gros Ventre Range	un-colonized	2,251	350	175	291
5	Wyoming Range	colonizing	7,344	1,608	804	1,335
6	Wind River Range	un-colonized	8,084	1,074	537	891
YNP	Yellowstone N.P.	colonized	8,865	495	247	411
GTNP	Grand Teton N.P.	colonizing	1,253	284	142	236
GYA	Entire GYA	-	58,994	10,745	5,372	8,918

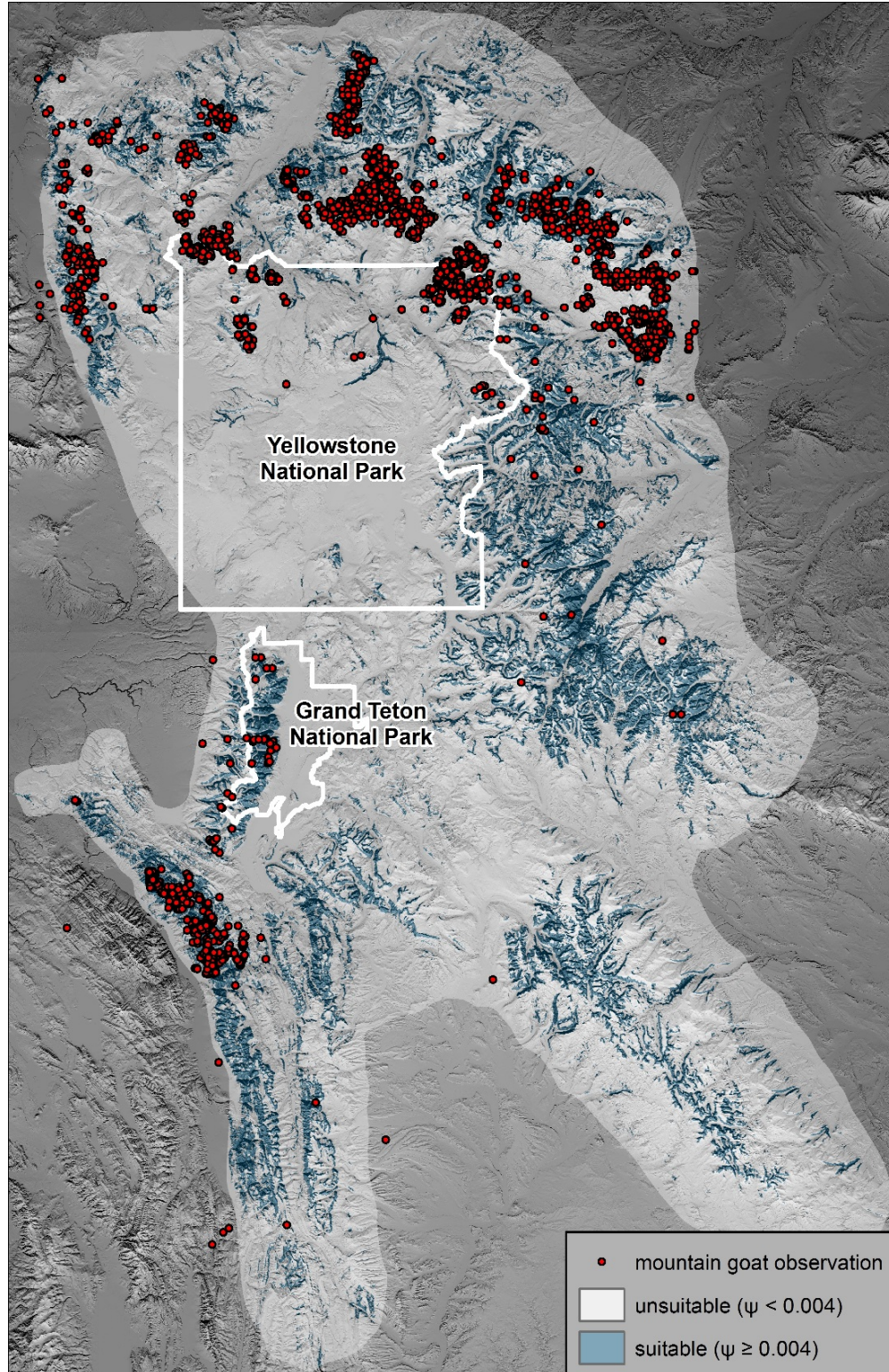


Figure 4. Predicted suitable summer habitat of mountain goats for the greater Yellowstone area overlaid by data collected from 1968-2012 by management agency personnel showing the general, current distribution of mountain goats.

DISCUSSION

Habitat Selection

This study used an occupancy design employing independent, double-observer surveys of a fine-scale grid for understanding spatial scale-specific habitat selection for mountain goats, a relatively rare species inhabiting a large, mountainous landscape. Through analysis of detection and non-detection observations collected from two mountain ranges across three summer seasons, I found evidence that mountain goat habitat selection occurred at two distinct spatial scales. The among suite model comparison and effect sizes indicated that mountain goats more strongly selected for mean slope and slope variance terrain attributes at a broader scale of 500 m than for characteristics of canopy cover, heat load, and forage availability, which are selected at a finer scale of 100 m or less. Some uncertainty exists for selection of canopy cover, heat load, and forage at scales finer than the 100 m spatial scale due to the size constraint of the sampling units; however, a clear distinction is evident between the spatial scales of the terrain covariates and the other covariates. The evidence for the importance of these two spatial scales likely indicates a hierarchal structuring of mountain goat habitat selection (i.e., mountain goats first select for slope attributes at a broader scale and then, within that slope habitat, secondarily select for finer scale habitat components); however, this study did not directly address hierarchical selection.

At the broader spatial scale, these results support mountain goat selection for intermediate (optimal 36.8°) and higher variability slopes. This highlights the advantage of using slope and slope variance over distance to escape terrain covariates that constrain

selection to an arbitrary threshold value and assume equal selection of slopes greater than that threshold. Contrary to this, my results indicate that not all steep slopes are alike; intermediate slopes and highly variable terrain are important components of terrain selected by mountain goats. The optimal slope value is similar to average slopes previously reported to be used by mountain goats, ranging from 33-41° (Foster 1982, Varley 1996, Poole and Heard 2003). Slope and slope variance covariates are strongly recommended in place of distance to escape terrain covariates for future modeling efforts and understanding of mountain goat habitat, and are likely applicable in habitat studies of other species associated with steep and variable terrain, such as bighorn sheep. Distance-based covariates should be carefully considered to determine if less constraining and more biologically meaningful covariates exist (Martin and Fahrig 2012).

At the finer scale, my results support mountain goat selection for lower canopy cover, lower heat load, and higher values of NDVI. Based on effect sizes, selection occurred strongest for canopy cover and weakest for NDVI. Reduced canopy cover may be related to increased availability and productivity of shade-intolerant graminoids and forbs that are desirable as forage for mountain goats (Pallister 1974, Varley 1996). Alternatively, mountain goats may be minimizing the amount of immediate forest structure to increase visibility for predator detection, as demonstrated for nursery groups in interior Alberta, Canada (Festa-Bianchet and Côté 2008). Mountain goats may also be attempting to thermoregulate by seeking cooler microclimates created by terrain features. Mountain goats were commonly observed in deeply shaded aspects or couloirs or near persistent snow patches as had been observed in other studies in the GYA (Varley 1996).

These responses to warmer summer temperatures during the day appear to be similar to those of Alpine ibex (*Capra ibex*; Aublet et al. 2009) and desert ungulates in temperate systems (Cain et al. 2006), but contrast with Shafer et al. (2012) who found that mountain goats in coastal southeastern Alaska selected for sites with higher heat loads during the summer. This inconsistency may be due to regional climate differences. In the more northern, cooler climates, sites with higher heat loads may support the most vegetatively productive habitats and have less persistent snow, while in the warmer and drier interior temperate regions, lower heat loads provide cooler microsites for avoiding exposure to high temperatures and reducing metabolic water loss. These sites are also likely to retain snowpack longer, providing foraging opportunities as the snow slowly recedes over the summer and new plant growth becomes available (Varley 1996). Higher NDVI values are likely capturing these and other fine scale sites containing more palatable vegetation irrigated by melting of persistent snowpack or by spring seeps.

Mountain goats are physiologically adapted to and tightly associated with steep and complex terrain. This adaptation has been primarily perceived as a strongly selected evolutionary strategy to minimize predation risk, presumably based on observations that mountain goats quickly move to steep and complex terrain in the presence of predators and hypotheses that mountain goats can be found further from steep and complex terrain in systems lacking predators (Adams et al. 1982, Fox and Streveler 1986). This “escape terrain” undoubtedly provides escape opportunities from certain predators, however, mountain goats are likely adapted to these sites for a host of reasons, including, for example, reduced effects of interference and exploitative competition with other

mountain ungulates (like bighorn sheep), increased access to a diversity of microsites for foraging, or increased access to cool, shaded environments for thermal regulation. Terrain with high variance in slope at a broader spatial scale may be particularly important for providing sufficient foraging and shade opportunities at a finer scale. Therefore, it is reasonable that mountain goat association with steep and complex terrain is not simply the result of a predation risk trade-off strategy (especially considering that predation risk by mountain lions, *Puma concolor*, and golden eagles, *Aquila chrysaetos* may be elevated compared to gentler slopes and more homogenous terrain), but is rather a function of an assemblage of environmental characteristics created by the terrain that provides the necessary resources for survival and reproduction to which mountain goats are specifically adapted (i.e., their ecological niche). Future interpretation and modeling of habitat selection for mountain goats and other animals associated with similar terrain may be improved by the de-emphasis of “escape terrain” terminology.

Adequately modeling detection probability was particularly challenging using the methods employed by this study. I found little evidence for an association of canopy cover or terrain complexity with detection probability, a relationship that has been previously found in studies from aerial surveys (Poole 2007, Rice et al. 2009). Based on the inferential model, estimates of detection probability, ranging from 0.43 to 0.52, were roughly constant regardless of canopy cover. Additionally, the post hoc evaluation of covariates on detection resulted in considerable model selection uncertainty, with the most-supported model predicting constant detection at approximately 0.47. This result may have been due to lack of relevant covariates or dependence among the data as a

result of subsequent recording of detections as groups traveled across sampling units during the viewshed survey. The subsequent detections may have eroded any signal of the effect of canopy cover or terrain complexity because observers were more likely to record a group in forested or more rugged areas if it had been previously detected. In addition, detection probabilities were likely underestimated because of two possible reasons: 1) non-simultaneous viewing of each sampling unit by double observers while groups traveled across the viewshed, and 2) unmodeled variation in detection probability from lack of relevant covariates (MacKenzie et al. 2006). As a consequence, estimates of occupancy probabilities were likely overstated (MacKenzie et al. 2006, Rota et al. 2009). If detections of groups were scaled up to the viewshed, average detection probability was approximately 0.65, similar to estimates found in previous studies from aerial surveys in other regions (0.59-0.69; Houston et al. 1986, Poole et al. 2000, Gonzalez-Voyer et al. 2001, Pauley and Crenshaw 2006, Poole 2007, Rice et al. 2009).

Future applications of these methods may consider increasing the size of the sampling units to reduce the chance of animal movement among sampling units during surveys, as well as enacting stricter survey protocols to increase the chance that observers look in the same sampling units at the same time. This may be possible with larger sampling units or smaller viewshed extents. Trade-offs of these strategies would include reduced sample sizes (with potential increased model convergence issues) as well as less discernment of habitat associations at finer scales. Although modeling detection was a limitation in this study, the inferential model performed well in predicting observations from an independent data source with a reasonably conservative spatial error of 200 m

across a broad geographic area, lending support for a reasonable prediction of habitat selection.

Habitat Suitability and Abundance in the GYA

I present a landscape-wide prediction for the spatial distribution and abundance of mountain goats for the GYA given colonization of all suitable summer habitats. The model depicted clear spatial delineation of areas projected to be suitable habitat. About 18% of the GYA extent in consideration contained predicted suitable habitat which was primarily associated with heterogeneous terrain and indicated varying extents and connectivity of suitable patches. The currently colonized areas of the GYA, including the northern GYA and the Palisades area (i.e., southwestern GYA survey region), contained about 43% of the total predicted suitable habitat. The remaining, un-colonized area was projected to be 6,131 km², or about 1.3 times larger than the area currently colonized. Focal concentrations of un-colonized suitable habitat occurred in the South Absaroka, Teton, Gros Ventre, Wyoming, and Wind River Ranges (see Table 4 & *Regions of Management Interest* below). The best-guess abundance of mountain goats potentially supportable by the suitable habitat in the GYA ranged from 5,372 to 8,910. Given the most recent abundance estimate for the GYA of 2,104 mountain goats (*unpublished manuscript*), these figures suggest that when mountain goats have expanded their range throughout the GYA, they may be 2.5 to 4.2 times more abundant than currently.

Suitable habitat overlaps considerably with the general summer distribution of bighorn sheep observations throughout the GYA (e.g., Figure 5; *unpublished data*). Limited observations of interactions between the two species have indicated presence of

interference competition with mountain goats dominating (Reed 1986), however, the biological effects of any potential competition are largely unknown. Adams et al. (1982) and Varley (1996) suggest that bighorn sheep and mountain goats in native sympatric areas occupy separate niches that overlap only marginally, alleviating potential competition for scarce resources. Adams et al. (1982) hypothesized, however, that non-native mountain goat populations occupied a broader niche during rapid population growth and range expansion in Colorado, where native bighorn sheep were allopatric. Conceivably, the bighorn sheep niche may also be broader in the absence of mountain goats due to lack of competition. This reasoning indicates that competitive overlap may be increased during the initial expansion phase of mountain goats, but may be alleviated as populations stabilize, reflecting reduced niche overlap present in native sympatric populations. Given that the data for this study was collected from areas with well-established, sympatric populations, my prediction of suitable habitat likely reflects the latter condition in the GYA and inference may be stronger for regions currently occupied by bighorn sheep. My results may be conservative in areas where mountain goats are predicted to be allopatric where a broader niche may be sustained due to lack of competition.

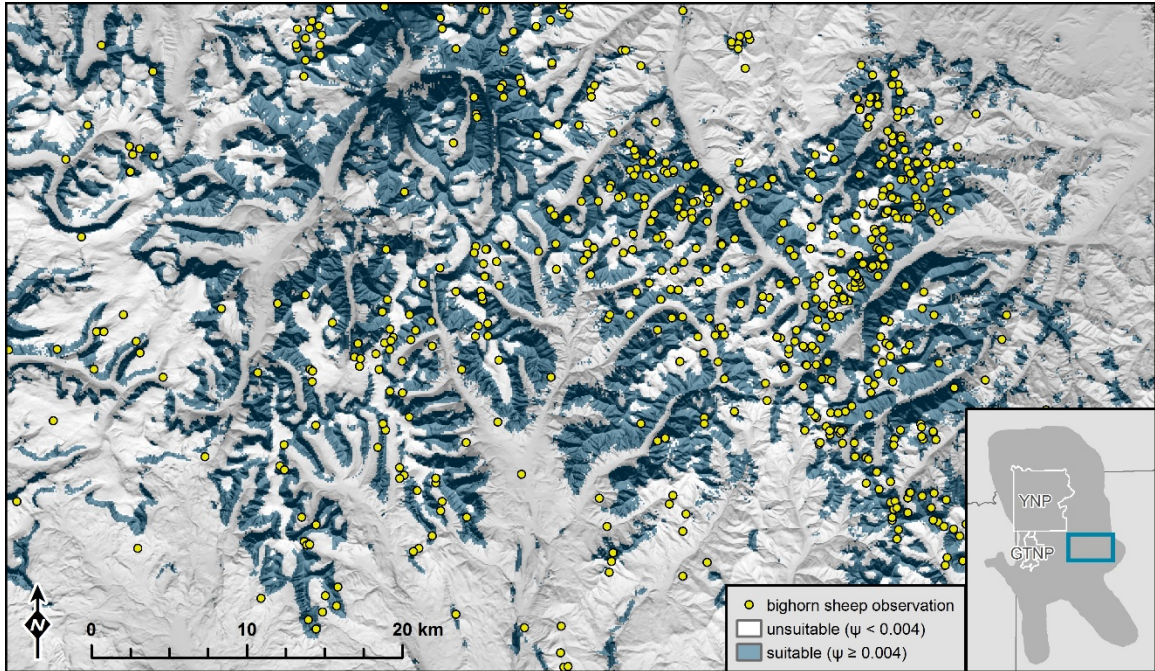


Figure 5. Predicted suitable summer habitat for mountain goats overlaid by summer locations of bighorn sheep collected by management agency personnel for an example area in the South Absaroka Range of the greater Yellowstone area.

In addition, the realized occupancy and abundance of suitable habitat may be constrained due to competition for scarce resources in shared winter habitats, such as on high elevation, wind-swept ridges, limiting population sizes in certain regions of the GYA (Adams et al. 1982, Varley 1996). It is unknown to what extent such conditions existed for my study areas, and there is likely large variation in the amount of shared winter habitats throughout the GYA. This study also did not take into account the potential effects of different regional climatic conditions on patterns of habitat selection and abundance of mountain goats. For example, the southern, more arid regions of the GYA may induce higher metabolic demand for thermoregulation and water (Cain et al. 2006), prompting greater preference for sites with lower heat loads, more canopy cover, or more succulent vegetation. Additionally, regions that experience harsher winter

conditions (e.g., deep snow accumulations) and have less available winter habitat (steep, snow-shedding slopes or wind-swept ridges) may reduce the number of mountain goats occupying the predicted suitable summer habitat. Lastly, areas that are predicted as suitable habitat but have no historic observations of mountain goats from management agency surveys (e.g., the West Boulder Plateau in the northern GYA) may indicate that an important habitat covariate not considered in this study was not captured in the inferential model. Therefore, suitable habitat and abundance estimates of mountain goats should be interpreted carefully.

Future research focused on understanding the ecological niches and overlap of bighorn sheep and mountain goats in both summer and winter ranges in multiple regions of the GYA would provide valuable insight into the dynamics and effects of potential competition. Ongoing studies across the GYA utilizing global positioning systems (GPS) technologies are collecting such data and will provide a comparative method with new insight into patterns of habitat selection for both species and provide further insight into potential competition between these two mountain ungulates.

Regions of Management Interest

The following sections provide information about the projected distribution of suitable habitat and abundance of mountain goats for specific regions across the GYA that may be valuable foresight for land and wildlife resource agencies concerned with developing management strategies for mountain goats and bighorn sheep.

Yellowstone National Park

The National Park Service in YNP and GTNP is guided by policy and statutory law to evaluate impacts of non-native species to park resources and preserve the natural integrity of the parks (National Park Service 2006). Suitable habitat for mountain goats in YNP was patchily distributed, primarily along the northern and eastern boundary (Figure 6), and predicted to support 247-411 mountain goats. Previous abundance estimates were 95-500 by Laundré (1990) and 270-365 by Lemke (2004). The majority of the suitable habitat is currently colonized; however, un-colonized patches occur in the southeast corner adjacent to the continuous habitat of the South Absaroka Range and in isolated “islands” elsewhere that are likely too small to support breeding populations. Given the limited amount of un-colonized habitat and the most recent abundance estimate of 299 individuals (adjusted for a 0.7 detection rate; *unpublished manuscript*), YNP may be at or near a state of complete colonization, having reached a density of 0.6/km² of predicted habitat.

