University of Nevada, Reno

Do regional habitat models outperform a single-model approach for resource selection at a population scale? A case study with mule deer in Nevada

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By

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**Do regional habitat models outpreform a single-model
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requirements for the degree of

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ABSTRACT:

Effective conservation and management of ungulate species requires characterization of resource availability, selection, and use. Mule deer (*Odocoileus hemionus*) in the Great Basin are experiencing population reductions that are generally thought to be driven by declines in their preferred sagebrush-dominated habitats. In many parts of the Great Basin, sagebrush habitats are being rapidly lost or degraded due to wildfire, energy development, mining, anthropogenic development, climate change, and overgrazing. Robust models of resource selection by mule deer allow wildlife managers to make more informed decisions about habitat protection and permitting for development projects. We used machine learning (random forest) to evaluate patterns of habitat selection at the population level (second order) during summer by GPS-collared mule deer ($n = 630$) across northern Nevada. We divided our study area into four ecologically distinct regions. We compared two alternative modeling approaches: a "region-specific" modeling approach, in which we fit separate resource selection models for each region (thereby accommodating distinct patterns of resource selection within each region), and an "all-regions" modeling approach, in which we fit a single model of mule deer habitat selection for our study region (assuming similar resource patterns across all four regions). The all-regions model outperformed the regional models in cross-validation, indicating that patterns of selection of resources by mule deer were similar across northern Nevada. Our models indicated that mule deer favored summer habitats near perennial water sources, with higher cover of perennial grasses and forbs, less bare ground, and cooler temperatures than expected on the basis of available resources. Our research is important for mule deer conservation by comparing model

performance of summer resource selection at the landscape level (second order), which

highlights areas of conservation need from future anthropogenic alterations within the

Great Basin.

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TABLE OF CONTENTS

List of Tables

LIST OF FIGURES

INTRODUCTION:

Effective conservation and management of ungulate species requires characterization of resource availability, selection, and use. Availability of key resources such as forage quality and availability, and refuge from predators can directly affect survival and reproductive fitness of individuals (Monteith et al. 2014). Four different "orders" of resource selection have been identified, the broadest (first-order selection) representing a species geographical range, and the narrowest (fourth-order selection) representing resource selection at the microhabitat level (Johnson 1980; Manly et al, 2007). Resource selection functions (RSFs) typically assess selection of resources at one of these scales, with RSF order determined largely by the research question and management objectives (Boyce 2006). Second order RSFs characterize relative resource use intensity at the population level within a species range (or large regions within the range) and are particularly relevant for wildlife management and conservation at the regional or range-wide scale. Analyses of resource selection at this scale can help wildlife ecologists and resource managers to better understand how a species uses the landscape and which segments of the landscape most warrant protection or restoration (Guisan and Thuiller 2005; Elith and Leathwick 2009).

Species whose ranges span multiple different ecosystems may exhibit different patterns of second-order resource selection in different parts of their range. For example, white-tailed deer (*Odocoileus virginianus*) in Idaho have been shown to favor old growth timber or second growth timber habitats during times of heavy snowfall to reduce the

energetic cost of moving through deep snow >40 cm (Pauley et al. 1993). In contrast, Webb et al. (2010) showed that white-tailed deer in southern latitudes tended not to exhibit strong changes in patterns of selection in response to extreme weather conditions (e.g., snowfall and prolonged temperatures <0°). Consequently, assessments of resource selection across large geographic areas (75,000 km^2) could fail to capture key regional differences in patterns of selection.

Selection of resources often varies across seasons as a result of changes in nutrient demand, availability of resources, and reproductive state (Morano et al. 2019). For example, nutritional requirements for ungulates are highest for females following parturition and while provisioning dependent young (Pettorelli et al. 2003; Stewart et al. 2005; Parker et al. 2009; Monteith et al. 2014). Following parturition, female mule deer (*Odocoileus hemionus*) need to provision dependent young, while simultaneously replenishing fat stores to increase reproductive fitness and over-winter survival (Monteith et al. 2014). Furthermore, forage quality for ungulates can vary substantially across seasons (Alldredge et al. 2002; Zweifel-Schielly 2012). For example, unlike northern environments with winter snow, winter in South Texas has higher availability of forage for white-tailed deer than most other seasons, while summer is the most nutritionally stressful time of year (Stewart et al. 2000). In addition, overwinter survival of juvenile mule deer is largely determined by nutritional resources acquired during summer (Monteith et al. 2014). If summer habitat is lost or degraded, ungulates in particular might lose valuable nutrients which in turn could decrease survival and recruitment of young (Monteith et al. 2014, Heffelfinger et al. 2018).

The landscape of the Great Basin is characterized by valleys surrounded by mountains, which has been described as basin and range topography, (Grayson 1993; Andreasen et al. 2018) dominated by a sagebrush-steppe at low-mid elevations (1200-1800m) with increased tree cover at higher elevations (West 1983). Arid and semiarid environments such as the Great Basin are extremely susceptible to landscape level alterations, making it critical to understand current and future degradation of these ecosystems (Chambers and Wisdom 2009). The Great Basin is located in the Western United States of America bound by Sierra Nevada and cascade ranges to the west and Rocky Mountains on the east, characterized by an internally draining basin. The Great Basin has been largely affected by biotic, invasive annual plants and conifer encroachment, and abiotic changes such as mining activity, road developments, fire, urban expansion, and energy development (Osterhout et al. 2024). Across the Western United States approximately 28,000 km^2 are proposed to convert native rangelands to solar farms in efforts to increase renewable resources (U.S. Department of Interior 2024). Therefore, understanding how future alternative energy, mining activity, and urban expansion will affect species dependent on sagebrush steppe ecosystems such as mule deer, greater sage-grouse (*Centrocercus urophasianus*) and pygmy rabbit (*Brachylagus idahoensis*) is paramount.

Mule deer are an important native species across the western USA with aesthetic, economic, and environmental values, and in recent decades populations have been declining (Unsworth et al. 1999; Johnson et al. 2000; Stewart et al. 2002; Bishop et al. 2009; Hurley et al. 2011). Mule deer are the most important game species in Nevada, providing hunting opportunities across most of the state. In 2024, $18,269,558 in match

funding was provided for the management of game species and their habitats such as mule deer from the Pittman-Robertson wildlife restoration fund (U.S Fish and Wildlife Services, 2024). Mule deer also offer opportunities for non-consumptive users such as wildlife viewers and photographers. Mule deer are prey for many carnivore species such as wolves (*Canus Lupus*), mountain lion (*Puma concolor*), black bear (*Ursus americanus*), grizzly bears (*Ursus actors*), and coyotes (*Canis latrans*). Because of their cultural, economic and ecological importance, mule deer have been well studied across their geographic range, including the Great Basin (Pierce et al. 2004; Shields et al. 2012; Blum et al. 2015; Shoemaker et al. 2018; Morano et al. 2019). Mule deer range from Baja California to the Yukon in Alaska, and expanding into much of the Great Plains with noticeable differences in skull and body measurements (Heffelfinger, 2006; Heffelfinger and Krausman, 2023). Selection of resources by mule deer changes across their range however, little is known about intrapopulation variation across large scales (75,000 km^2), specifically those in homogeneous habitats.