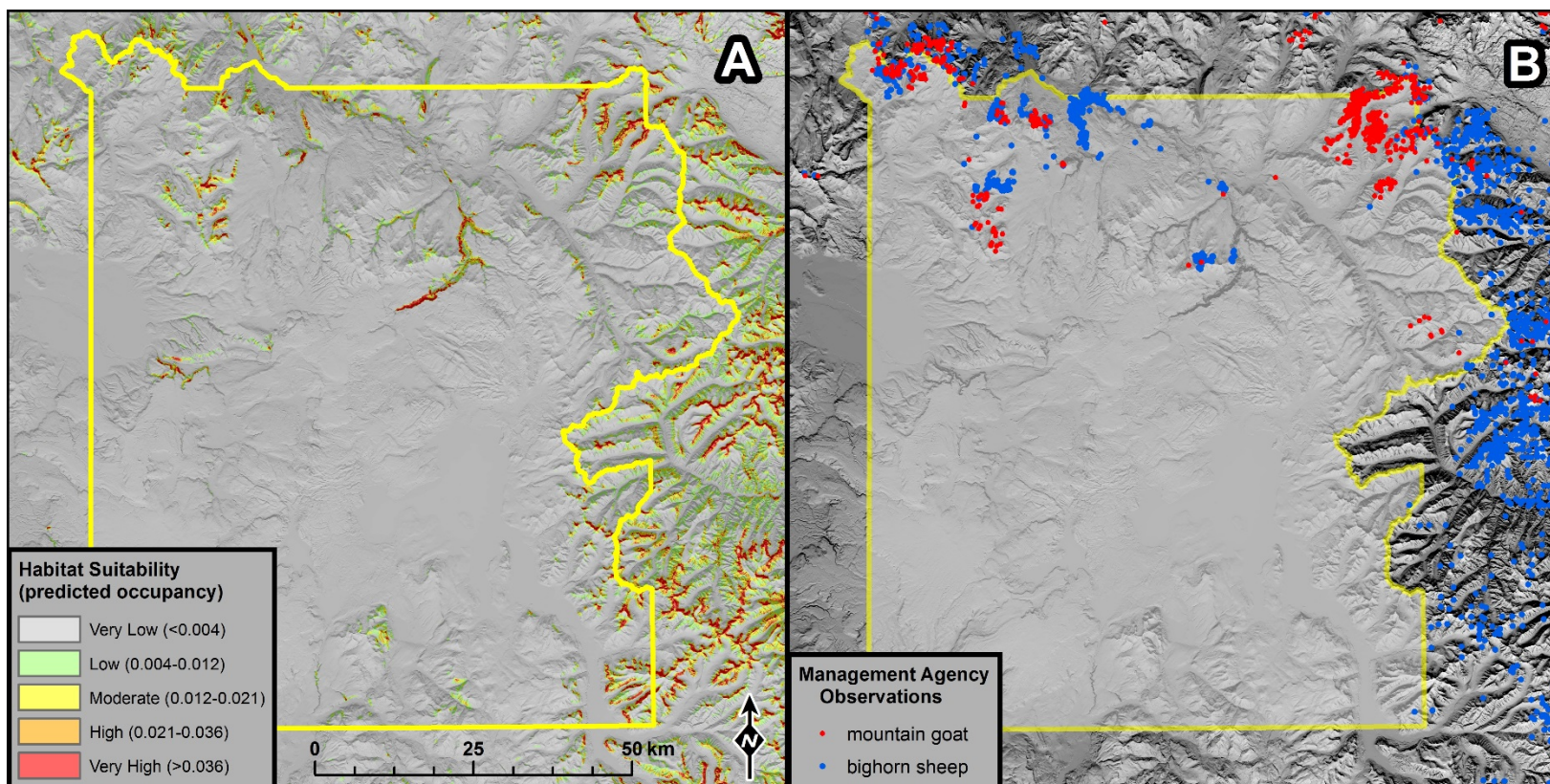


Figure 6. (A) Suitable habitat classifications of predicted occupancy probabilities for the Yellowstone National Park (YNP in Table 4 and Figure E1). (B) Observations of mountain goats and bighorn sheep obtained from summer surveys performed by wildlife and land management agency personnel from 1968-2012 (*unpublished data*) for Yellowstone National Park.

Teton Range & Grand Teton National Park

In contrast, the Teton Range (Figure 7) located partly within GTNP, is currently undergoing colonization, with recent reports of nanny and kid groups indicating a breeding population is establishing (GTNP Science and Resource Management, Wildlife Monitoring: Mountain Goats,

http://www.greateryellowstonescience.org/download_product/3987/0, accessed 11/2014).

The Teton Range also supports about 100-150 native, non-migratory bighorn sheep that have been subjected to habitat loss and restriction caused by human development and winter recreation (Courtemanch 2014). Suitable habitat for mountain goats was predicted throughout the Teton Range, predominating the more rugged eastern front of the GTNP and overlapping substantially with the current range of bighorn sheep. The predicted habitat for the Teton Range was estimated to support 248-411 mountain goats. The corridor between the Teton Range and the colonized Palisades area, where dispersing mountain goats are likely originating from, has relatively patchy and thinly distributed suitable habitat, spanning 9-10 km N-S and about 11 km E-W at its narrowest.

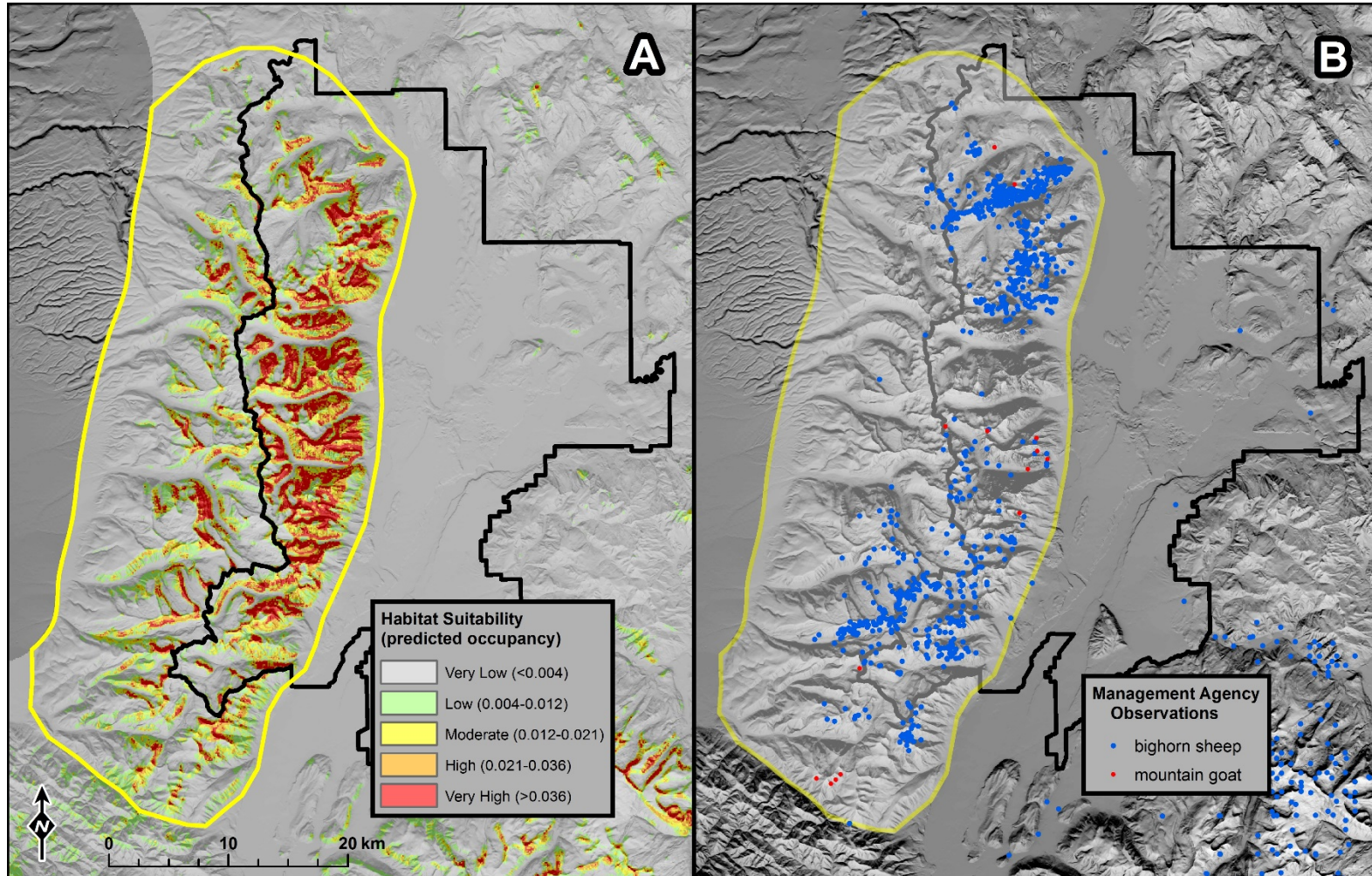


Figure 7. (A) Suitable habitat classifications of predicted occupancy probabilities for the Teton Range and Grand Teton National Park (Region 3 and GTNP, respectively, in Table 4 and Figure E1). (B) Observations of mountain goats and bighorn sheep obtained from summer surveys performed by wildlife and land management agency personnel from 1968-2012 (*unpublished data*) for the Teton Range and Grand Teton National Park.

South Absaroka Range

The South Absaroka Range contains one of the largest, core populations of native bighorn sheep in North America. This region is largely devoid of mountain goats, with only a small number of isolated mountain goat observations beginning in the mid-1980's (*unpublished data*), and represents the largest core area of suitable habitat remaining to be colonized in the GYA (Figure 8). The South Absaroka contains about 26% of the total suitable habitat in the GYA, and is estimated to support an equal or greater abundance of mountain goats than bighorn sheep currently occurring in this area (D. McWhirter, *personal communication*). Given the continuous distribution of suitable habitat and absence of movement barriers from areas to the north that are currently colonized, the South Absaroka is likely to be one of the first regions to experience rapid expansion and colonization of mountain goats.

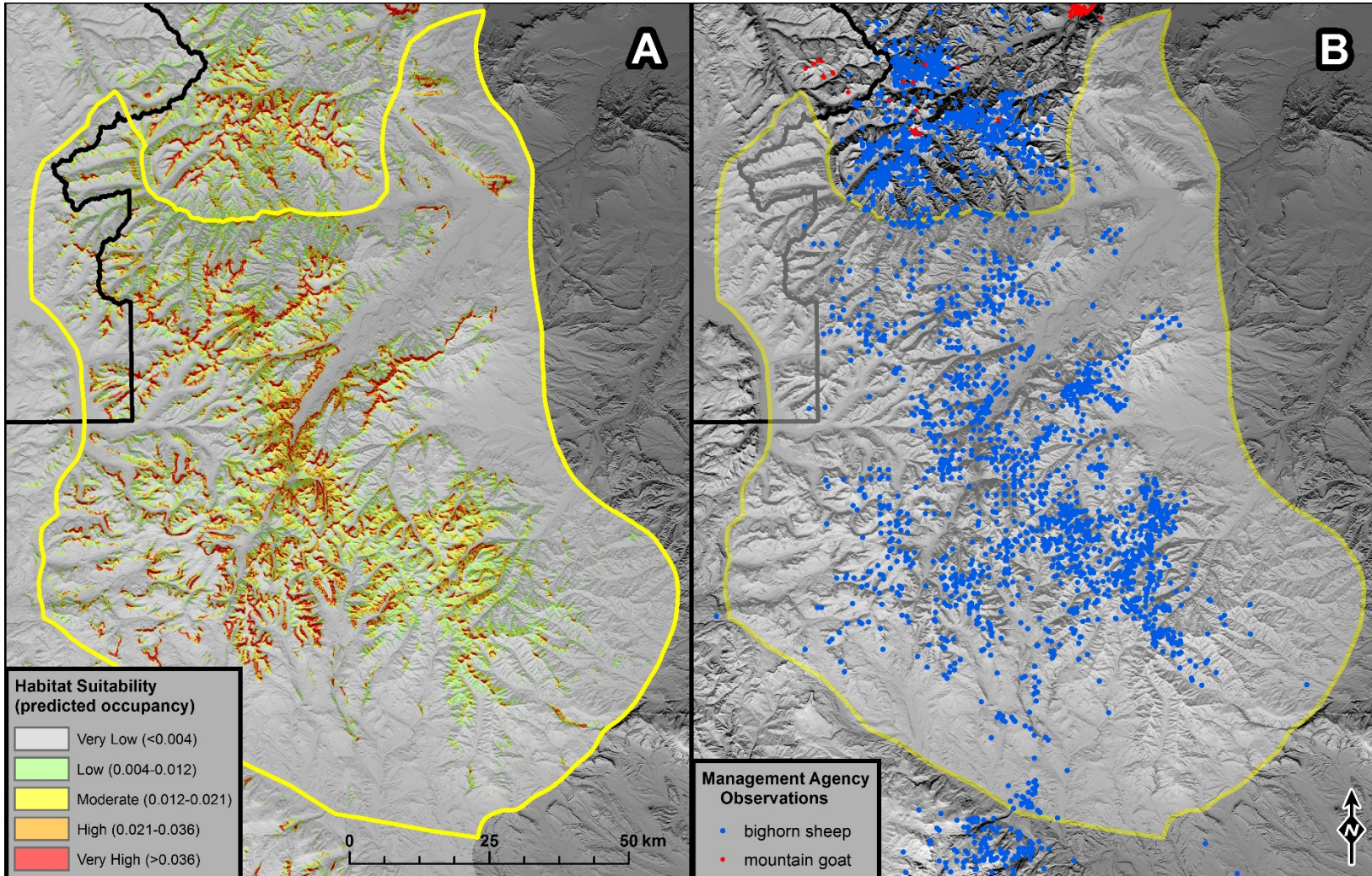


Figure 8. (A) Suitable habitat classifications of predicted occupancy probabilities for the South Absaroka Range (Region 2 in Table 4 and Figure E1). (B) Observations of mountain goats and bighorn sheep obtained from summer surveys performed by wildlife and land management agency personnel from 1968-2012 (*unpublished data*) for the South Absaroka Range.

Gros Ventre Range

The un-colonized Gros Ventre Range (Figure 9) may be expected to experience colonization over a lengthier period of time than for previous regions due to the relatively deep and fast-flowing Snake River bisecting this region and the neighboring Palisades area. Rare observations of mountain goats in the Gros Ventre Range do occur, indicating the river is not a complete barrier, and the patchy suitable habitat spanning about 18 km E-W and 15 km N-S between these two areas may serve as a movement corridor. Additionally, future dispersal from the post-colonized South Absaroka could occur across stepping-stone habitat patches, a total distance of about 40 km with each patch no further than 6.5 km from the next. The Gros Ventre Range is estimated to contain suitable habitat adequate to support 175-291 mountain goats, mostly restricted to small areas occurring between the forested lower elevation valleys and large, flat topped plateaus at high elevation, areas across which summering bighorn sheep are broadly distributed.

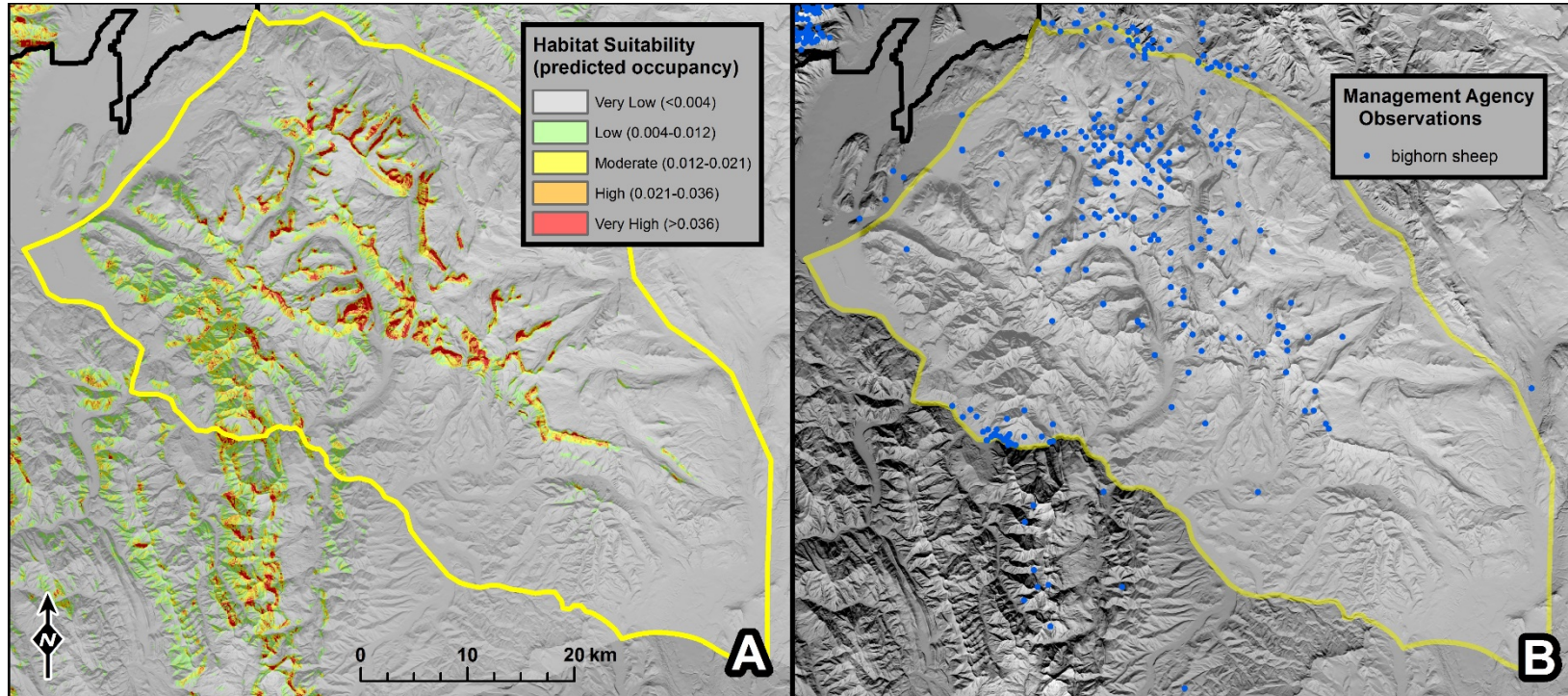


Figure 9. (A) Suitable habitat classifications of predicted occupancy probabilities for the Gros Ventre Range (Region 4 in Table 4 and Figure E1). (B) Observations of bighorn sheep obtained from summer surveys performed by wildlife and land management agency personnel from 1968-2012 (*unpublished data*) for the Gros Ventre Range.

Wyoming Range

Suitable habitat in the Wyoming Range (including the Palisades area; Figure 10), comprises 15% of the total predicted for the GYA, and occurs along two mountain spines on the western and eastern front. The current abundance estimate of the established Palisades population is about 316 (adjusted for 0.7 detection rate; *unpublished manuscript*), representing 24-39% of the predicted ultimate abundance for the entire range. Expansion through the southern portion of the mountain range is expected to be restricted by the Snake River; however, considerable, largely contiguous suitable habitat lies within this area.

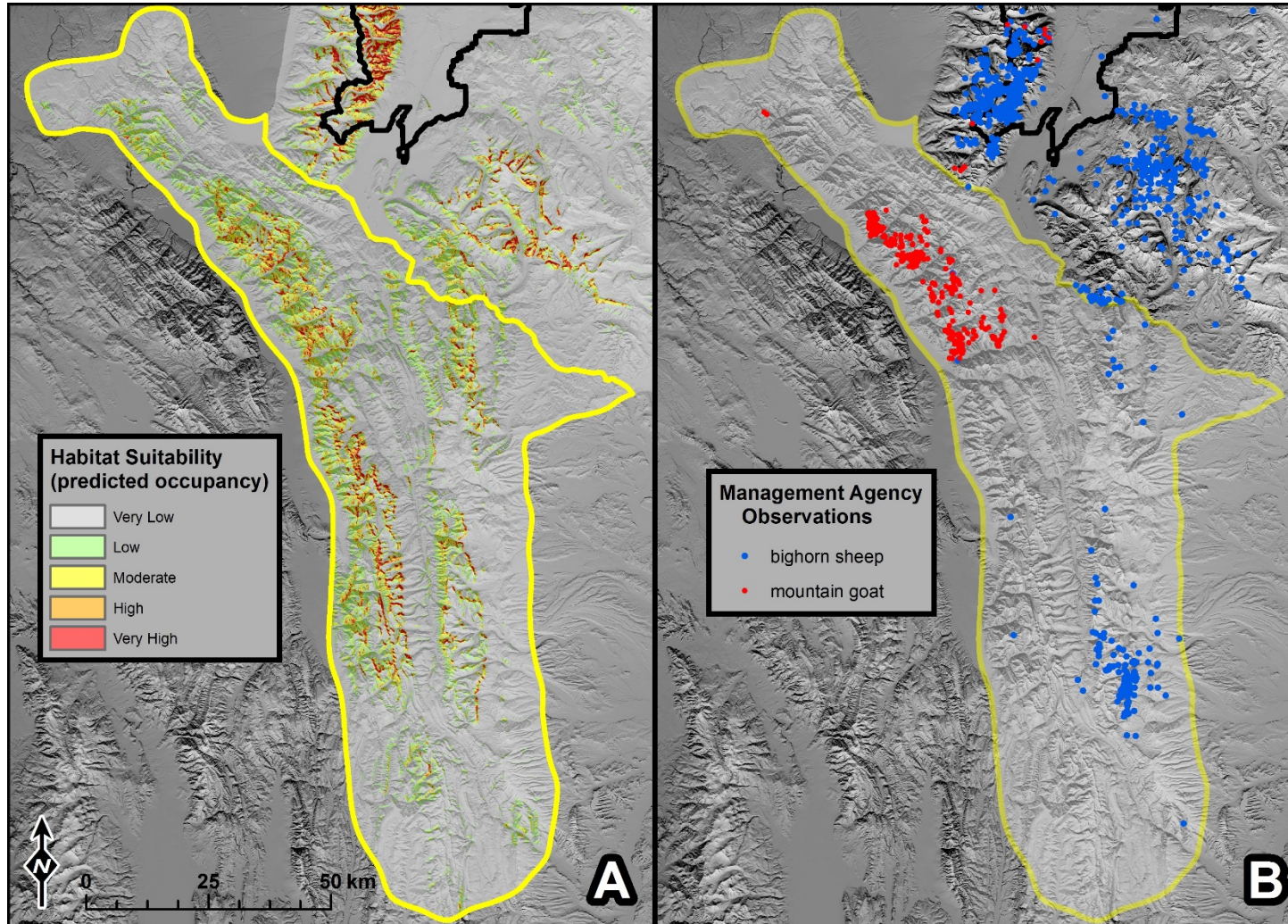


Figure 10. (A) Suitable habitat classifications of predicted occupancy probabilities for the Wyoming Range (Region 5 in Table 4 and Figure E1). (B) Observations of mountain goats and bighorn sheep obtained from summer surveys performed by wildlife and land management agency personnel from 1968-2012 (*unpublished data*) for the Wyoming Range.

Wind River Range

The last sizeable extent of predicted suitable habitat, comprising 10% of the total in the GYA, occurs in the un-colonized Wind River Range (Figure 11). Most of the suitable habitat is predicted in the northern half of the mountain range, with the remaining mostly restricted to the core spine of the range and several deep side-canyons on the NE front. This area is considered to be an important core area for native bighorn sheep, supporting about 1,000 individuals (Toweill and Geist 1999). No mountain goats are known to occur here, though a few historic records exist (*unpublished data*). This mountain range is predicted to support an estimated 537-891 mountain goats, but is likely to be the last region to be colonized given that the nearest neighboring regions are currently un-colonized and it is isolated, being about 11 km from any suitable patches in the Gros Ventre Range and 16 km from any substantial suitable habitat in the South Absaroka Range.

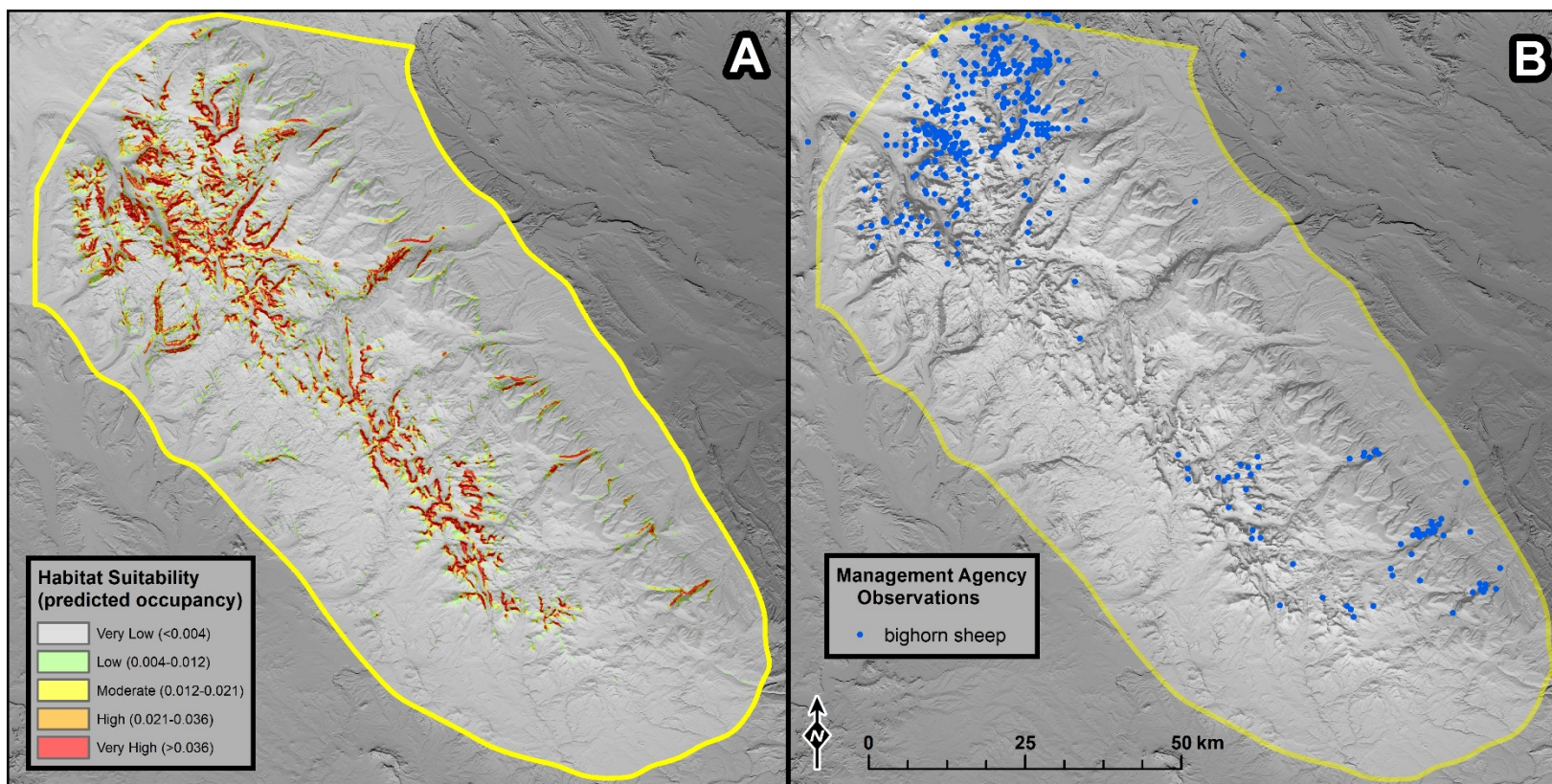


Figure 11. (A) Suitable habitat classifications of predicted occupancy probabilities for the Wind River Range (Region 6 in Table 4 and Figure E1). (B) Observations of bighorn sheep obtained from summer surveys performed by wildlife and land management agency personnel from 1968-2012 (*unpublished data*) for the Wind River Range.

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APPENDICES

APPENDIX A

DEVELOPMENT OF HABITAT COVARIATES

Defining “scale”. This project combined two disciplines: geographic information science (GI Science) and ecology. Both fields use the term “scale” but define it in different ways. In GI Science, scale refers to cell size and resolution, with emphasis on representing the data correctly. For example, representing small scale data (which is coarse scale in GI Science mapping) at a large scale (fine scale in GI Science) can infer accuracy that isn’t inherent in the source data; therefore, analysis and results should reflect the appropriate scale. In ecology, scale often refers to the size or extent of the landscape that animals are responding to and selecting for. For example, the results of this project suggest that mountain goats select for landscapes of steep and variable-steepness terrain that are 0.25 km² (500 x 500 m) in area while also selecting for landscapes of lower canopy cover that are 0.01 km² (100 x 100 m) in area. These areas represent the size of the response by mountain goats, and, in GI Science, are considered a neighborhood analysis of the underlying habitat raster that may be at the 30 x 30 m scale (resolution). For this project, in order to clarify scale terms used in the development of covariates and habitat rasters in GIS for understanding ecological relationships, I reserved the term “**scale**” to mean the neighborhood of influence (i.e., the size of the area mountain goats are responding to or “scale of effect”; Wiens 1989), and the term “**resolution**” to mean the raster cell size that the data can be represented accurately at. I use the spatial scale modifiers “fine” and “broad” to describe the size of the neighborhood of influence when comparing habitat covariates relative to others (smaller and larger, respectively). For this project, rasters were collected from various sources (see Appendix G for the Data Dictionary) at various resolutions. The explanatory variables in the analysis were based on the average values of those rasters within the 100 x 100 m sampling units (zonal mean). For understanding different spatial scales mountain goats may be responding to, a neighborhood analysis (e.g., 3x3 for the 300 m scale) of the resulting 100 m resolution grid was calculated. Therefore, the results of this analysis were at the 100 m resolution and were not represented at any finer detail.

100 x 100 m polygon sampling units. The 100 x 100 m polygon grids used for field sampling and generating explanatory values were developed using the “genvecgrid” command in Geospatial Modelling Environment software (<http://spatial ecology.com>). The polygon sampling units were used as zonal features to calculate means and, for slope variance, standard deviations that were used as covariates in the occupancy analysis.

Mean slope (SLP) & slope variance (SLPv). Slope covariates (SLP and SLPv at 100-900 m spatial scales) were developed from a slope (in degrees) raster calculated from a 1-arc-second (approximately 30 meter) resolution National Elevation Dataset (NED). For the 100 m spatial scale slope covariate, zonal mean and standard deviation using the 100 m polygon grid as the zonal feature were calculated for each sampling unit from this raster

layer. For the 300 to 900 m spatial scales, I calculated focal mean and standard deviation of the slope raster with environment settings set at a larger extent around each region of interest (for accurate calculation of periphery sampling units) and the cell size of 100 m so that each cell precisely lined up with the polygon sampling units. The neighborhood sizes for focal calculations were then set to 3x3 for the 300 m spatial scale, 5x5 for the 500 m scale, and so on. Zonal mean for both the mean and standard deviation raster layers using the 100 m polygon grid as the zonal feature was then calculated for each sampling unit and outputted to a table. Standard deviations were later squared to calculate slope variances. This process was automated in one GIS using Python scripting (<https://code.google.com/p/pyscripter>). Following is example Python coding for the 300 m spatial scale for development in ArcMap 10.2:

```
#-----
# Name:      Slope at 300m Scale (Python code)
# Purpose:   For each region of interest, calculate focal stats (mean and standard deviation) at 300m scale for surveyed polygon
             grid cells. Code developed for PyScripter and ArcMap 10.2.
# Author:    Jesse DeVoe
# Created:   24/06/2014
#-----

import arcgisscripting #import the core GeoProcessing module
import sys #import the sys module
import time #import the time module
import arcpy
from arcpy import env
from arcpy.sa import *
gp = arcgisscripting.create(9.3) #create the geoprocessor object

# set to desired folder for storage of rasters from focal stats
myFocalStatsFolder = r"C:\...\Covariates\Slope\300m"

# set to desired folder for storage of zonal stat tables
myZonalStatsFolder = r"C:\...\Covariates\Slope\zstat_tables\300m"

gp.Workspace = myZonalStatsFolder
arcpy.env.overwriteOutput = True # overwrite files ON

print "Started processing at " + time.ctime()

# REGION 1
env.cellSize = 100
# set extent to coordinates of region of interest (expanded extent of surveyed polygon grids)
env.extent = arcpy.Extent(489158.457682,4996337.788360,497858.457682,5005037.788360)

arcpy.CheckOutExtension("Spatial")

# Focal Statistics

# Slope raster as input
inRaster = r"C:\...\slope30_gc" # Gallatin Crest 30m Slope raster, as an example

# set to covariate spatial scale of interest. For 300 m, neighborhood size (300x300) = 3 x 3:
neighborhood = NbrRectangle(3,3,"CELL")

outFocalStatistics = FocalStatistics(inRaster, neighborhood, "MEAN", "DATA") # calculate mean
outFocalStatistics.save(myFocalStatsFolder + "\\ " + "r1slp30_300") # save raster

outFocalStatistics = FocalStatistics(inRaster, neighborhood, "STD", "DATA") # calculate standard deviation
```

```

outFocalStatistics.save(myFocalStatsFolder + "\\" + "r1slp30_300sd") # save raster

# Zonal Statistics as Table

# for MEAN:
inZoneData = r"C:\...\REGION1\region1_grid.shp" # region 1 zonal input (original polygon grid)
inValueRaster = r"C:\...\r1slp30_300" # region 1 focal mean raster previously created
zoneField = "pc_id" # unique polygon grid unit identifier
outTable = myZonalStatsFolder + "\\" + "r1slp30_300.dbf" # save zonal statistics table as a DBF file
outzSaT = ZonalStatisticsAsTable(inZoneData,zoneField,inValueRaster,outTable,"DATA","MEAN")

# for Standard Deviation:
inValueRaster = r"C:\...\r1slp30_300sd" # region 1 focal standard deviation raster previously created
zoneField = "pc_id" # unique polygon grid unit identifier
outTable = myZonalStatsFolder + "\\" + "r1slp30_300sd.dbf" # save zonal statistics table as a DBF file
outzSaT = ZonalStatisticsAsTable(inZoneData,zoneField,inValueRaster,outTable,"DATA","MEAN")

# Join mean and standard deviation zonal statistics tables for more efficient data management
joinTable = myZonalStatsFolder + "\\" + "r1slp30_300.dbf"
joinTablesD = myZonalStatsFolder + "\\" + "r1slp30_300sd.dbf"

joinField = "pc_id"
arcpy.JoinField_management(joinTable,joinField,joinTablesD,joinField,"MEAN")

# Add field in zonal mean table to copy standard deviation values
fieldName = "SD"
arcpy.AddField_management(joinTable,fieldName,"DOUBLE")

# Copy standard deviation values
arcpy.CalculateField_management(joinTable,"SD",'!MEAN_1!',"PYTHON")

# Clean up so no confusion (delete MEAN_1 field)
arcpy.DeleteField_management(joinTable,"MEAN_1")

# If running for multiple regions of interest, can append all regions together:

# Save a raw copy (for each region) for appending at end
reg1_300 = myZonalStatsFolder + "\\" + "r1slp30_300.dbf"

# Append all regions to one table file
finaltableFolder = r"C:\...\zstat_tables\finaltables" # create new folder for final, appended DBF file

# copy one region to be target dataset
arcpy.Copy_management("r1slp30_300.dbf", finaltableFolder + "\\" + "slp30_300.dbf")

# append all other regions
arcpy.Append_management([reg1_300, reg2_300, reg3_300, reg4_300, reg5_300, mt_300], finaltableFolder + "\\" +
"slp30_300.dbf", "TEST")

arcpy.CheckInExtension("Spatial")

```

Distance to escape terrain (DET). Distance to escape terrain covariates (DET for 25°, 33°, 40°, 45°, 50° slope thresholds) were developed from the 30 m resolution slope raster by first calculating “escape terrain” based on each of the desired slope thresholds. Slope values were partitioned into two nominal categories, “0” for slopes less than the desired cutoff value and “1” for slopes greater than or equal to the desired cutoff value. The Euclidean distance (in meters) from each 30m pixel to the nearest pixel with values of 1 (i.e., escape terrain) was then calculated. The zonal mean using the 100 m polygon grid

as the zonal feature was calculated in one GIS for each sampling unit from this raster layer and outputted to a table.

Terrain ruggedness (RUG). Terrain ruggedness covariates (RUG at 100-900 m spatial scales) were obtained from a 30 m resolution ruggedness raster developed using a profile curvature function in one GIS measuring the second derivative (rate of change of the slope) of the surface from a 30 m resolution NED (M. Zambon, *personal communication*). Positive curvature indicates convexity (concave up), negative curvature indicates concavity (concave down), and values of 0 indicate flat surfaces. From the curvature raster, focal standard deviation was calculated within a 100 m radius neighborhood to produce a measure of the variability of the rate of change in slope for each pixel (Poole et al. 2009). The RUG raster was used to develop each RUG covariate spatial scale using the same methods described for the mean SLP covariates.

Vector ruggedness measure (VRM). Vector ruggedness measure covariates (VRM at 100-900 m spatial scales) were developed from the 30 m resolution NED raster (see Slope and Slope Variance) using the *Terrain Ruggedness (VRM)* tool in the *Terrain Tools* toolbox for ArcMap 10.2 (Sappington et al. 2007; <http://resources.arcgis.com/gallery/file/geoprocessing/details?entryID=F65FF927-1422-2418-A02A-EE72574A8C26>). This tool uses a vector analysis to calculate the dispersion of vectors orthogonal (normal) to pixels within a specified neighborhood, capturing the variation in the three-dimensional orientation of the pixels. Values are unit-less and range from 0 indicating no terrain variation (e.g., flat or steep areas) to 1 indicating high variation (e.g., steep and rugged areas). A 7x7 neighborhood was used to produce a VRM raster from the 30 m resolution NED that was then used to develop each VRM covariate spatial scale employing the same methods described for the mean SLP covariates.

Solar radiation index (SRI). Solar radiation index covariates (SRI at 100-900 m spatial scales) came directly from a hillshade raster layer estimated by a combination of slope and aspect data from a 30 m NED (personal communication: M. Zambon). Hillshade has been used as a surrogate for solar insolation (the total amount of solar radiation energy received on a given surface area during a given time) as it varies with topography, measuring the average amount of shade during the course of the year at any pixel (Ciarniello et al. 2005). The hillshade was calculated with an azimuth of 180° and a slope of 45° to give south-facing (180°) slopes the most solar radiation. Values ranged from -1 (low solar radiation) to 1 (high solar radiation). The hillshade raster was used to develop each SRI covariate spatial scale using the same methods described for the mean SLP covariates.

Global radiation (GRAD). Global radiation covariates (GRAD at 100-900 m spatial scales) were calculated using the *Area Solar Radiation* tool in the *Solar Radiation* toolbox in ArcMap 10.2 (Fu and Rich 1999) and a 1 arc-second (approximately 30 m) resolution NED. A larger extent than the 100 m polygon sampling grids was used to ensure accurate calculation of periphery pixels (for incorporation of sky obstructions during tool calculations). The global radiation raster output was selected as a measure of solar insolation (combining direct and diffuse radiation). User-defined options were set as follows: latitude = 45°, sky size = 512, time configuration = multiple days in a year, date/time (in Julian dates) = 171 to 289 for 2012, day interval = 7 (weekly), and hour interval = 0.5 (default). All other settings were left as default. The resulting GRAD layer values represent watt per square meter for each pixel for June 19 to October 15, spanning the range of dates of field data collection. The GRAD raster was used to develop each GRAD covariate spatial scale using the same methods described for the mean SLP covariates.

Forest canopy cover (COV). Canopy cover covariates (COV at 100-900 m spatial scales) were derived from the 30 m resolution 2001 NLCD (National Land Cover Database) Percent Tree Canopy (Version 1.0) raster using the same methods described for the mean SLP covariates.