Our objective was to examine patterns of summer resource selection at the population level by mule deer in the sagebrush-steppe ecosystem across northern Nevada, USA. We chose to evaluate selection of resources during summer, because acquisition of resources during summer can be a limiting factor for many large mammals in unpredictable environments such as the Great Basin (Bender et al. 2007; Bårdsen et al. 2010). We built resource selection models at the population level (second-order) using locations of individual mule deer collected by the Nevada Department of Wildlife (NDOW). We divided our study area into distinct regions and hypothesized that selection of resources by mule deer would differ substantially across regions, such that models fit

to data from specific regions would outperform a single model fit to data from across the entire study area. Further, we hypothesized that mule deer select habitats with cooler temperatures during the summer season because nutrition quality tends to decline with increased temperatures (Marshal et al. 2005; Jamieson et al. 2012). Finally, we used our models of summer resource selection to generate predictive maps for mule deer across Northern Nevada.

MATERIAL AND METHODS:

Study Area

Our study area encompassed most of Northern Nevada, about 75,000 km^2, which included the diverse habitats characteristic of the Great Basin ecosystem (Figure 1). We excluded southern Nevada because that landscape is more representative of the Mojave Desert rather than the Great Basin ecosystem, and our data on locations of mule deer was specific to the Great Basin. The landscape of the Great Basin is characterized by valleys surrounded by mountains, which has been described as basin and range topography, (Grayson 1993; Andreasen et al. 2018). Elevations within our study region range from a minimum of 1,000 m to a maximum of 3,900 m. Annual precipitation within our study area averages 300 mm, with the most falling in winter in the form of snow. Summer is the driest period in the Great Basin with an average precipitation of 13.8mm (SD = 6.3), and the majority of that rainfall occurs at high elevations (PRISM 2022). Summer temperatures are highly variable across our study area as a result of the changing topography, with mean temperature of 18.48 °C (SD = 3.4). Dominant vegetation in low elevations includes bitterbrush (*Purshia tridentana*), green rabbitbrush (*Chrysothamnus*

viscidiflorus), and other species characteristic of Great Basin desert shrub communities. At mid-elevations the dominant shrub is sagebrush (*Artemisia spp.*), and tree species include Utah juniper (*Juniperus osteosperma*) and singleleaf pinyon pine (*Pinus monophylla*). In recent decades, pinyon-juniper cover has increased dramatically within sagebrush communities (Miller at al., 2013). Dominant vegetation communities at high elevations include singleleaf pinyon pine (*Pinus monophylla*) and stands of quaking aspen (*Populus tremeloides*) (Richart et al. 2013). We defined summer as the months of June, July, August, and September using a climograph, on the basis of similar precipitation and temperature regimes within our study area (Stewart et al., 2002, McKee et al. 2015).

Field data collection

Adult mule deer were captured by NDOW using helicopter-netgun technique between 2009 and 2019 (Krausman et al. 1985). A total of 39 males and 591 female mule deer were equipped with global positioning system (GPS) collars. Fix rates varied across individuals, with GPS locations recorded every 4-12 hours. We discarded all locations recorded within one week of release because of the potential bias resulting from effects of handling on movements and patterns of resource selection. We also discarded GPS locations associated with high positional uncertainty (PDOP > 10), locations that implied unrealistically rapid movements exceeding 5 km per hour (Dussault et al. 2001), and locations outside the geographic boundaries of our study region. Because the focus of our study was on summer, we only included locations recorded within summer months (June-September). To minimize temporal autocorrelation in our data and model bias towards

individuals with high numbers of locations, we thinned our data by retaining no more than 100 used locations for each individual, with locations distributed evenly (maximal duration between locations) across the summer months. If an individual had fewer than 100 locations recorded during summer, we retained all data for that individual for analysis. All geographic data processing was performed using ArcGIS (ArcGIS 10.8.1 Environmental Systems Research Institute [ESRI], Redlands, CA, USA). We began with approximately 480,000 GPS locations prior to thinning those data. Because collars on mule deer were distributed as a result of management driven objectives by NDOW, we observed substantial variation in numbers of collars across our designated regions (Table 1). Region 4 had the greatest number of individuals with 434 adult mule deer compared with Region 1 that had only 26 marked individuals which we thinned region 4 to a maximum of 50 points per individual. The all-region dataset, which included mule deer from all regions combined, had a total of 630 individuals. Then we extracted random points within regions at a 1:1 ratio using ArcGIS (ArcGIS 10.8.1 Environmental Systems Research Institute [ESRI], Redlands, CA, USA), each random point was paired with a used GPS location in each region.

Environmental covariates

We compiled spatial data for multiple environmental attributes that have been previously shown to influence selection of resources by mule deer during summer. All spatial grids included the entire study region with an additional 10 km buffer to help prevent edge effects (mostly relevant for variables representing distance to potentially important environmental features). We derived elevation, slope, aspect, and topographic ruggedness (modified vector ruggedness metric; Dilts et al. 2022) from a digital elevation

model (DEM) at 30 m grid resolution (www.usgs.gov/the-national-map-data-delivery).
Because aspect is a circular variable, we transformed the raster for aspect by sine
("eastness") and cosine ("northness") functions (Stewart et al. 2002, Heffelfinger et al.
2020). We obtained monthly rasters for temperature and precipitation from the PRISM
database (PRISM 2022; 800 m grid resolution), and summarized mean precipitation and
temperature across summer months for each year. We downloaded spatial grids for our
study region representing summer vegetation cover from the Rangeland Analysis
Platform (RAP; Allred et al. 2021), including cover of trees, shrubs, perennial forbs and
grasses, annual forbs and grasses, litter, and bare ground. We obtained information on the
timing and spatial extent of wildfires within our study region to derive spatial grids of our
study area for each year representing the years since the most recent fire (Eidenshink et
al. 2007, Walters et at. 2008). We obtained data on water developments for large
mammals from NDOW; and, we obtained locations of lakes, perennial streams, rivers
(www.usgs.gov/the-national-map-data-delivery), and springs (Springs Stewardship
Institute, 2022). We used locations of all of those water sources to derive a raster layer
representing the Euclidean distance to the nearest known water source. We obtained
information on the locations of all roads within our study region (Open Street Map
Foundation, 2022); and derived Euclidean distance from roads classified as "medium
use" roads. Medium-use roads were defined as state highways and well-maintained
county roads. Major roads, such as interstate freeways, were not included in our analyses
primarily because of the extremely low density of such roadways in the study region,
whereby most mule deer and their habitats were unlikely to be influenced by those roads.