Rock (RCK) & meadow (MDW). Proportion rock (RCK) and meadow (MDW) covariates (at 100-900 m spatial scales) were developed from preprocessed 30 m resolution land cover classifications (personal communication: K. Proffitt). Methods for developing the preprocessed classifications were found in the metadata for Montana Land Cover Framework 2013 (http://geoinfo.msl.mt.gov/home/msdi/land_use_land_cover.aspx). From this classification, all cover types corresponding to cliff/canyon/bedrock, scree, and ice field were reclassified to 1 for “rock” and 0 otherwise (Table B1). All cover types corresponding to open habitats and meadows, including alpine fell-fields, alpine turf, grasslands, meadows, marshes, steppe, shrublands, and badlands, were reclassified to 1 for “meadow” and 0 otherwise.

Table A1. Reclassifications of land cover classifications to rock and meadow.

Classification	Rock Reclass	Meadow Reclass
Open Water	0	0
Developed, Open Space	0	0
Developed, Low Intensity	0	0
Developed, Medium Intensity	0	0
Quarries, Strip Mines and Gravel Pits	0	0
Pasture/Hay	0	0
Cultivated Crops	0	0
Cultivated Cropland	0	0

Great Plains Badlands	0	1
Rocky Mountain Cliff, Canyon and Massive Bedrock	1	0
Alpine Ice Field	1	0
Alpine Bedrock and Scree	1	0
Geysers and Hot Springs	0	0
Aspen Forest and Woodland	0	0
Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest	0	0
Rocky Mountain Subalpine Woodland and Parkland	0	0
Rocky Mountain Foothill Limber Pine - Juniper Woodland	0	0
Rocky Mountain Lodgepole Pine Forest	0	0
Rocky Mountain Ponderosa Pine Woodland and Savanna	0	0
Rocky Mountain Subalpine Dry-Mesic Spruce-Fir Forest and Woodland	0	0
Rocky Mountain Subalpine Mesic Spruce-Fir Forest and Woodland	0	0
Rocky Mountain Montane Douglas-fir Forest and Woodland	0	0
Rocky Mountain Poor Site Lodgepole Pine Forest	0	0
Aspen and Mixed Conifer Forest	0	0
Mountain Mahogany Woodland and Shrubland	0	0
Inter-Mountain Basins Aspen-Mixed Conifer Forest and Woodland	0	0
Middle Rocky Mountain Montane Douglas-fir Forest and Woodland	0	0
Alpine Dwarf-Shrubland	0	1
Low Sagebrush Shrubland	0	1
Inter-Mountain Basins Montane Sagebrush Steppe	0	1
Rocky Mountain Montane-Foothill Deciduous Shrubland	0	1
Rocky Mountain Subalpine Deciduous Shrubland	0	1
Big Sagebrush Steppe	0	1
Montane Sagebrush Steppe	0	1
Wyoming Basins Dwarf Sagebrush Shrubland and Steppe	0	1
Rocky Mountain Lower Montane-Foothill Shrubland	0	1
Rocky Mountain Lower Montane, Foothill, and Valley Grassland	0	1
Rocky Mountain Subalpine-Upper Montane Grassland	0	1
Alpine Fell-Field	0	1
Alpine Turf	0	1
Rocky Mountain Subalpine-Montane Mesic Meadow	0	1
Northern Rocky Mountain Lower Montane, Foothill and Valley Grassland	0	1
Harvested Forest - Northwestern Conifer Regeneration	0	1
Harvested Forest-Shrub Regeneration	0	1
Harvested Forest - Grass/Forb Regeneration	0	1
Recently burned forest	0	0
Rocky Mountain Lower Montane-Foothill Riparian Woodland and Shrubland	0	0
Rocky Mountain Wooded Vernal Pool	0	0
Rocky Mountain Subalpine-Montane Riparian Woodland	0	0
Rocky Mountain Subalpine-Montane Riparian Shrubland	0	1
Alpine-Montane Wet Meadow	0	1
Emergent Marsh	0	1
North American Arid West Emergent Marsh	0	1
Rocky Mountain Subalpine-Montana Fen	0	1
Great Plains Riparian	0	1
Columbia Plateau Vernal Pool	0	0
Western Great Plains Saline Depression Wetland	0	0
Western Great Plains Riparian Woodland and Shrubland	0	0

To calculate proportions within each 100 x 100 m sampling unit for multiple scales, I first resampled the “rock” and “meadow” raster reclassifications to 5x5 m cells in order to improve accuracy and reduce cell boundary effects during calculation. Mean zonal statistics for the sampling units were calculated and outputted as rasters, with values representing proportions of rock and meadow, respectively. These rasters were used for the 100 m spatial scale of RCK and MDW covariates. For the remaining 300-900 m spatial scales, these rasters were resampled to 100x100 m cells in order to calculate focal summation of the proportions for a neighborhood (e.g., 3x3 for 300 m spatial scale). A mean zonal statistic, which returned the summed proportion value, was calculated to

output the values for each sampling unit into a table. An additional field was calculated by dividing the summed proportion value of the neighborhood by the number of cells in the neighborhood (e.g., 9 for 3x3 neighborhood), giving a proportion for the specific spatial scale. This process was automated in one GIS using Python scripting (<https://code.google.com/p/pyscripter>). Following is example code for the 300 m spatial scale for development in ArcMap 10.2:

```
#-----
# Name:      Meadow Proportion at 300m Scale (Python code)
# Purpose:   For each region of interest, resample to 5x5m cells, calculate mean zonal stat raster, resample to 100x100 cells,
              calculate focal stats (SUM) at 300m scale (3x3), calculate MEAN zonal stat to .dbf table. Code developed for
              PyScripter and ArcMap 10.2.
# Author:    Jesse DeVoe
# Created:   08/07/2014
#-----

import arcgisscripting #import the core GeoProcessing module
import sys #import the sys module
import time #import the time module
import arcpy
from arcpy import env
from arcpy.sa import *
gp = arcgisscripting.create(9.3) #create the geoprocessor object

# set to desired folder for resample rasters, zonal raster, and focal stats raster
myFocalStatsFolder = r"C:\...\proportions\300m"

# set to desired folder for final zonal stats table
myZonalStatsFolder = r"C:\...\proportions\zstat_tables\300m"

gp.Workspace = myFocalStatsFolder
arcpy.env.overwriteOutput = True # overwrite files ON

print "Started processing at " + time.ctime()

# Resample meadow raster (reclassified from land cover data) to 5x5m cells
inRaster = r"C:\...\meadow_reclass" # input meadow raster
arcpy.Resample_management(inRaster, r"C:\...\Proportions\resamp5_mead", "5", "NEAREST")
resamp5_mead = r"C:\...\Proportions\resamp5_mead" # grab for further processing

# REGION 1
# set extent to coordinates of region of interest (expanded extent of surveyed polygon grids)
env.extent = arcpy.Extent(489158.457682,4996337.788360,497858.457682,5005037.788360)

arcpy.CheckOutExtension("Spatial")

# Zonal Stats (to raster) - MEAN - calculates proportion of rock in each cell
inZoneData = r"C:\...\Proportions\expandedgrids\reg1_newgrid.shp" # Region 1 zonal input (expanded extent polygon grid)
inValueRaster = resamp5_mead # 5x5 resample layer just created
zoneField = "FID"
outRaster = r"C:\...\Proportions\r1zst5_md" # name and folder for saving raster

outZonalStatistics = ZonalStatistics(inZoneData,zoneField,inValueRaster,"MEAN","DATA")
outZonalStatistics.save(outRaster)

# Resample to 100x100m cells - bring back to 100m scale (same raster as previous, but different scale)
arcpy.Resample_management(outRaster, r"C:\...\Proportions\r1res100_md", "100", "NEAREST") # grabbing raster from
                                              previous output

# Focal Statistics - calculate raster for 300 m spatial scale variable
inRaster = r"C:\...\Proportions\r1res100_md" # grab 100x100 resampled raster just created
neighborhood = NbrRectangle(3,3,"CELL") # set to neighborhood size (300x300)
```

```

outFocalStatistics = FocalStatistics(inRaster, neighborhood, "SUM", "DATA") # sums proportions for neighborhood
outFocalStatistics.save("r1_foc_300md")

# Final Zonal Stats – MEAN returns same value for each grid calculated in focal statistics
inZoneData = r"C:\...\REGION1\region1_grid.shp" # region 1 zonal input (original polygon grid)
inValueRaster = "r1_foc_300md" # focal stats raster just created
zoneField = "pc_id" # unique polygon grid unit identifier
outTable = myZonalStatsFolder + "\\\" + "r1_300md.dbf" # save table as DBF file
outZonalStatistics = ZonalStatisticsAsTable(inZoneData, zoneField, inValueRaster, outTable, "DATA", "MEAN")

# Add proportion field
fieldName = "prop"
arcpy.AddField_management(outTable, fieldName, "DOUBLE")

# Calculate field
# for 3x3 focal stats, divide MEAN by 9 = proportion md within 300x300m
arcpy.CalculateField_management(outTable, "prop", "!MEAN!/9", "PYTHON")

# If running for multiple regions of interest, can append all regions together:

# Save a raw copy (for each region) for appending at end
r1_300 = outTable

# Append all regions to one table file
finaltableFolder = r"C:\...\proportions\zstat_tables\finaltables" # create new folder for final, appended DBF file

# copy one region to be target dataset
arcpy.Copy_management(outTable, finaltableFolder + "\\\" + "mead_300.dbf")

# append all other regions
arcpy.Append_management([r1_300, r2_300, r3_300, r4_300, r5_300, mt_300], finaltableFolder + "\\\" + "mead_300.dbf",
"TEST")

arcpy.CheckInExtension("Spatial")

```

Normalized difference vegetation index (NDVI). Normalized Difference Vegetation Index covariates (NDVI at 100-900 m spatial scales) were developed from a 30 m resolution Landsat 7 ETM+ (Enhanced Thematic Mapper) image acquired for a cloud-free period in July 2000 (personal communication: M. Zambon). All spectral and thermal bands collect data with 8-bit radiometric resolution producing a range of digital numbers from 0 to 255. These digital numbers were converted to at-sensor reflectance values for normalization across scenes. Values for NDVI were calculated from thematic mapper (TM) bands 3 and 4, representing the visible red range and the near infrared range of the electromagnetic spectrum, respectfully, using the following equation:

$$NDVI = \frac{(TM4 - TM3)}{(TM4 + TM3)}$$

The NDVI metric was intended to be a quantification of the amount of forage available to mountain ungulates during a month of alpine green-up. Values range from -1.0 (non-vegetated features) to 1.0 (higher concentrations of green vegetation). This NDVI raster was used to calculate each spatial scale using the same methods described for the mean

SLP covariates, however, because forest canopy cover, which was not considered forage, results in high NDVI values, NDVI values for sampling units that had greater than or equal to 15% canopy cover were converted to the average NDVI value of sampling units that had less than 15% canopy cover. This value varied depending on the spatial scale being considered. This process essentially masked out the forested areas in the logistic regression analysis to isolate the effect of NDVI in open areas and meadows where mountain ungulates may be more likely to feed. This was done for each of the NDVI spatial scales. It was important to note that application of NDVI to mountainous environments can produce erroneous values, with shadows and soil reflectance negatively impacting results (Jiang et al. 2006). In addition, the Landsat image represents a snapshot in time (e.g., the month of July from which the images were taken) and may not be representative of forage availability across the season or years.

Tasseled cap wetness (TCAP). Tasseled Cap Wetness covariates (TCAP at 100-900 m spatial scales) were derived from the same July 2000 Landsat ETM+ data layer described for NDVI covariates (personal communication: M. Zambon). The tasseled cap wetness transformation uses coefficients for each TM band in the following equation (Crist and Cicone 1984):

$$Wetness = 0.0315_{TM1} + 0.2021_{TM2} + 0.3102_{TM3} + 0.1594_{TM4} - 0.6806_{TM5} - 0.6109_{TM7}$$

This transformation identifies a “wetness” component from the TM bands sensitive to both moisture in vegetation and soil. Wetness values were therefore interpreted as quantifying the amount of forage vegetation that may be available to mountain ungulates. Values ranged from 0 to 0.26. Non-intuitively, low values indicate higher wetness. Each spatial scale for the TCAP covariate was developed using the same methods described for the NDVI covariates (including “masking” of forested areas). This variable was interpreted with caution due to evidence that sensors may be more sensitive to moisture in soil than in vegetation (Crist and Cicone 1984).

Literature Cited

- Crist, E. P., and R. C. Cicone. 1984. A physically-based transformation of thematic mapper data-the TM tasseled cap. *IEEE Transactions on Geoscience and Remote Sensing* 22:256–263.
- Jiang, Z., A.R. Huete, J. Chen, Y. Chen, J. Li, G. Yan, and X. Zhang. 2006. Analysis of NDVI and scaled difference vegetation index retrievals of vegetation fraction. *Remote Sensing of Environment* 101:366-378.

APPENDIX B

PAIRWISE CORRELATION PLOTS

Sloped Terrain Suite

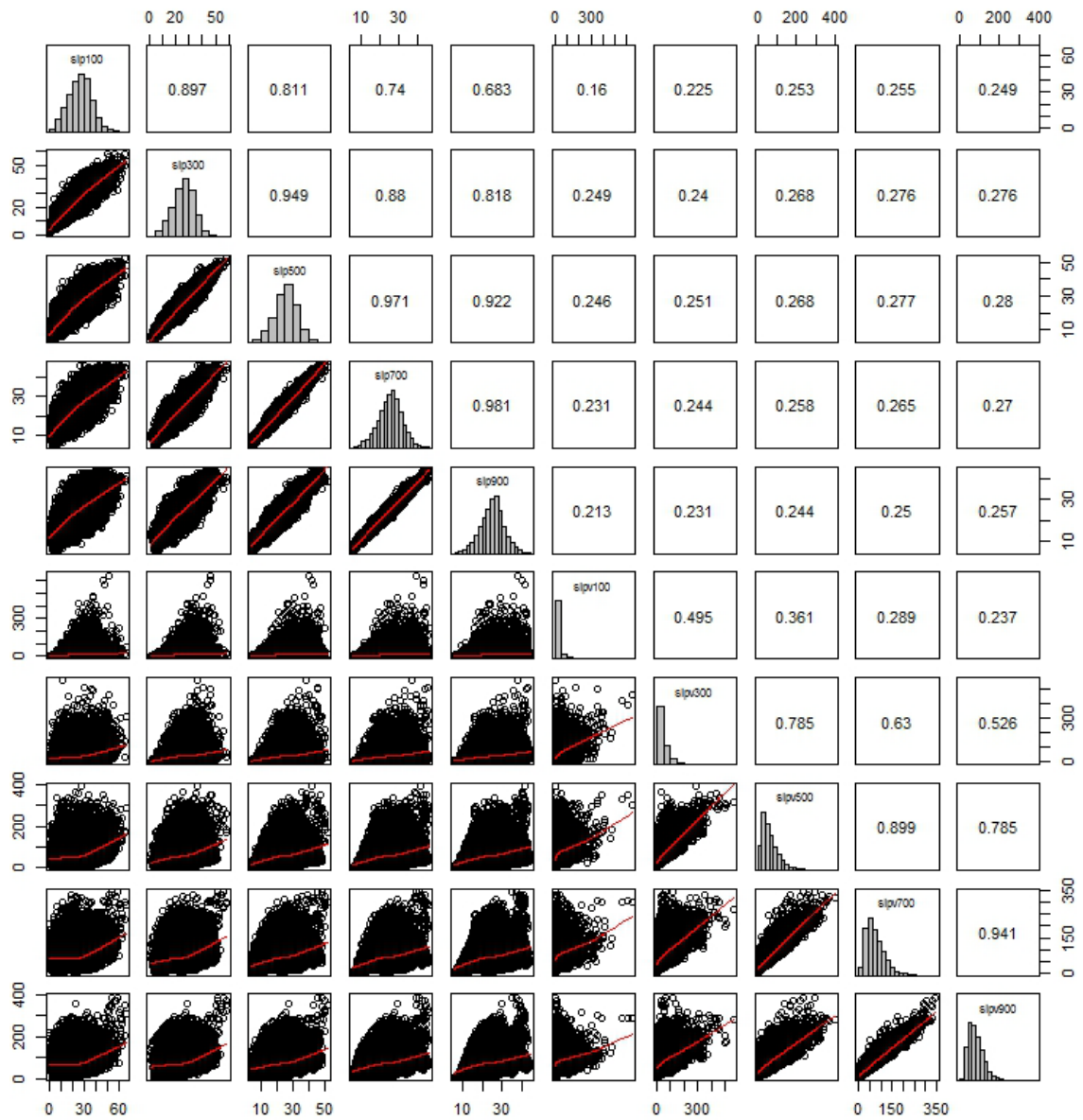


Figure B1. Pairwise plots of Pearson correlation coefficients, histograms, and x-y scatter plots of covariates considered in the sloped terrain model selection suite for modelling mountain goat occupancy probability in the greater Yellowstone area.

Ruggedness Suite

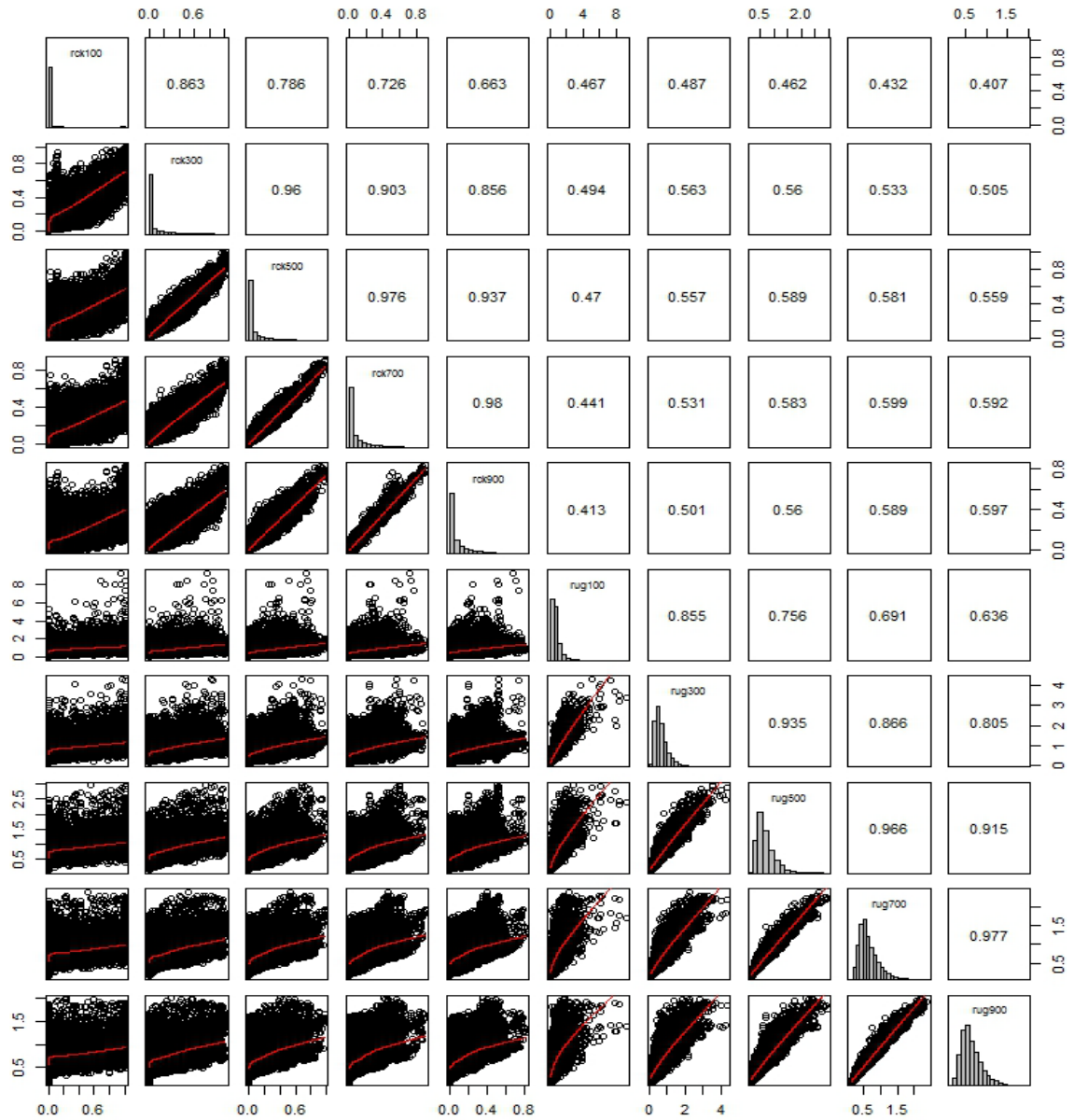


Figure B2. Pairwise plots of Pearson correlation coefficients, histograms, and x-y scatter plots for multiple scales of the RCK and RUG covariates considered in the ruggedness model selection suite for modelling mountain goat occupancy probability in the greater Yellowstone area.

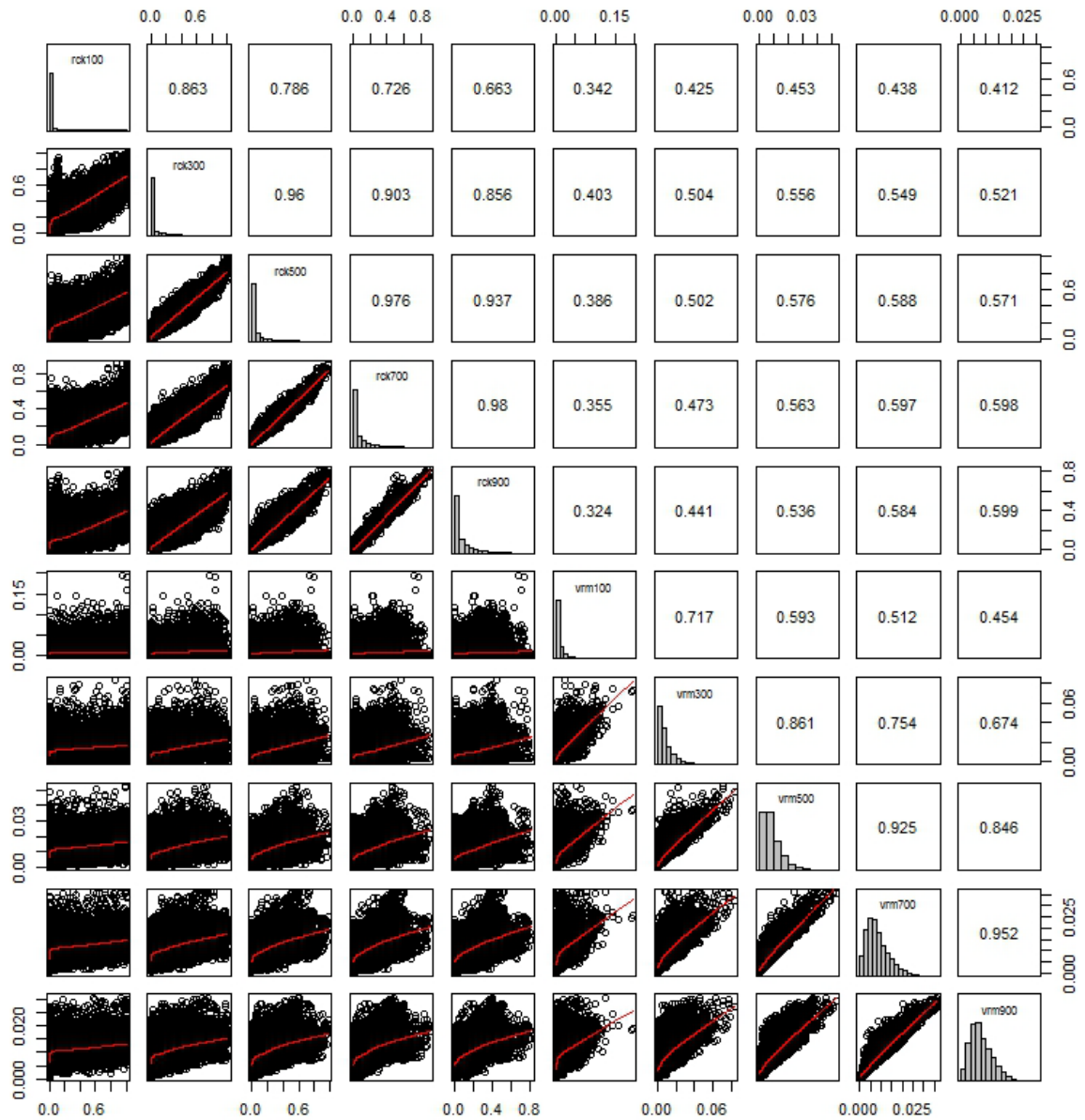


Figure B3. Pairwise plots of Pearson correlation coefficients, histograms, and x-y scatter plots for multiple scales of the RCK and VRM covariates considered in the ruggedness model selection suite for modelling mountain goat occupancy probability in the greater Yellowstone area.

Forage Suite

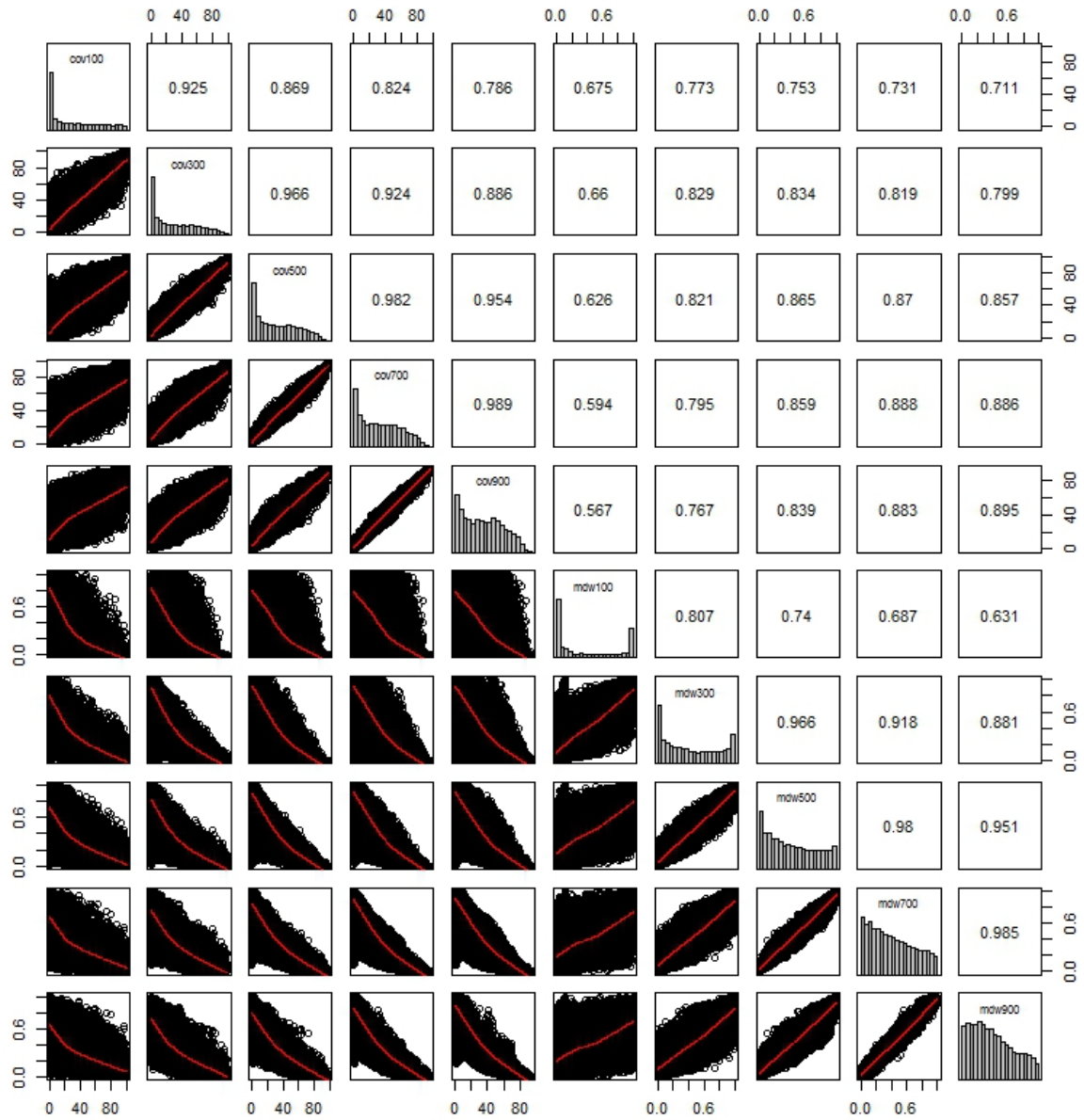


Figure B4. Pairwise plots of Pearson correlation coefficients, histograms, and x-y scatter plots for multiple scales of the COV and MDW covariates considered in the forage model selection suite for modelling mountain goat occupancy probability in the greater Yellowstone area.

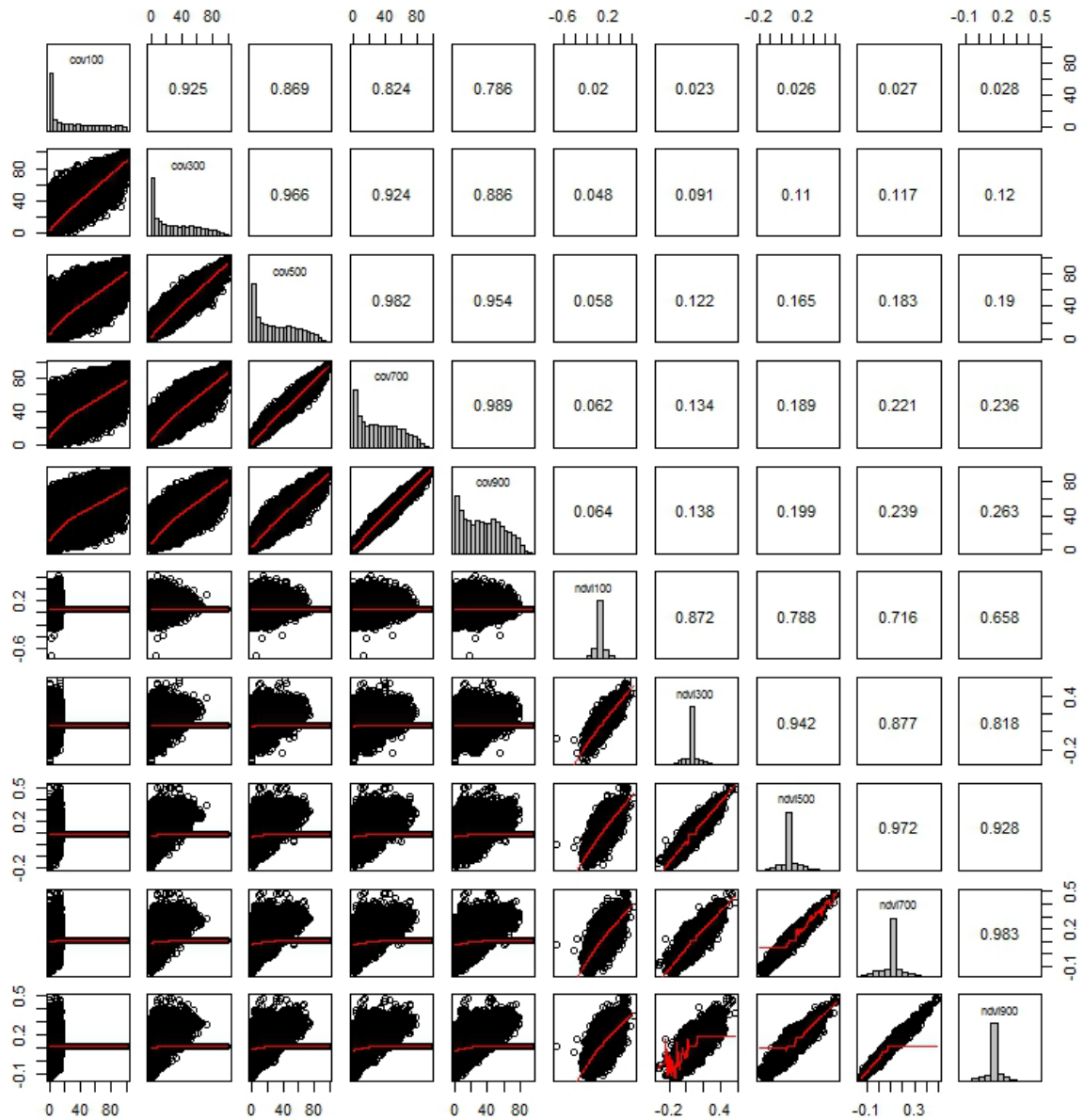


Figure B5. Pairwise plots of Pearson correlation coefficients, histograms, and x-y scatter plots for multiple scales of the COV and NDVI covariates considered in the forage model selection suite for modelling mountain goat occupancy probability in the greater Yellowstone area.

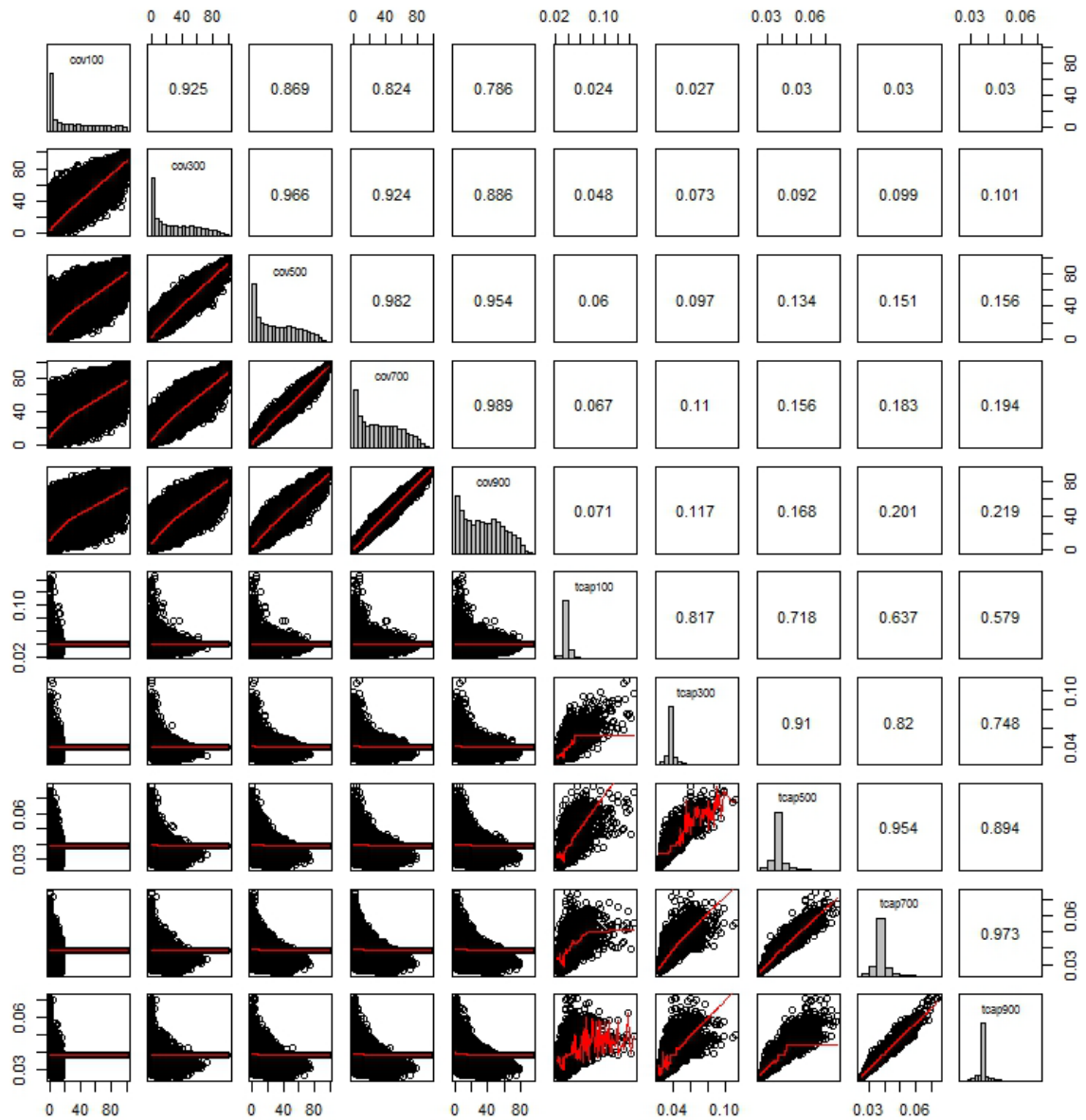


Figure B6. Pairwise plots of Pearson correlation coefficients, histograms, and x-y scatter plots for multiple scales of the COV and TCAP covariates considered in the forage model selection suite for modelling mountain goat occupancy probability in the greater Yellowstone area.

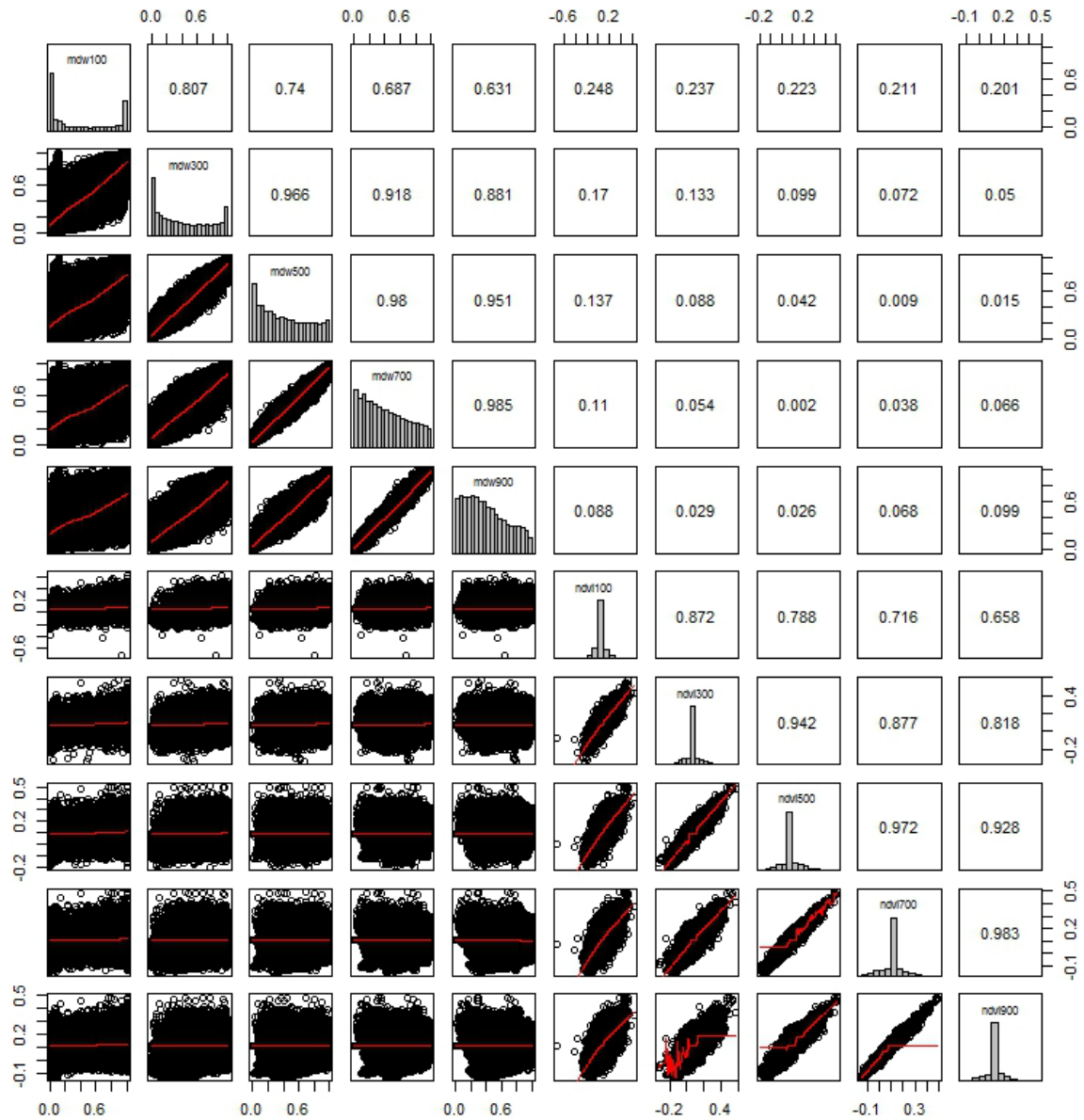


Figure B7. Pairwise plots of Pearson correlation coefficients, histograms, and x-y scatter plots for multiple scales of the MDW and NDVI covariates considered in the forage model selection suite for modelling mountain goat occupancy probability in the greater Yellowstone area.