Minor roads also were removed from the analysis because we were unable to validate their placement and traffic volumes.

Modeling summer resource selection

We used a multi-stage approach to reduce the set of predictor variables to reduce multicollinearity, model overfitting, and to improve interpretability. First, we assessed pairwise correlations among variables using Pearson's correlation coefficient, and removed variables when pairwise correlations were ≥ 0.75. Only elevation and temperature were highly correlated (Pearson $r > 0.75$). Temperature was a time-varying covariate, and was related to variation in nutrition quality and quantity (Marshal et al. 2005; Jamieson et al. 2012). Therefore, we retained temperature instead of elevation, but we realize that variation in temperature at this scale likely also reflected differences in elevation.

We embedded 2 uncorrelated random variables within the covariates then fitted a random forest model (Breiman, 2001) using the 'ranger' package in R ver. 4.2.1 (R Core Team 2022, Wright and Ziegler 2017). We removed any variable whose importance value (computed using the 'permutation-importance' method in 'ranger') was lower than any of the uncorrelated random variables. We then used a recursive feature elimination algorithm ('rfe' function in package caret; Kuhn 2021) to identify the smallest set of predictor variables that were able to perform as well as (or better than) more complex models under rigorous cross-validation. Specifically, we fitted random forest models (using 'ranger') using alternative sets of predictor variables and assessed model performance using 5-fold spatial cross-validation (5 sets of 5 folds each). We performed

spatial cross-validation by splitting each region into *ad hoc* subdivisions (to ensure

sufficient known-use points were contained within each spatial subdivision), which were

approximately 3,300 km^2. As a result of the number of GPS locations in each region, the

number and sizes of grids varied (Table 1.).

We used two different modeling techniques to assess habitat selection by mule

deer in Northern Nevada. First, we created region-specific models ("region") whereby we

fit a different model for each of the 4 regions. The second modeling technique (the "all-

regions" model) combined data for the 4 designated regions to fit a single habitat-

selection model (Figure 1.). We validated both modeling approaches using the same

spatial cross-validation procedure described previously. We assessed two different

metrics: Area Under the Curve (AUC) which was derived from Receiver Operating

Characteristic (ROC) and represents that ability of a model to correctly classify used vs

background observations (Zweig and Campbell, 1993; Fielding and bell, 1997). Scores

higher than 0.5 indicate better-than-random performance and a score of 1 represents

perfect classification accuracy (Hanley 2014). A perfect score, however, can seldom be

achieved in a used-available framework (Pearce and Ferrier, 2000). We ran a k-fold cross

validation and used the Boyce index as a measure of model performance. (Boyce et al.

2002, Osterhout et al. 2024). We created Boyce indices and plots from the Boyce index

generated using the 'ecospat' package in R (Hirzel et al. 2006). Boyce index values were

calculated by a Spearman-rank correlation between habitat suitability classes and the

ratio of used:available points .

Prediction mapping

We generated predictive maps (hereafter: "random forest") of summer resource use intensity for mule deer generated for both region-specific and all-regions modeling approaches. Each of the regions were mosaicked and stitched together from the 4 different areas creating a single 'regional' map. Region specific maps were extended 1000 m around each region, and values that overlapped were then averaged to yield smooth transitions in predicted resource use intensity values between regions.

Because some environmental covariates (e.g., temperature) varied across years, we generated 11 maps of summer habitat (representing all years from 2010-2020). We then computed the per-pixel average intensity of habitat use across the 11 years as a static representation of habitat use for northern Nevada. To visualize the spatial differences in predicted habitat suitability between region-specific and the all-regions approach, we calculated the per-pixel difference between the two maps (hereafter: "Random Forest difference map").

Scaled maps were then created by categorizing areas into 4 classes (high, moderate, low, non-habitat) (hereafter: "suitability") following the method of Coates et al. (2016). Categories were created based on the standard deviation (SD) from the mean ($\bar{x}$) from all used points extracted values from the region and all-regions Random Forest map, data were grouped within regions for the all-region and region models, bins were defined separately for each region. High suitability (HS) habitat was comprised of all habitat suitability values greater than 0.5 SD below $\bar{x}$. Moderate suitability was comprised of HS values between 1.0 and 0.5 SD below $\bar{x}$. Low suitability habitat was

comprised of HS values between 1.5 and 1.0 SD below $\bar{x}$. Non-suitable habitat was comprised of HS values 1.5 SD below $\bar{x}$. Where cells overlap we took the minimum value. We then created a difference map between the two scaled maps to visualize differences in predicted habitat suitability. Furthermore, to assess the statistical differences in the scaled maps we calculated a confusion matrix.

RESULTS:

Based on our random forest analysis, we identified a total of seven variables as important predictors of resource selection by mule deer in at least one of the five models (four region-specific models and one all-regions model): cover of perennial forbs and grasses, temperature, bare ground, tree cover, distance to water, slope, and shrub cover (Figure 2). Perennial forbs and grasses, temperature, and distance to water were consistently identified as the top three variables in selection of resources by mule deer during the summer season. In contrast, shrub cover was only identified as an important factor predicting summer resource use intensity for one of the five models (Region 1) (Figure 2). In addition, topographic slope was identified as an important factor for mule deer second order selection in two regions (Regions 3 and 4).

Shapes of the functional relationships describing intensity of selection by mule deer as a function of each predictor variable were similar across regions (Figure 3). Intensity of resource use tended to increase monotonically with increased cover of trees and perennial forbs and grasses (Figure 3). In all models, (four region-specific and the all-regions model) intensity of selection during summer was highest in areas with the lowest mean summer temperatures (Figure 3). In models where slope was an important

predictor of summer resource selection, mule deer tended to occur in areas with steeper slopes relative to available habitat. For all models in which distance to water was identified as important (all models except for Region 1), mule deer selected areas closer to water. In regions where bare ground was included in the top model (all models except for Region 3) mule deer selected areas with the least amount of bare ground and appeared to avoid areas with >20% bare ground. Our rigorous spatially structured cross-validation trials indicated that model predictive performance was relatively high (AUC ≥ 0.83, Boyce Index ≥ .92) when region-specific models were validated using data from the same region to which the model was trained (diagonal panels in Figure 4 and 5). Furthermore, regional models generally exhibited strong performance when used to predict intensity of resource use for regions other than the training region (AUC ≥ 0.79, Boyce Index ≥ 0.68; Figure 4 and 5). Overall, the all-regions model exhibited the strongest and most robust performance in cross-validation (AUC = 0.87; Figure 4 and Boyce Index = 0.99; Figure 5). In general, Boyce Indices (association between the observed density of [out-of-bag] used points and the predicted resource use intensity) were high in our cross-validation trials, indicating strong predictive performance (Figure 5). However, the positive correlation between predicted resource use intensity and density of mule deer locations tended to break down at high levels of predicted habitat suitability (Figure 5), possibly due to insufficient data and overfitting models.

When we used our random forest models to generate predictions of resource use intensity across our study region, we found that predicted intensity of resource use during summer was generally highest at the highest elevations (often the tops of mountains) across northern Nevada (Figure 6). Although we can see apparent differences in habitat

quality from the difference map (Figure 6) overall both models showed high similarities with one another (Table 2; 0.892% mean (0.892-0.892, 95% CI), kappa =0.754).

DISCUSSION:

Our findings indicated that patterns of resource selection by mule deer were highly conserved across our Northern Nevada study area. Not only were the top variables and their functional relationships very similar across regions, regional models also generally performed well even when validated with data from a completely different geographic region. Given that data were not limited within any region, we are confident that our results reflect fundamental similarities in the way that mule deer selected resources during summer across Northern Nevada. Poor performance of regional models in cross validation likely arose from over fitting data within specific regions. Random forest can be susceptible to overfitting, especially in large datasets (Olden et al. 2008), however our all region model outperformed the regional models in spatial cross validation highlighting the robust predictive performance of the all region model.

The Great Basin is a relatively uniform ecosystem in resource availability across our study area (West 1983), which likely caused similar selection of resources by mule deer at the population level. Conversely, in heterogeneous landscapes mule deer likely differ in selection of resources at the population level, meaning regional models could outperform a single model. Furthermore, mule deer are large ungulates able to move long distances in short periods of time, which allows easier and faster movement to different areas (Sawyer et al. 2005; Lendrum et al. 2013; Blum et at. 2015). With the ability to move long distances mule deer likely are not especially specialized to specific resources,

something more prominent in smaller mammals. For example in homogeneous landscapes smaller mammals limited by movement might exhibit regional specialization in resource selection. Overall, the differences in ecosystems and species can determine what scale correctly identifies how species select resources, further demonstrating the need to compare model performance at multiple scales.

Although temperature and elevation were highly correlated, we chose to remove elevation because of the lack of temporal variation and kept temperature, allowing managers to determine how annual variation in temperature will affect mule deer in the Great Basin. Temperature is directly tied to actual evapotranspiration (AET), which has direct effects on forage quality (Stephenson 1998, Morano et al. 2019). Mule deer in the White Mountains in California, selected areas with higher AET, which were more productive than other areas (Morano et al. 2019). Because of the large scale of our study area, we were not able to assess AET directly, but we used temperature as a surrogate for the corresponding effects on movement and space use by mule deer. When unusually high temperatures occur during spring and summer, green-up of vegetation may occur earlier with vegetation senescence also happening faster, which results in earlier loss of forage availability and declining quality during summer (Doi and Katano 2008 and Pettorelli et al. 2007). High temperatures at low elevations may lead to earlier emergence and lower quality forage during summer, also causing mule deer to move to higher elevations where nutrients are highest (Marshal et al. 2005; Jamieson et al. 2012).

During summer, mule deer remained relatively close to sources of water, which is well documented in the literature (Boroski and Mossman 1996, Ordway and Krausman

1986, McKee et al. 2015, and Eckrich et al. 2020). Our results show that mule deer

tended to stay close to water (<1200m) probably because of high water requirements for

lactating females and lack of precipitation during summer in the Great Basin. Lactating

females have higher water requirements than non-lactating females or males during

summer (Barboza et al. 2009; McKee et al. 2015; Heffelfinger et al, 2018). Eckrich et al.

(2020) reported mule deer in the summer stayed within a kilometer of water sources

(~0.7km) in Central Oregon. Summer is also time for individuals to replenish somatic

reserves before winter and mule deer require high quality forage, especially lactating

females (Barboza et al, 2009; Tollefson et al, 2010; Monteith et al, 2014). Additionally,

in desert ecosystems, abundance and quality of vegetation has been shown to be higher in

areas close to water (Miller et al, 2013; McKee et al. 2015), and soil moisture tends to be

the highest in close proximity to water allowing for greater nutrient uptake by plants

(Comstock and Ehleringer 1992, Krausman et al. 1993; McKee et al. 2015).

Mule deer selected areas with >20% cover of perennial forbs and grasses and

avoided areas with bare ground. Perennial forbs and grasses offer consistent forage

availability, however quality in the summer season is dictated by winter precipitation

(Heffelfinger et al. 2018). Furthermore, of the cover classes available at the landscape

scale perennial forbs and grasses include more nutritious and palatable forage for the

duration of summer compared with annual plants or shrubs (Kelsey et al. 1982; Ganskopp

and Bohnert 2001). The Great Basin Ecosystem has been drastically altered by fire,

which has resulted in loss of productive habitat to greater coverage of invasive annual

grasses of low forage quality (Knapp, 1996). Areas across the Great Basin that are still

dominated by perennial grasses and forbs should continue to be conserved to maintain

productive habitat for mule deer. Shrub cover only entered one of our models, but sagebrush and other shrubs tend to be most important forages for mule deer during winter (Anderson et al. 2012). In the summer, sagebrush is low in crude protein and digestible energy, however, in the winter sagebrush is an important forage for mule deer (Kelsey et al. 1982; Personius et al, 1987). Our results indicate that mule deer tended to select areas with more nutritious forage, such as locations close to water sources, and high cover of perennial forbs and grasses. Selection of high quality and quantity forages help mule deer to raise young and replenish somatic reserves to get through winter (Mautz 1978; Monteith et al. 2011).

Mule deer have been in decline across their geographic range largely attributed to the loss of habitat (Unsworth et al. 1999; Johnson et al. 2000; Stewart et al. 2002; Bishop et al. 2009; Hurley et al. 2011). Mule deer in Nevada are currently managed at the scale of the Game Management Unit (GMU) and the ability to understand how resources are selected at the population level (second order; Johnson 1980) are critical for their management; because the ability to identify large spatial areas of conservation needed allow managers to maintain critical areas and determine how habitat alterations could impact mule deer. The Great Basin is similar across most of the range (vegetation communities, precipitation, and temperature) (West 1983) however, patches of high quality habitat such as riparian areas are interspersed across the Great Basin offering critical resources for mule deer in the summer. Energy development, mining exploration, and urban development are all driving factors in habitat loss in the Great Basin (Osterhout et al. 2024), however the loss of resources caused by each alteration has different impacts on local flora and fauna. Furthermore, human caused habitat loss and

degradation are not uniform within the Great Basin, highlighting the importance of analysis across large areas critical for mule deer within the summer. Identifying how mule deer select resources at the population level helps identify how future landscape alterations will affect regional areas of the Great Basin differently.