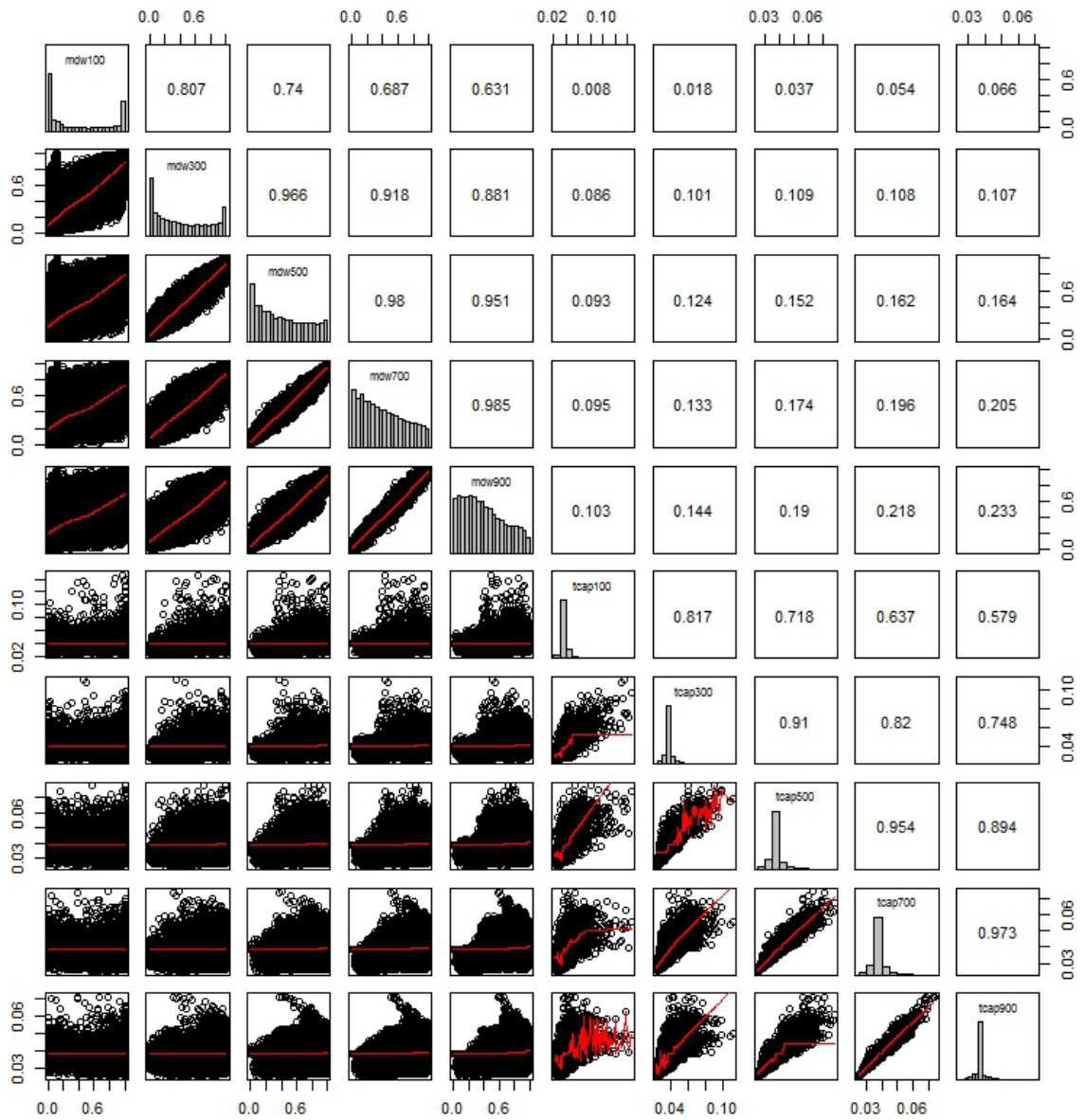


Figure B8. Pairwise plots of Pearson correlation coefficients, histograms, and x-y scatter plots for multiple scales of the MDW and TCAP covariates considered in the forage model selection suite for modelling mountain goat occupancy probability in the greater Yellowstone area.

Combined Suite

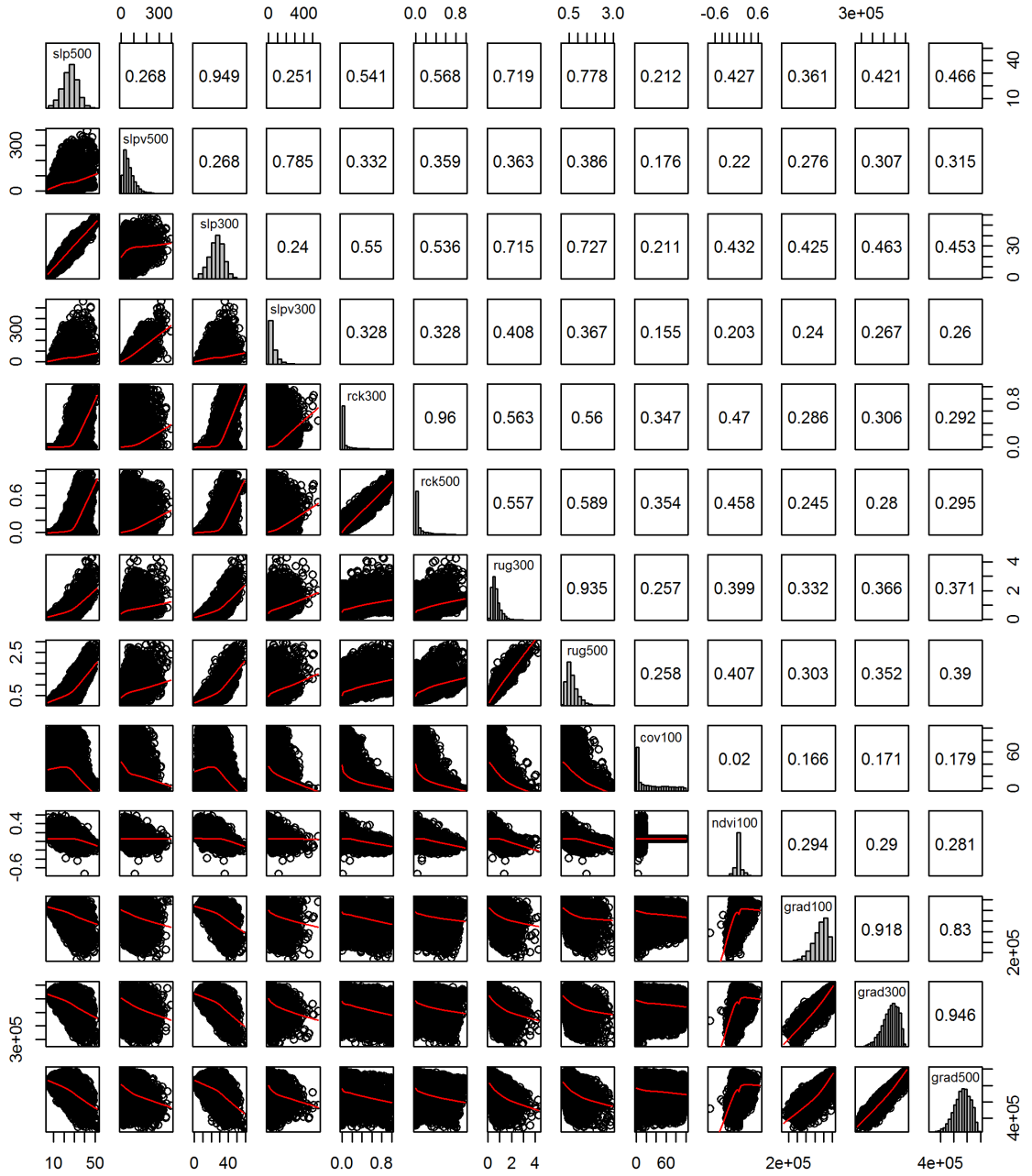


Figure B9. Pairwise plots of Pearson correlation coefficients, histograms, and x-y scatter plots for covariates considered in the combined suites for AIC and QAIC model selection for modelling mountain goat occupancy probability in the greater Yellowstone area.

APPENDIX C

DEVELOPMENT OF THE GYA OCCUPANCY

PREDICTION RASTER

The logistic regression equation of the final model:

$$Y = -4.592 + 1.806(SLP_{500}) - 0.579(SLP_{500}^2) + 0.593(SLPv_{500}^{ps}) - 0.527(COV_{100}) - 0.265(GRAD_{100}) + 0.213(NDVI_{100})$$

was implemented in the GIS by combining 100 m resolution raster layers of mean slope, squared mean slope, slope variance, canopy cover, global radiation, and NDVI using a map calculator function for the extent of the entire GYA. Prior to combining, each raster layer was developed for the appropriate scale identified in the final model (see methods for each raster below) and centered and scaled (or pseudothreshold transformed) as performed in the analysis. Transformations of each raster were as follows:

Table C1. Equations and values used to transform rasters based on centering and scaling or pseudothreshold transforming methods completed prior to modeling.

Raster	Transformation	$\bar{x}$	sd
SLP ₅₀₀	$(x - \bar{x})/sd$	25.795	7.049
SLPv ₅₀₀	$\ln\left(\frac{x}{100}\right) + 0.005$	-	-
COV ₁₀₀	$(x - \bar{x})/sd$	30.794	31.338
GRAD ₁₀₀	$(x - \bar{x})/sd$	562638.3	85005.75
NDVI ₁₀₀	$(x - \bar{x})/sd$	0.0165	0.1579

The inverse logistic transformation:

$$\text{Probability of occupancy} = \exp(Y) / (1 + \exp(Y))$$

was then applied to the linear predictor (Y) to transform the predictors from the logit (log odds) scale to the probability scale. This resulted in a map depicting habitat-suitability of mountain goats for the entire GYA, represented by a continuous surface of the modelled occupancy probabilities at a 100 m resolution. All work was completed in WGS 1984 UTM Zone 12N.

500 m scale mean slope (SLP), squared slope (SLP²), & slope variance (SLPv) rasters. A slope raster was calculated from a 1-arc-second (approximately 30 m resolution) National Elevation Dataset (NED) raster. To simulate previous methods of averaging slope values for each 100x100 m sampling unit (using zonal mean), the 30 m resolution slope raster was resampled to 100 m resolution using cubic interpolation. Mean and standard deviation focal statistics were then calculated for each pixel from a neighborhood of 5x5 cells and outputted to two rasters calculated for the 500 m spatial scale at a 100 m resolution: mean slope (SLP) and slope standard deviation. The slope variance (SLPv)

raster was calculated by squaring the slope standard deviation raster. The squared slope (SLP²) raster was calculated by squaring the center- and scale-transformed (Table B2) SLP raster.

100 m scale global radiation (GRAD) raster. The heat load raster was calculated from the 1-arc-second National Elevation Dataset (NED) raster using the Area Solar Radiation tool in the Solar Radiation toolbox in ArcMap 10.2 (Fu and Rich 2002). This tool calculates insolation (termed “global radiation”) for each pixel measured as watt hours per square meter. To account for effects of latitude due to the broad north-south extent of the GYA, two heat load rasters were calculated for separate extents, the northern and southern half of the GYA, and mosaicked together after processing. Latitude was set at 44.75 for the northern half and 43.25 for the southern half. Other user-defined options were set as follows: 1) sky size = 200; 2) date/time settings = year 2012, days 171-289; 3) day interval = 14; and 4) all else default. The resulting 30 m resolution raster was resampled to a 100 m resolution using cubic interpolation to produce the final raster.

100 m scale forest canopy cover (COV) raster. The canopy cover raster was derived from the 30 m resolution 2001 NLCD (National Land Cover Database) Percent Tree Canopy (Version 1.0) raster dataset by resampling to the 100 m resolution using cubic interpolation.

100 m scale normalized difference vegetation index (NDVI) raster. Multiple Landsat 7 ETM+ SLC-on scenes (30 m resolution) were obtained for July 2000 to cover the extent of the GYA. Due to varying cloud cover conditions across this extent, the same day in July could not be used. Cloud-free scenes used were from July 15, 24, and 31. Thermal bands 3 and 4 from each scene were pre-processed individually in order to convert raw raster values to positive reflectance values before being combined to calculate NDVI and mosaicked with other NDVI scenes. Methods of pre-processing the thermal bands from Landsat scenes were as follows:

- 1) Pixels with values of 0 (those on the peripheries of the scene) were reclassified to “NoData” so that further calculations were not done where data is missing.
- 2) This reclassified raster was converted to radiance values based on the following equation and band-specific bias and gain adjustment values from Chander et al. (2009):

$$radiance_{raster} = (gain * reclass_{raster}) + bias$$

Band	Gain	Bias
3	0.621654	-5.62
4	0.639764	-5.74

- 3) The radiance raster was converted to reflectance values based on the following equation and values from Chander et al. (2009):

$$reflectance_{raster} = \frac{\pi * radiance_{raster} * d^2}{E_{sun} * \sin(\frac{\theta_{SE} * \pi}{180})}$$

where $\pi=3.141592654$, d =earth-sun distance (in astronomical units), E_{sun} =band-specific radiance emitted by the sun, and θ_{SE} =solar elevation angle.

Band	E_{sun}	Date	d^*
3	1533	July 15, 2000	1.01641
4	1039	July 24, 2000	1.01575
		July 31, 2000	1.01497

Values for d are found by locating day of year of the scene and extracting value from table in Chander et al. (2009). Values for θ_{SE} are found in the scene-specific “_MTL.txt” file included with the data. Search the file for a “SUN_ELEVATION” value.

- 4) The reflectance raster was converted to positive reflectances by a conditional statement to change any values less than 0 to 0.

The resulting rasters for bands 3 and 4 for each scene were converted to NDVI values, given by:

$$NDVI = \frac{(Band\ 4 - Band\ 3)}{(Band\ 4 + Band\ 3)}$$

All resulting NDVI rasters were mosaicked together into a new raster covering the extent of the GYA. This NDVI raster was resampled using cubic interpolation to 100 m grid cells. Following methods to mask out the effect of canopy cover on NDVI that was performed prior to occupancy analysis, NDVI grid cells where forest canopy cover (from 100 m resolution, 100 m spatial scale COV raster) was greater than or equal to 15% were converted to 0.0609.

Reference:

Chander, G., B. L. Markham, and D. L. Helder, 2009. Summary of current radiometric calibration coefficients for Landsat MSS, TM, ETM+, and EO-1 ALI sensors. *Remote Sensing of Environment*, 113, 893-903.

APPENDIX D

MODEL VALIDATION PLOTS

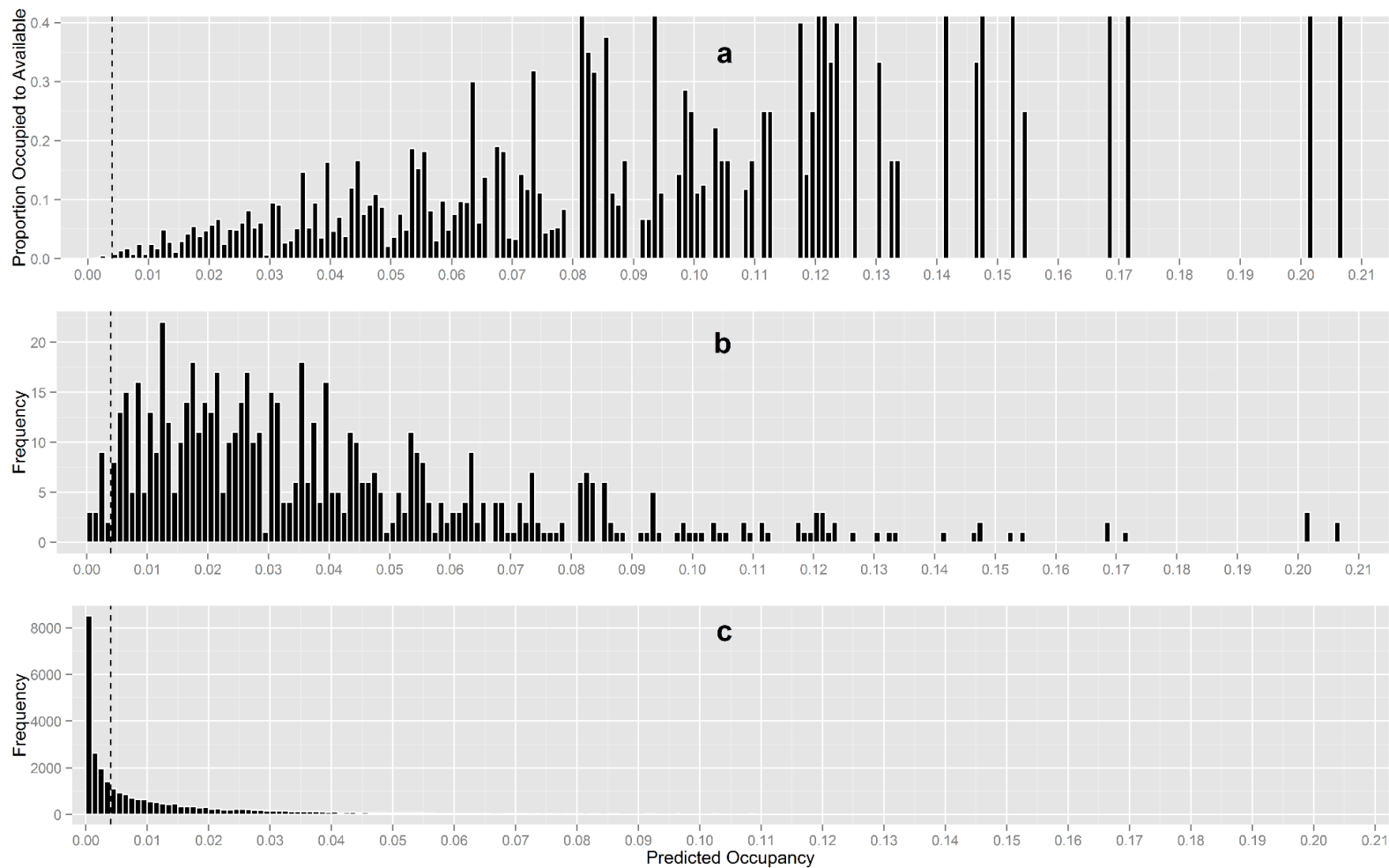


Figure D1. Estimated occupancy probability values for (a) the proportion of sampling units occupied by mountain goats to available, and the frequency of estimated occupancy probability values for occupied (b) and available (c) sampling units for viewsheds surveyed in two study areas of the northern greater Yellowstone. The dashed vertical line indicates the selected occupancy probability cutoff value (0.004) to represent suitable mountain goat habitat.