Climate change and anthropogenic alterations causing major landscape habitat loss within the Great Basin are expected to continue. The Great Basin is proposed to have major alternative energy projects within the next decade (U.S. Department of Interior 2024). Our analysis at the landscape scale gives managers a better understanding how human caused loss could negatively affect mule deer populations in the Great Basin, enabling informed decisions about key habitat areas that should remain free from development. Mule deer were similar across our study area in selection of resources. However, regional differences in anthropogenic land use practices such as mining, energy development and urban expansion will affect mule deer differently within the Great Basin. Furthermore, our research provides insight for population level resource selection, something that is important to not only the Great Basin ecosystem but for species management across the globe.

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Mule deer location data for Northern Nevada (2010-2019) and grid size within regions across our study area. Mule deer GPS points and years vary as a result of management decisions made by Nevada Department of Wildlife. Grid size was determined ad hoc due to GPS locations and size of regions.

Table 1. Mule deer location data for Northern Nevada (2010-2019) and grid size within regions across our study area. Mule deer GPS points and years vary as a result of management decisions made by Nevada Department of Wildlife. Grid size was determined ad hoc due to GPS locations and size of regions.

Regions	Number of mule deer	Number of used points	Years	Number of grids	Average grid size (km^2)
Region 1	26	100	2018-2019	12	3035.72
Region 2	59	100	2010-2019	14	1732.35
Region 3	116	100	2011-2019	19	4278.16
Region 4	434	50	2012-2020	19	4054.10

Table 2. Confusion matrix comparing categorized mapping techniques of mule deer in Northern Nevada, 2010-2019. The all region model was compared on a cell by cell basis to the region model. Values indicate the total number of cells for each category of habitat for GPS locations.

		All Region Model			
		No Habitat	Low	Moderate	High
	No Habitat	23313972	715004	10764	16
	Low	950896	2072847	442244	117295
Region	Moderate	28943	454159	467196	447179
Model	High	3717	68097	298778	674166
Accuracy = .892		CI = (.892-.892)		Kappa = .754	
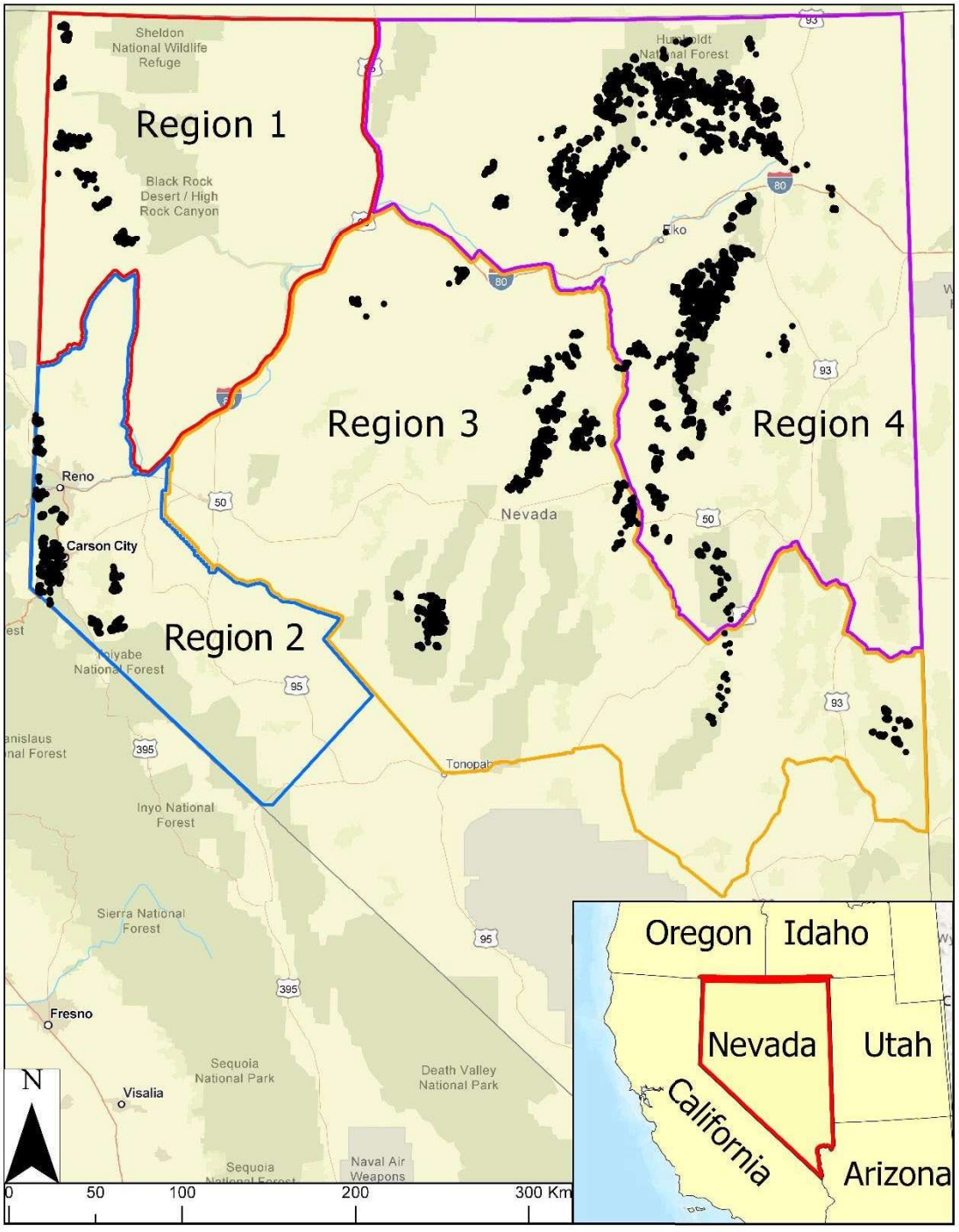
Figure 1. Figure 1. Map of the study area located in Northern Nevada along with mule

deer GPS points in black. Regions were defined by the combination of game management

units (GMU's) provided by the Nevada Department of Wildlife (NDOW). We created 4

different regions by combining GMU's based on similar landscape characteristics and

movement patterns of mule deer. All-region is defined by the combination of the 4

different regions across Northern Nevada for used locations of collared mule deer (2010-

2019).

Figure 2. Variables importance for all models for GPS radio collar locations of mule deer in Northern Nevada (2010-2019). Colored cells represent a variable that was used for a specific model. Shading of cells, in which darker cells represent higher variable importance along with numerical values from random forest.
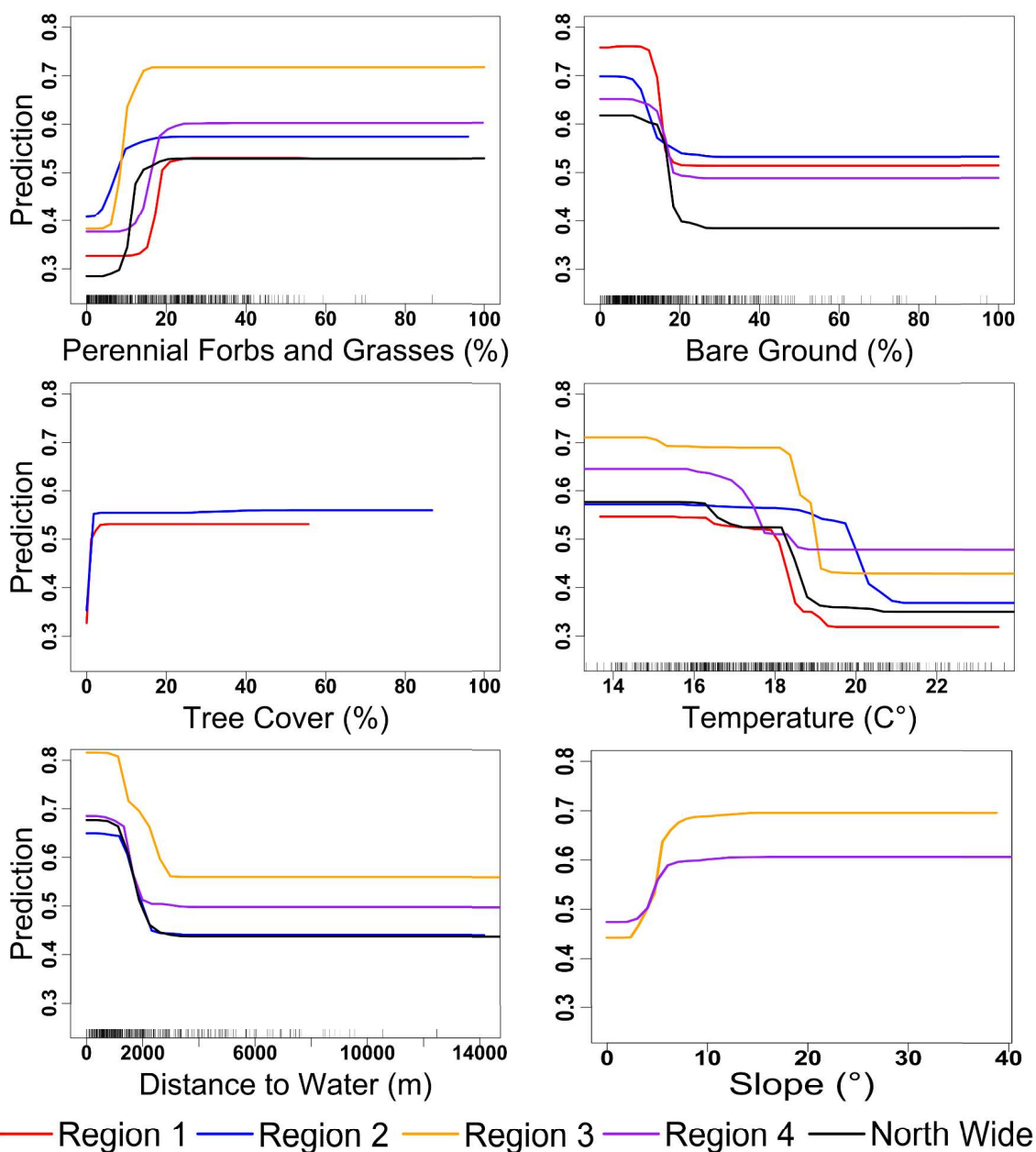
Figure 3. Partial dependence plots for variables that were in > 2 models. Predictions for each model were created by holding all other variables at their mean value and estimates for selection of covariates were then calculated from random forest analysis. For GPS radio collar locations of mule deer in Northern Nevada (2010-2019).
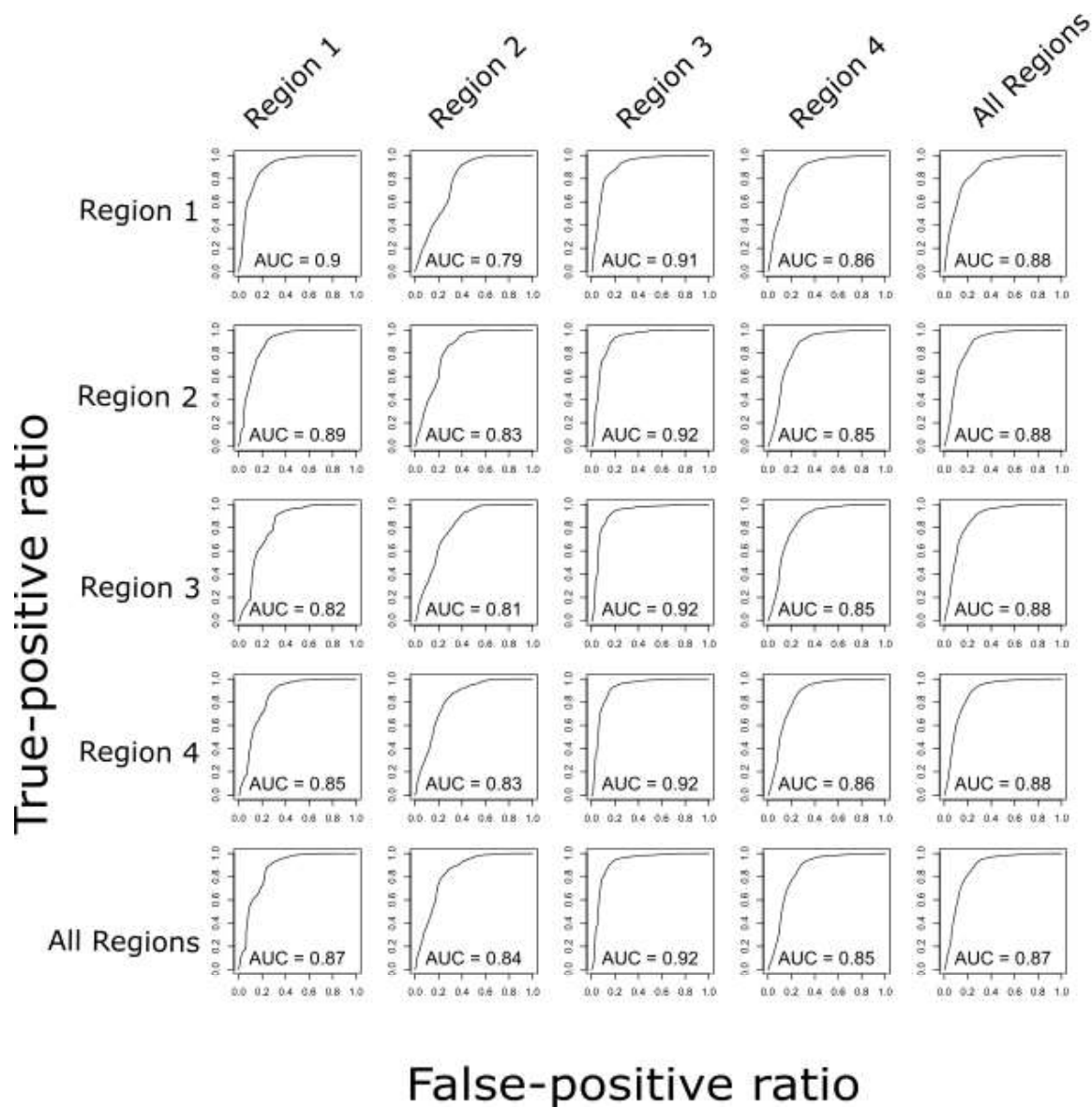