APPENDIX E

ADDITIONAL HABITAT SUITABILITY MAPS

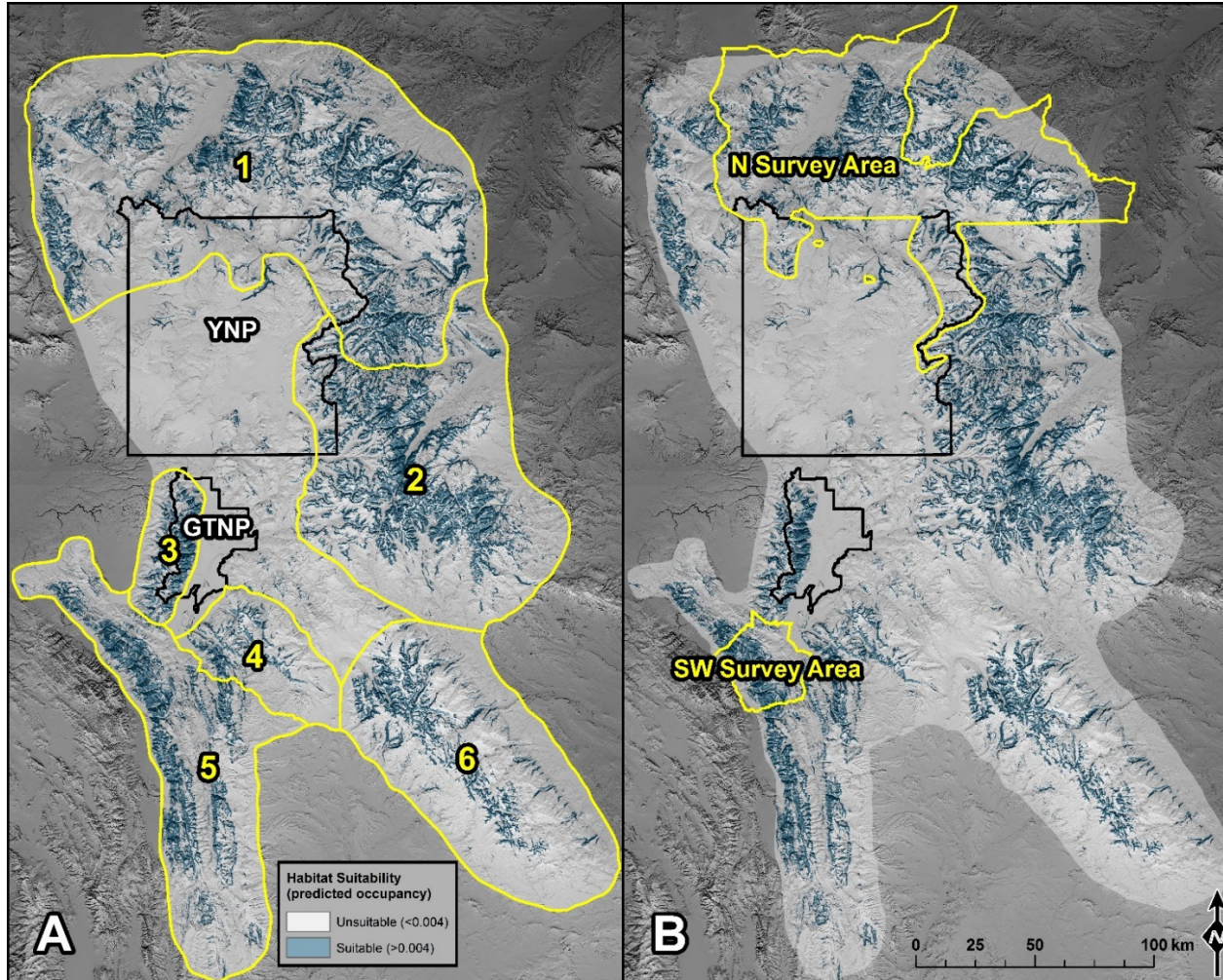


Figure E1. (A) Regions of management interest (numbered for reference with Table 4) where areas of predicted suitable habitat and potential abundances of mountain goats were estimated. (B) Survey areas (performed by wildlife and land management agency personnel; *unpublished data*) used to calculate density and estimate potential abundances of mountain goats.

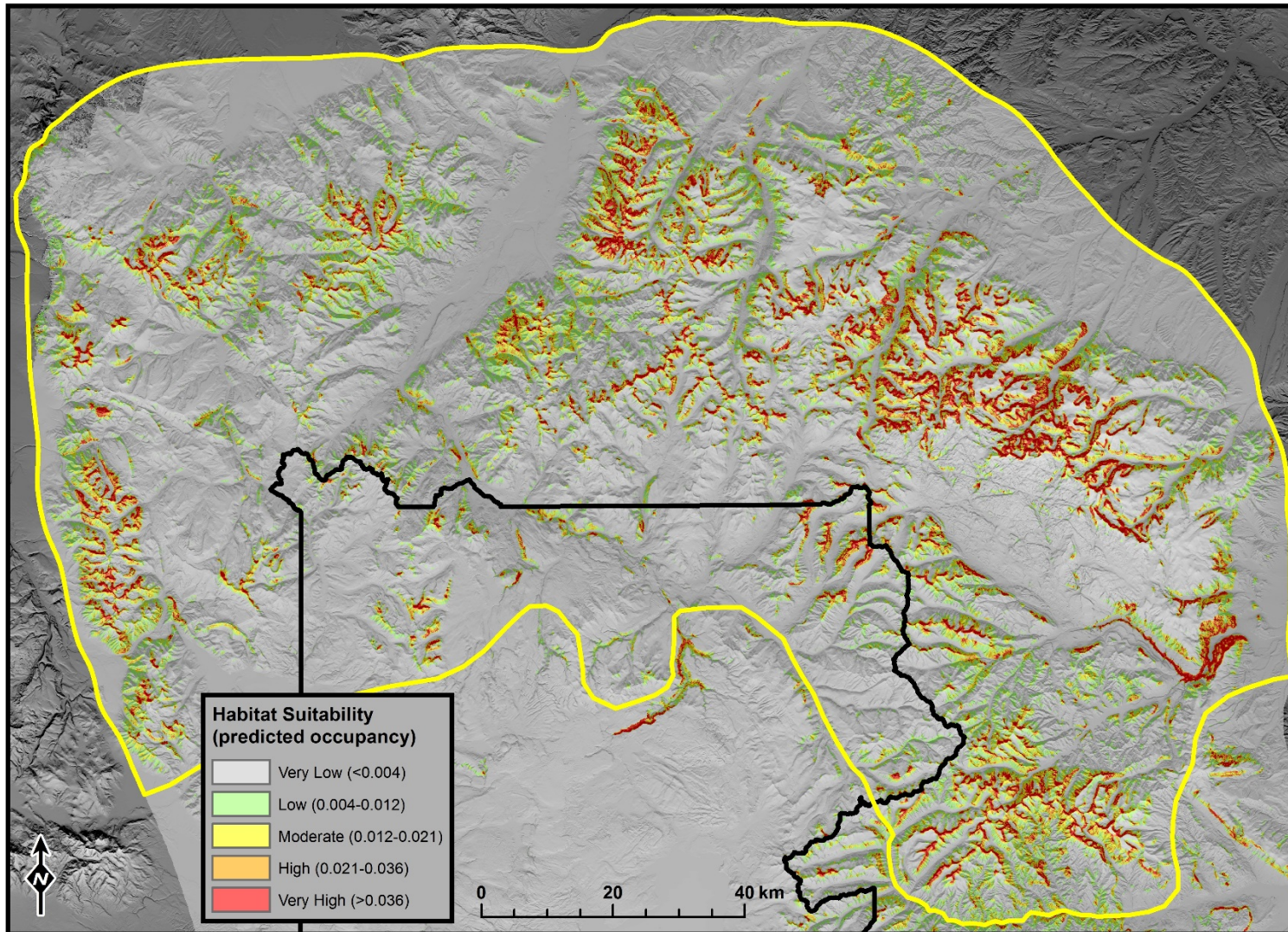


Figure E2. Suitable habitat classifications of predicted occupancy probabilities for mountain goats in the northern GYA (Region 1 in Table 4 and Figure E1).

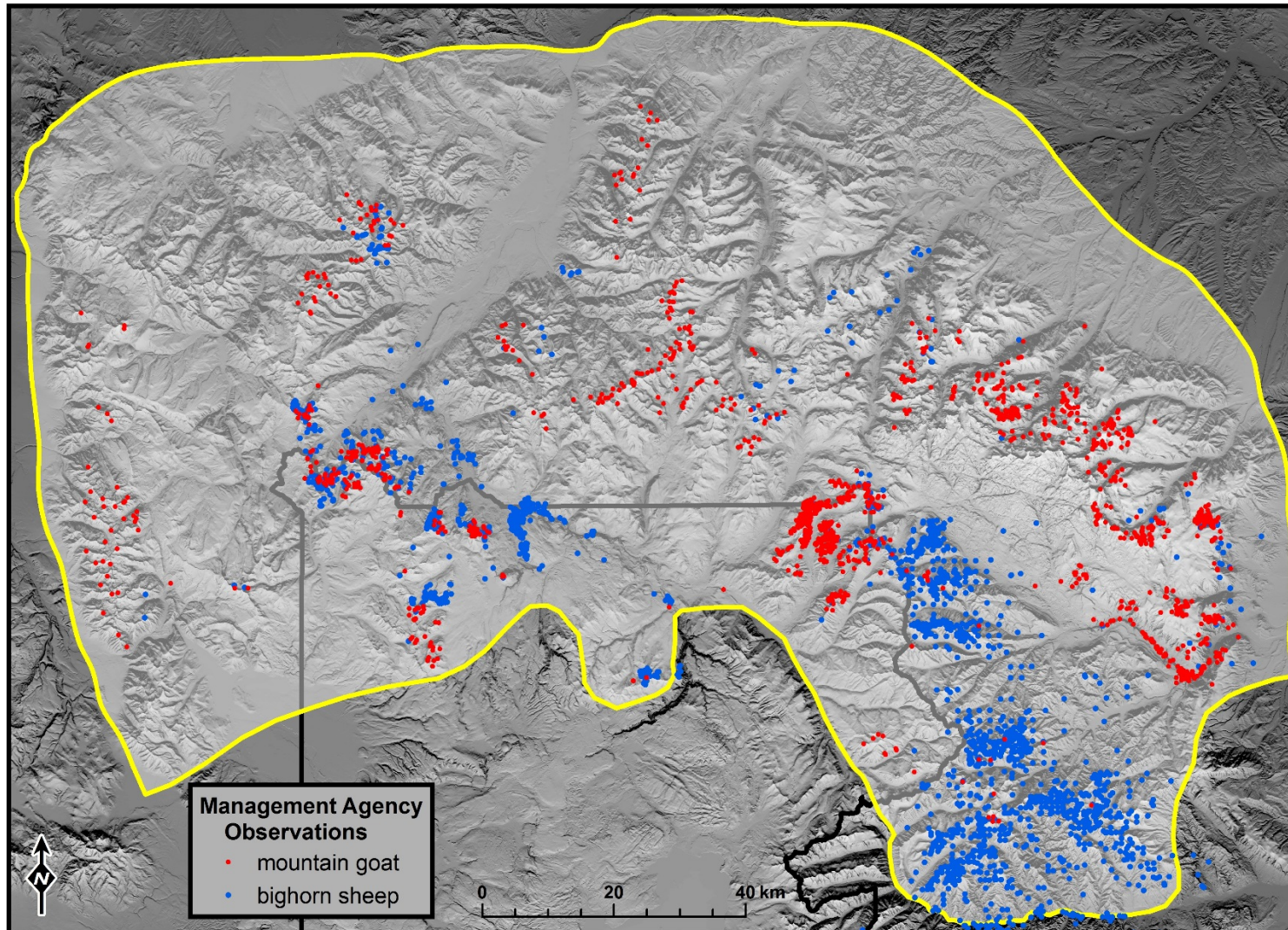


Figure E3. Observations of mountain goats and bighorn sheep obtained from summer surveys performed by wildlife and land management agency personnel from 1968-2012 (*unpublished data*) for the northern GYA (Region 1 in Table 4 and Figure E1).

APPENDIX F

MODEL SELECTION RESULTS

Table F1. Model rank and weight (w_{ti}) results of AIC selection within model suites for obtaining a complex model to estimate overdispersion ($\hat{c}$) for understanding mountain goat occupancy probability of sampling units in the greater Yellowstone area. The top models within 5 Δ AIC units of the overall top-ranked model within each suite are presented. Detection probability was parameterized using the 100 m scale pseudothreshold form of COV. Covariates on occupancy (ψ) probability are presented, with subscript indicating spatial scale and superscript indicating functional form (2=quadratic, ps=pseudothreshold, [none]=linear) of covariate. Model variables are defined in “Model Development.” K = no. of parameters. Negative log likelihood for the top model from the combined suite was 1932.87.

Model	K	AIC	Δ AIC	w_{ti}
<i>Sloped Terrain</i>				
$SLP_{500} + SLP_{500}^2 + SLP_{V500}^{ps}$	6	5960.35	0.00	0.78
$SLP_{500} + SLP_{500}^2 + SLP_{V500} + SLP_{V500}^2$	7	5963.78	3.43	0.14
$SLP_{300} + SLP_{300}^2 + SLP_{V300}^{ps}$	6	5964.99	4.64	0.08
<i>Ruggedness</i>				
$RCK_{300} + RCK_{300}^2 + RUG_{300} + RUG_{300}^2$	7	6142.10	0.00	0.92
$RCK_{300}^{ps} + RUG_{300}^{ps}$	5	6147.14	5.04	0.07
<i>Forage</i>				
$COV_{100} + NDVI_{100}$	5	6377.56	0.00	1.00
<i>Heat load</i>				
$GRAD_{100}$	4	6327.58	0.00	0.65
$GRAD_{100} + GRAD_{100}^2$	5	6329.15	1.58	0.30
<i>Combined</i>				
$SLP_{500} + SLP_{500}^2 + SLP_{V500}^{ps} + RCK_{300} + RCK_{300}^2 + COV_{100} + NDVI_{100} + GRAD_{100}$	11	5887.73	0.00	0.42
$SLP_{500} + SLP_{500}^2 + SLP_{V500}^{ps} + RCK_{300} + RCK_{300}^2 + COV_{100} + NDVI_{100} + GRAD_{100} + GRAD_{100}^2$	12	5888.96	1.23	0.23
$SLP_{500} + SLP_{500}^2 + SLP_{V500}^{ps} + COV_{100} + NDVI_{100} + GRAD_{100}$	9	5890.55	2.82	0.10
$SLP_{500} + SLP_{500}^2 + SLP_{V500} + SLP_{V500}^2 + RCK_{300} + RCK_{300}^2 + COV_{100} + NDVI_{100} + GRAD_{100}$	12	5891.45	3.72	0.07
$SLP_{500} + SLP_{500}^2 + SLP_{V500}^{ps} + COV_{100} + NDVI_{100} + GRAD_{100} + GRAD_{100}^2$	10	5891.97	4.23	0.05
$SLP_{500} + SLP_{500}^2 + SLP_{V500}^{ps} + RCK_{300}^{ps} + COV_{100} + NDVI_{100} + GRAD_{100}$	10	5892.41	4.68	0.04

Table F2. Estimated coefficients and 95% confidence intervals for the best-supported, competitive models from combinations of top models from four model suites (sloped terrain, ruggedness, forage, and heat load) for QAIC model selection, examining predicted effects of covariates on mountain goat occupancy (ψ) and detection (p) probabilities of sampling units in the greater Yellowstone area. Covariate subscripts indicate scale of covariate and superscripts indicate functional form (2=quadratic, ps=pseudothreshold, [none]=linear). Model variables defined in “Model Development.” ID number for reference to results in Table 3.

Model ID	1	2	3	4
Ψ (Intercept)	-4.59 (-4.96, -4.22)	-2.19 (-3.54, -0.84)	-4.95 (-5.30, -4.59)	-2.51 (-3.90, -1.12)
Ψ (SLP ₅₀₀)	1.81 (1.25, 2.36)	1.82 (1.27, 2.37)	1.83 (1.28, 2.38)	1.84 (1.29, 2.40)
Ψ (SLP ₅₀₀ ²)	-0.58 (-0.84, -0.32)	-0.58 (-0.84, -0.32)	-0.59 (-0.85, -0.33)	-0.59 (-0.85, -0.34)
Ψ (SLP _{V500} ^{ps})	0.59 (0.30, 0.89)	0.60 (0.30, 0.89)		
Ψ (SLP _{V500})			0.28 (0.14, 0.42)	0.28 (0.14, 0.42)
Ψ (COV ₁₀₀)	-0.53 (-0.84, -0.22)	-0.51 (-0.82, -0.21)	-0.55 (-0.86, -0.24)	-0.53 (-0.84, -0.23)
Ψ (NDVI ₁₀₀)	0.21 (0.04, 0.39)	0.21 (0.04, 0.39)	0.21 (0.03, 0.38)	0.20 (0.03, 0.38)
Ψ (GRAD ₁₀₀)	-0.27 (-0.42, -0.11)		-0.27 (-0.42, -0.12)	
Ψ (GRAD ₁₀₀ ^{ps})		-1.39 (-2.19, -0.59)		-1.41 (-2.21, -0.61)
p (Intercept)	0.09 (-0.55, 0.73)	0.10 (-0.55, 0.74)	0.09 (-0.56, 0.73)	0.09 (-0.55, 0.74)
p (COV ₁₀₀ ^{ps})	0.071 (-0.12, 0.26)	0.074 (-0.12, 0.27)	0.072 (-0.12, 0.26)	0.075 (-0.12, 0.27)

Table F3. Post hoc model rank and weight (w_{ti}) results for QAIC model selection of covariates for understanding detection probability of mountain goats for sampling units in the greater Yellowstone area. Occupancy probability (ψ) was parameterized in each model based on the inferential model from the combined QAIC model suite results. Covariates on detection probability (p) were measured at the 100 m spatial scale and are included in parentheses, with superscript indicating functional form (ps=pseudothreshold, [none]=linear). Model variables are defined in “Model Development.” K = no. of parameters. Negative log likelihood for the top model was -848.90.

Model	K	QAIC	Δ QAIC	w_{ti}
Intercept-only	9	1715.80	0.00	0.23
COV	10	1717.01	1.21	0.13
COV ^{ps}	10	1717.27	1.48	0.11
SLP _v	10	1717.67	1.87	0.09
RUG	10	1717.71	1.92	0.09
VRM	10	1717.79	1.99	0.09
COV + SLP _v	11	1718.85	3.06	0.05
COV + RUG	11	1718.88	3.08	0.05
COV + VRM	11	1719.00	3.20	0.05
COV ^{ps} + SLP _v	11	1719.17	3.37	0.04
COV ^{ps} + RUG	11	1719.22	3.42	0.04
COV ^{ps} + VRM	11	1719.27	3.48	0.04

APPENDIX G

DATA DICTIONARY

Source Data

Dataset:	National Elevation Dataset (NED)
Source:	The National Map Viewer, U.S. Geologic Society (USGS) (http://viewer.nationalmap.gov/viewer)
Resolution:	30 m (1 arcsec)
Description:	Raster elevation data (meters). ArcGrid format. Coverage extent for the entire GYA. Values range from 1219 to 3443.
Published:	2011
Coordinate System:	GCS North American Datum of 1983
Application:	Multiple chunks mosaicked for development of rasters related to covariates used in the occupancy analysis, including: slope, distance to escape terrain, vector ruggedness measure, and global radiation (see Derived Data).
Dataset:	Percent Tree Canopy Version 1.0 (NLCD2001)
Source:	Multi-Resolution Land Characteristics Consortium (MRLC) (http://www.mrlc.gov/nlcd01_data.php)
Resolution:	30 m
Description:	Raster of percent forest canopy cover. Coverage extent for the entire GYA. Values range from 0 to 100
Published:	2001
Coordinate System:	Albers Conical Equal Area
Application:	Development of multi-scale covariates, including percent canopy cover (COV) and masking of normalized difference vegetation index (NDVI) and tasseled cap wetness index (TCAP; see Appendix A), and development of 100 m spatial scale COV raster (100 m resolution) for extrapolating habitat suitability across the GYA (see Appendix C).
Dataset:	MTIDWY_GAP
Source:	Kelly Proffitt (Montana Fish Wildlife & Parks)
Resolution:	30 m
Description:	Land cover dataset adapted from the Montana Land Cover Framework 2010 (see metadata on the Montana Spatial Data Infrastructure website; http://geoinfo.msl.mt.gov/home/msdi/land_use_land_cover.aspx)
Published:	Unpublished
Coordinate system:	NAD 83 State Plane Montana FIPS 2500
Application:	Development of multi-scale covariates, including proportion rock (RCK) and proportion meadow (MDW; see Appendix A).
Dataset:	NDVI_clip.tif
Source:	Mike Zambon (Flat Earth, Inc.)
Resolution:	30 m
Description:	Raster of calculated normalized difference vegetation indices processed from a Landsat 7 ETM+ July 2000 scene. Values range from -1.0 to 1.0.
Published:	Unpublished
Coordinate system:	WGS 1984 UTM Zone 12N
Application:	Development of multi-scale NDVI covariates (see Appendix A).