Figure 4. Area Under the Curve (AUC) values for spatial cross validation using mule deer data in Northern Nevada (2010-2019). Horizontally, for each row models accuracy was measured with different datasets (vertically) where a subset of data was withheld using spatial cross validation. Figures were then created by a models' ability to determine correctly classified habitat suitability areas versus False-positive classifications. AUC score of 1 indicates a perfect model.
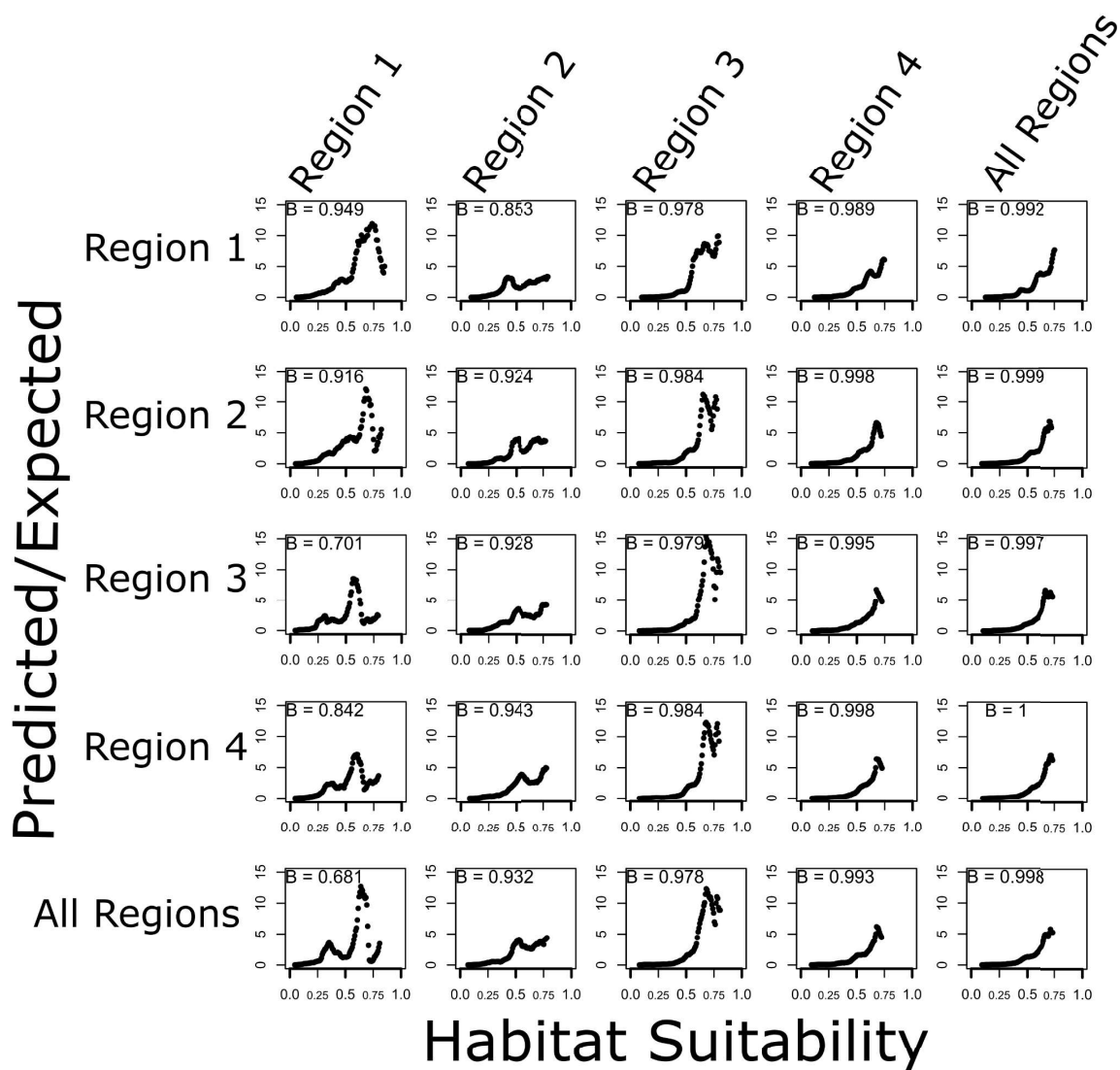
Figure 5. Boyce index plots for models with different datasets using GPS points from Northern Nevada (2010-2019). Plots were created by testing each model with spatial cross validation. Models are indicated horizontally and each dataset (vertical) was tested to compare predictive performance. X-axis represents a change in habitat suitability ranging from 0-1, while the Y-axis represents the ratio of predicted/expected points along