Dataset:	TCAP_wet_b.tif
Source:	Mike Zambon (Flat Earth, Inc.)
Resolution:	30 m
Description:	Raster of calculated tasseled cap wetness values processed from a Landsat 7 ETM+ July 2000 scene. Values range from 0.0 to 0.26
Published:	Unpublished
Coordinate system:	WGS 1984 UTM Zone 12N
Application:	Development of multi-scale TCAP covariates (see Appendix A).
Dataset:	sri_surr.tif
Source:	Mike Zambon (Flat Earth, Inc.)
Resolution:	30 m
Description:	Raster of solar radiation index values (Ciarniello et al. 2005). Values range from -1.0 to 1.0
Published:	Unpublished
Coordinate system:	WGS 1984 UTM Zone 12N
Application:	Development of multi-scale SRI covariates (see Appendix A).
Dataset:	ruggedness_b.tif
Source:	Mike Zambon (Flat Earth, Inc.)
Resolution:	30 m
Description:	Raster of terrain ruggedness index values (Poole et al. 2009). Values range from 0.0 to 19.2
Published:	Unpublished
Coordinate system:	WGS 1984 UTM Zone 12N
Application:	Development of multi-scale RUG covariates (see Appendix A).
Dataset:	Landsat 7 ETM+ SLC-on scenes
Source:	EarthExplorer, U. S. Geologic Survey (USGS) (http://earthexplorer.usgs.gov/)
Resolution:	30 m
Description:	Thematic mapper (bands 3 and 4) raster dataset scenes for July 2000 (15 th , 24 th , and 31 st).
Published:	Variable (metadata review date: 2006)
Coordinate system:	WGS 1984 UTM Zone 12N
Application:	Multiple, cloud-free thematic mapper raster scenes processed and mosaicked for development of 100 m spatial scale normalized difference vegetation index (NDVI) raster (100 m resolution) for extrapolating habitat suitability across the GYA (see Appendix C).

Derived Data

Dataset: Master Observations Point Database
 Resolution: 100 m
 Description: Vector database containing detection and non-detection point data of mountain goats and bighorn sheep collected from 2011-2013 within surveyed 100 m grid sampling units. Contains a total of 88,510 observations that were restructured (Appendix H) so that each sampling unit per survey contained a detection (0 or 1) for each of the observers (total of 53,098 sampling units). Combined with covariate values for each sampling unit (obtained by zonal statistics) and used for occupancy analysis.

Coordinate system: WGS 1984 UTM Zone 12N

Attributes of Master Observations table:

Field	Description
date	date of observation (d/m/yyyy)
time	time of observation (2400)
species	“NONE” (non-detection) or “GOAT” or “SHEEP” (detection)
id	unique ID for each group observed
cell_id	unique ID for each grid cell (4376.3 = cell 4376 in region 3)
region	region within study areas
survey_id	survey ID unique to specific survey event + observer ID (219.3 = survey #219, observer 3)
observer	first name of observer
total_num	total number of animals in the group
num_mat_ma	number of mature males in group
num_yng_ma	number of young males in group
num_female	number of adult females in group
num_yearling	number of yearlings in group
num_yoy	number of young of year in group
num_unknown	number of unknown animals in group
behavior	overall behavior of group
point_x	UTM x coordinate of observation
point_y	UTM y coordinate of observation
event	opportunistic observations indicated by “1”, otherwise “0”

Dataset: 100 x 100 m grids (separate shapefile for each region)
 Description: Polygon 100 m grids for different regions across the study areas. Developed for field data collection of response variables (detection/non-detection of mountain ungulates within each sampling unit) and for development of covariates (i.e., calculating covariate raster data for each sampling unit with zonal and neighborhood statistics)

Coordinate system: WGS 1984 UTM Zone 12N

Attributes of 100 m grid tables:

Field	Description
cell_id	Unique ID for each grid (sample) unit
xmin	UTM x coordinate of left border

xmax	UTM x coordinate of right border
ymin	UTM y coordinate of bottom border
ymax	UTM y coordinate of top border

Dataset:	Slope
Resolution:	30 m & 100 m
Description:	Rasters of degree slope values for the coverage extent of the GYA. Developed from 30 m (1 arcsec) National Elevation Dataset. <u>30 m raster</u> : values range from 0.0 to 81.6. Used to develop multi-scale slope (SLP) and slope variance (SLPv) covariates (Appendix A) and 100 m resolution slope rasters for extrapolating suitable habitat across the GYA, including slope, squared slope, and slope variance (Appendix C). <u>100 m raster</u> : values range from 0 to 79.6. Represents the 500 m spatial scale slope variable used in extrapolating suitable habitat across the GYA.
Coordinate system:	WGS 1984 UTM Zone 12N
Dataset:	Squared slope
Resolution:	100 m
Description:	Raster of squared slope values for the coverage extent of the GYA. Developed from 30 m slope raster (Appendix C). Values range from 0 to 6336.16. Represents the 500 m spatial scale slope variance variable used in extrapolating suitable habitat across the GYA.
Coordinate system:	WGS 1984 UTM Zone 12N
Dataset:	Slope variance
Resolution:	100 m
Description:	Raster of variance in slope values for the coverage extent of the GYA. Developed from 30 m slope raster (Appendix C). Values range from 0 to 882. Represents the 500 m spatial scale slope variance variable used in extrapolating suitable habitat across the GYA.
Coordinate system:	WGS 1984 UTM Zone 12N
Dataset:	Distance to escape terrain ($\geq 25^\circ$, 33° , 40° , 45° , and 50°)
Resolution:	30 m
Description:	Raster of distance (meters) to specified slope threshold values (i.e., escape terrain). Developed from the 30 m slope raster and used as distance to escape terrain (DET) covariates (Appendix A).
Coordinate system:	WGS 1984 UTM Zone 12N
Dataset:	Vector ruggedness measure
Resolution:	30 m
Description:	Raster of (unit-less) values capturing variability in slope. Values range from 0.0 to 0.42. Developed from the 30 m (1 arcsec) National Elevation Dataset. Used to develop multi-scale vector ruggedness measure (RUG) covariates (Appendix A).
Coordinate system:	WGS 1984 UTM Zone 12N

Dataset:	Global radiation
Resolution:	30 m & 100 m
Description:	Raster of watts/m² values capturing heat load. Developed from the 30 m (1 arcsec) National Elevation Dataset. <u>30 m raster</u>: values range from 38331.8 to 828400. Used to develop multi-scale global radiation (GRAD) covariates (Appendix A) and 100 m resolution global radiation raster for extrapolating suitable habitat across the GYA (Appendix C). <u>100 m raster</u>: values range from 66356.4 to 59788.9. Represents the 100 m spatial scale variable used in extrapolating suitable habitat across the GYA.
Coordinate system:	WGS 1984 UTM Zone 12N
Dataset:	Canopy cover
Resolution:	100 m
Description:	Raster of percent forest canopy cover values for the coverage extent of the GYA. Values range from 0 to 100. Developed from the 30 m NLCD2001 Percent Canopy Cover dataset (see Source Data and Appendix C). Represents the 100 m spatial scale canopy cover variable used in extrapolating suitable habitat across the GYA.
Coordinate System:	WGS 1984 UTM Zone 12N
Dataset:	NDVI
Resolution:	100 m
Description:	Raster of normalized difference vegetation index values for the coverage extent of the GYA. Values range from -1 to 0.9. Developed from the 30 m Landsat dataset (see Source Data and Appendix C). Represents the 100 m spatial scale NDVI variable used in extrapolating suitable habitat across the GYA.
Coordinate system:	WGS 1984 UTM Zone 12N
Dataset:	GYA habitat suitability
Resolution:	100 m
Description:	Raster of suitability values of mountain goat habitat for the coverage extent of the GYA. Developed from the 100 m resolution slope, slope variance, canopy cover, NDVI, and global radiation rasters (Appendix C). Values range from 0 to 0.42.
Coordinate system:	WGS 1984 UTM Zone 12N

APPENDIX H

FORMATTING RESPONSE VARIABLE

FOR DETECTION HISTORIES

```

#=====
# Program: Occupanator.R (r code)
# Author: Michael Ebinger
# Created on: 11/01/2013
# Last Modified on: 5/12/2014
#-----
# Note: The following code overcame a monumental obstacle in formatting the immense amount of detection and
# non-detection observations (Master Observation Database – see Appendix G, “Derived Data” – collected on
# Juniper Mesa Geo tablets and ArcPad) for each sampling unit in a manner suitable for analysis in program
# “unmarked” for R. This code also created sequential numbering for groups observed moving across multiple grid
# sampling units (path id coding below).
#=====

rm(list = ls())
library(matlab)
library(tcltk)
options(digits=13)

#-----
# READ IN DATA
# Read in the initial occupancy dataset (converted to CSV)
#-----

occ_dat <- read.delim('C:\\filelocation\\datafile.csv', head=TRUE, sep=",", na.strings = "", stringsAsFactors=FALSE, as.is=T)

occ_dat <- subset(occ_dat, subset = event == 0); # remove the opportunistic sightings (where “event” = 0)

occ_dat$grid_id <- occ_dat$Sid_1 + occ_dat$region/10 # create a unique grid id variable

uni_grid_id <- unique(occ_dat$grid_id)
uni_obsr <- unique(occ_dat$observer)
occ_dat$pnt_xy <- floor(occ_dat$point_x) + (floor(occ_dat$point_y)/10000000)

# create a numeric observer id field called ‘observer2’
occ_dat$observer2 = NA
for(i in 1:length(uni_obsr)){
  rep_ix <- occ_dat$observer==uni_obsr[i]
  occ_dat$observer2[rep_ix] = i
}

#-----
# START: PATH ID CODING
#-----

occ_dat$temp_00 <- occ_dat$date2 + (occ_dat$survey_id/1000);
subby = which(occ_dat$Sid > 0);
dat2=occ_dat[subby,];
uni_dat2 = unique(dat2$temp_00);

for(i in 1:length(uni_dat2)){
  subby2 = which(dat2$temp_00 == uni_dat2[i]); # loop through the unique date-surveys
  uni_grp = unique(dat2$Sid[subby2]); # subset the dataset to the unique date-survey[i]
  # find the number of unique groups in the subset
  for(j in 1:length(uni_grp)){
    subby3 = which(dat2$Sid[subby2]==uni_grp[j]); # loop through the unique groups nested in the unique date-survey[i]
    # subset the dataset to the unique groups
    srt = sort(dat2$time2[subby2[subby3]], index.return = TRUE); # sort the data by time2 field
    dat2$track_id[subby2[subby3[srt$ix]]] = seq(1,length(srt$ix),1); # insert the correct path order sequence
  }
}
occ_dat$track_id = 0 # create a new field
occ_dat$track_id[subby] = dat2$track_id # update new field with track id's

occ_dat <- occ_dat[,-28] # drop the temp field

#-----
# END: PATH ID CODING
#-----
#-----

```

```

# START: basic front end coding to get started
#-----

occ_dat$survey_id2 = occ_dat$survey_id*10      # turn survey_id into an integer incorporating observer id
occ_dat$grid_id2 = occ_dat$grid_id*10        # turn grid into a unique integer
occ_dat$grid_date = occ_dat$grid_id2 + occ_dat$date2/100000 # make grid and date combination

uni_grid_id <- unique(occ_dat$grid_id)
uni_grid_date <- unique(occ_dat$grid_date)
uni_obser <- unique(occ_dat$observer)
uni_spp <- unique(occ_dat$species)
tag <- c(2,0,1)
occ_dat$species2 = NA
#-----
# END: basic front end coding to get started
#-----
# START: species coding
#-----
for(i in 1:length(uni_spp)){
  rep_ix <- occ_dat$species==uni_spp[i]
  occ_dat$species2[rep_ix] = tag[i]
}
#-----
# END: species coding
#-----
# START: create new fields for the data
#-----
new_grid <- data.frame(numeric())
new_sid <- data.frame(cbind(numeric(),numeric()))
new_date <- data.frame(character(0),character(0),stringsAsFactors=FALSE)
new_time <- data.frame(character(0),character(0),stringsAsFactors=FALSE)
new_ehn <- data.frame(cbind(numeric(),numeric()))
new_grp <- data.frame(cbind(numeric(),numeric()))
new_ehc <- data.frame(cbind(character(),character()),stringsAsFactors=FALSE)
new_ohn <- data.frame(cbind(numeric(),numeric()))
new_ohc <- data.frame(cbind(character(),character()),stringsAsFactors=FALSE)
new_vis <- data.frame(cbind(numeric(),numeric()))
new_ohb <- data.frame(cbind(character(),character()),stringsAsFactors=FALSE)
new_trk <- data.frame(cbind(numeric(),numeric()))

occ_raw = occ_dat # keep a raw file untouched (just in case)

#-----
# END: create new fields
#-----
#-----
#!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!
#!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!
# START: SPECIES SPECIFIC PROCESSING
#-----
# MUST SELECT GOAT OR BIGHORN FOR ANALYSIS IN THE
# TWO BLOCKS OF CODE BELOW (highlight and run only one)
#-----
#!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!
#!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!
#-----

# SUBSET DATA FOR BIGHORN ANALYSIS:
sub_both = which(occ_dat$species=="GOAT")
occ_dat$species[sub_both] = "NONE" # from bighorn perspective, goat obs are "NONE" so recode them
occ_dat$species2[sub_both] = 2
occ_dat$behavior[sub_both] = NA
occ_dat$track_id[sub_both] = NA

# SUBSET DATA FOR SHEEP ANALYSIS:

```

```

sub_both = which(occ_dat$species=="SHEEP")
occ_dat$species[sub_both] = "NONE"      # from goat perspective, bighorn obs are "NONE" so recode them
occ_dat$species2[sub_both] = 1
occ_dat$behavior[sub_both] = NA
occ_dat$track_id[sub_both] = NA

#####
#####
#####

total <- length(uni_grid_date)
pb <- tkProgressBar(title = "progress bar", min = 0,
                    max = total, width = 300)

tracker <- 1;
for(i in 1:length(uni_grid_date)){
  subset_ix <- which(occ_dat$grid_date==uni_grid_date[i])
  uni_check <- unique(occ_dat$observer[subset_ix])
  uni_surv <- unique(occ_dat$survey_id[subset_ix])

  #-----
  # BEGIN: SUBROUTINE
  # sub routine to remove triple observer cells where
  # alternative survey_id's are looking into grid.
  #-----
  temp_v1 <- as.numeric(names(which.max(table(fix(uni_surv)))))
  subset_ix <- subset_ix[which(fix(occ_dat$survey_id[subset_ix]) == temp_v1)]
  uni_check <- unique(occ_dat$observer[subset_ix])
  uni_surv <- unique(occ_dat$survey_id[subset_ix])
  #-----
  # END: SUBROUTINE
  #-----
  #-----
  # BEGIN: SUBROUTINE
  # sub routine to remove the extra "none" cell from grid
  # sampling events where both species were observed and
  # we overwrote the non-target spp to be "NONE"
  #-----
  keeper = NA;
  for(q in 1:length(uni_surv)){
    sub_surv = which(occ_dat$survey_id[subset_ix] == uni_surv[q])
    TF<- isempty(subset_ix[sub_surv[which(occ_dat$species2[subset_ix[sub_surv]] != 2)]])
    TF<- isempty(subset_ix[sub_surv[which(occ_dat$species[subset_ix[sub_surv]] != "NONE")]])
    if(TF==FALSE){
      keeper[q] = subset_ix[sub_surv[which(occ_dat$species2[subset_ix[sub_surv]] != 2)]]
      keeper[q] = subset_ix[sub_surv[which(occ_dat$species[subset_ix[sub_surv]] != "NONE")]]
    }else{
      keeper[q] = subset_ix[sub_surv[1]]
    }
  }
  #if(TF==FALSE){
  subset_ix <- keeper # overwrite the subroutine to get ride of the "NONE" cells
  # }
  #-----
  # END: SUBROUTINE
  #-----
  #-----
  # START: ASSIGN DATA TO NEW FIELDS
  #-----

  for(j in 1:length(subset_ix)){
    new_grid[tracker,j] <- occ_dat$grid_id[subset_ix[j]]
    new_date[tracker,j] <- as.character(occ_dat$date[subset_ix[j]])
    new_time[tracker,j] <- occ_dat$time[subset_ix[j]]
    new_ehc[tracker,j] <- occ_dat$species[subset_ix[j]]
    new_grp[tracker,j] <- occ_dat$total_num[subset_ix[j]]
    new_ehn[tracker,j] <- occ_dat$species2[subset_ix[j]]
  }
}

```

```

new_ohc[tracker,j] <- occ_dat$observer[subset_ix[j]]
new_ohn[tracker,j] <- occ_dat$observer2[subset_ix[j]]
new_vis[tracker,j] <- occ_dat$grid_vis[subset_ix[j]]
new_ohb[tracker,j] <- occ_dat$behavior[subset_ix[j]]
new_trk[tracker,j] <- occ_dat$track_id[subset_ix[j]]
new_sid[tracker,j] <- occ_dat$survey_id[subset_ix[j]]
}
tracker <- tracker+1
setTkProgressBar(pb, i, label=paste( round(i/total*100, 0),
                                     "% done"))

#-----
# END: ASSIGN DATA TO NEW FIELDS
#-----
}

close(pb)

new_super_dat = cbind(new_grid,new_sid,new_date,new_time,new_ehc,new_ohc,new_ehn,new_ohn,new_vis,new_ohb,new_trk)

colnames(new_super_dat)[1] <- "grid_id_1"
colnames(new_super_dat)[2] <- "grid_id_2"
colnames(new_super_dat)[3] <- "survey_id_1"
colnames(new_super_dat)[4] <- "survey_id_2"
colnames(new_super_dat)[5] <- "date_1"
colnames(new_super_dat)[6] <- "date_2"
colnames(new_super_dat)[7] <- "time_1"
colnames(new_super_dat)[8] <- "time_2"
colnames(new_super_dat)[9] <- "spp_txt_1"
colnames(new_super_dat)[10] <- "spp_txt_2"
colnames(new_super_dat)[11] <- "grp_size_1"
colnames(new_super_dat)[12] <- "grp_size_2"
colnames(new_super_dat)[13] <- "obs_txt_1"
colnames(new_super_dat)[14] <- "obs_txt_2"
colnames(new_super_dat)[15] <- "spp_num_1"
colnames(new_super_dat)[16] <- "spp_num_2"
colnames(new_super_dat)[17] <- "obs_num_1"
colnames(new_super_dat)[18] <- "obs_num_2"
colnames(new_super_dat)[19] <- "grid_vis_1"
colnames(new_super_dat)[20] <- "grid_vis_2"
colnames(new_super_dat)[21] <- "BEH_1"
colnames(new_super_dat)[22] <- "BEH_2"
colnames(new_super_dat)[23] <- "track_id_1"
colnames(new_super_dat)[24] <- "track_id_2"

#-----
# START: EXPORT DATASETS
#-----

write.csv(new_super_dat, "C:\\filelocation\\newfilename.csv",row.names = T)

#-----
# END: EXPORT DATASETS
#-----

```