a range of different habitat suitable values. B represents the Boyce index value calculated

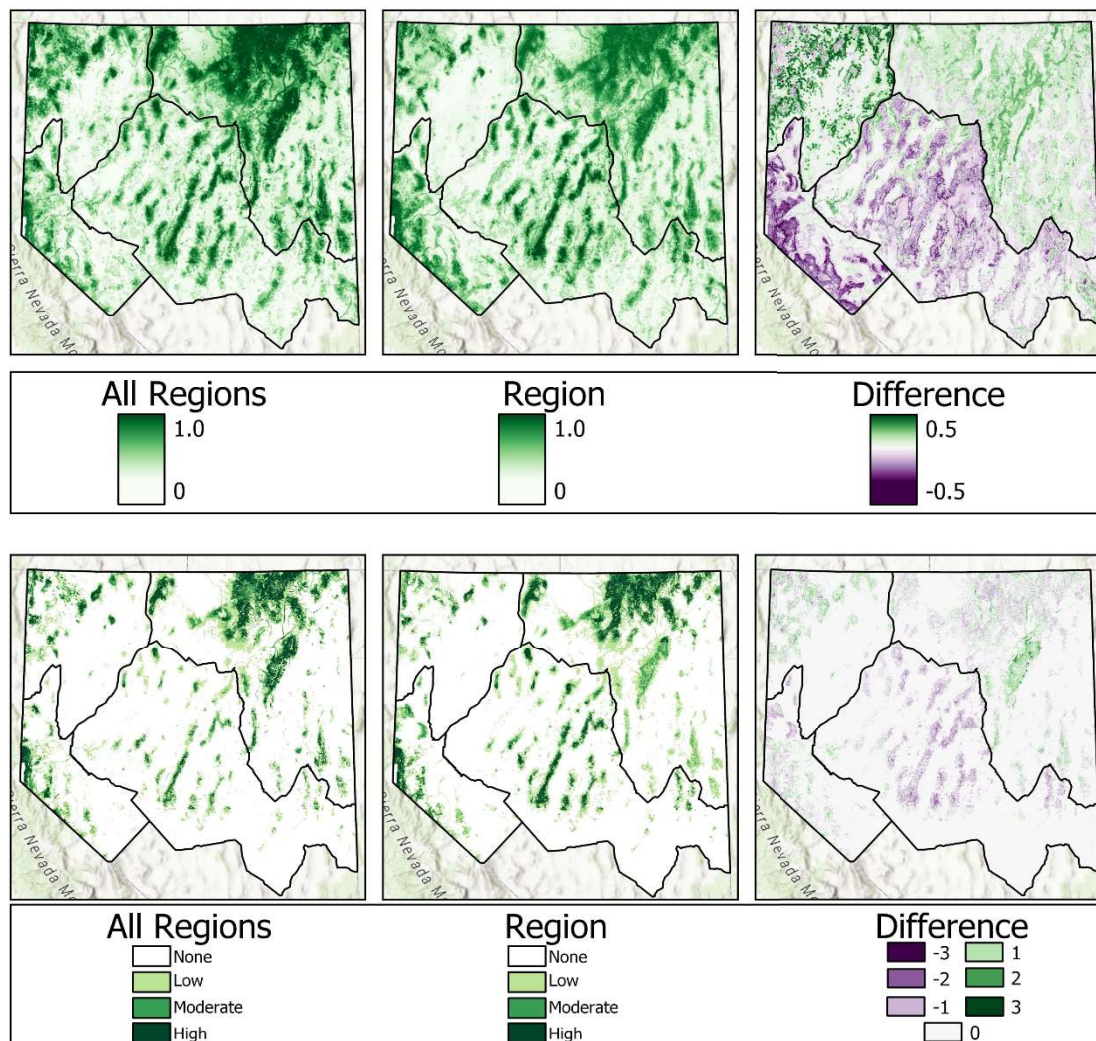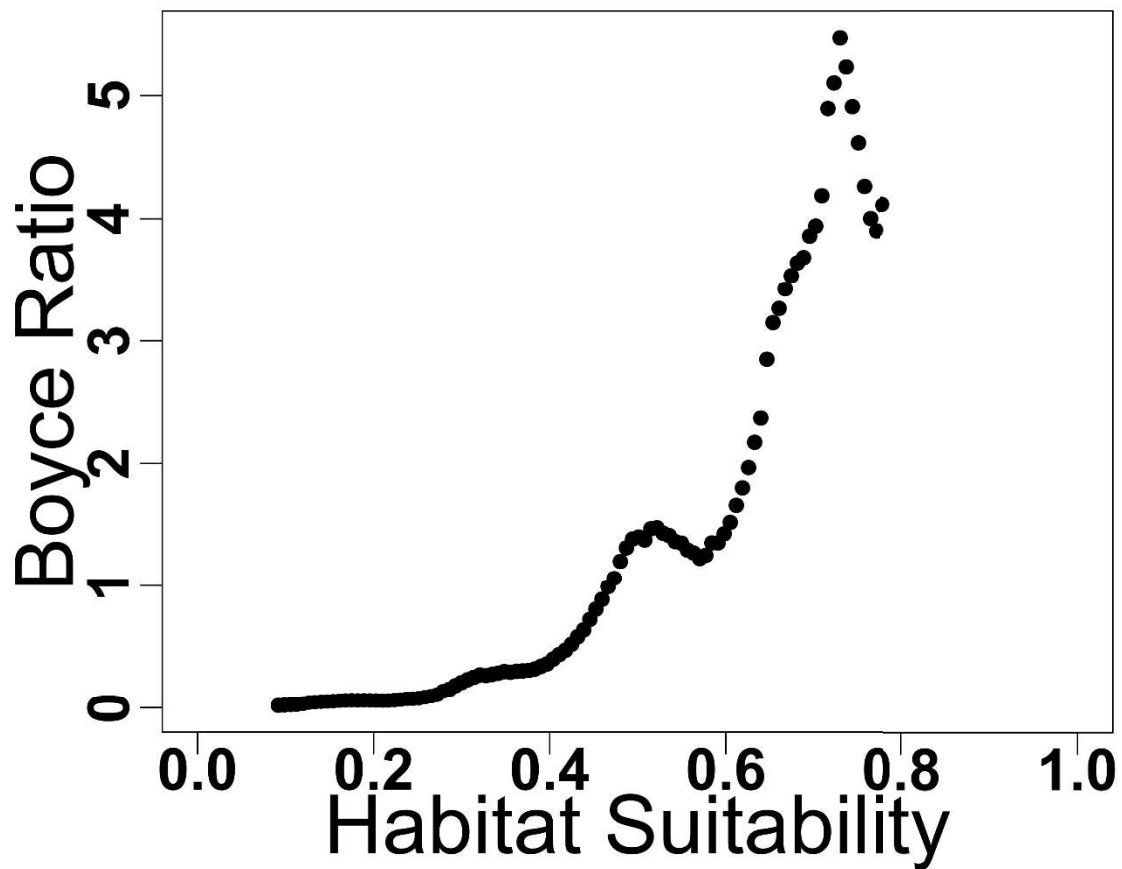by a Spearman-rank correlation between points within individual bins.

Figure 6. Prediction maps for 2 different modeling techniques (top panel), Categorized maps based on used GPS points from Northern Nevada (2010-2019) within each region (bottom panel). Top panel illustrates random forest habitat suitability maps created for All- region prediction which is based on all thinned data located in the study area, while regional based models are from thinned data located within a specific region. Values closer to 1 indicate perfect habitat for mule deer. The panel on the right illustrates the difference in predictions between the 2 different modeling approaches. Positive values

show higher model prediction for the All-region model when compared to regional based models. Bottom panel maps were created by extracting values of the habitat suitability from the mule deer used points within each region. Then a difference between the two maps was created to highlight the areas where predictions differed.

Supplemental Figure 1. Boyce index for all-region model created from mule deer data from Northern Nevada (2010-2019) when spatial cross validation is done. Cross validation was done by withholding entire regions of data and making a prediction on how well the model is doing with missing data.