GENERALIZING AND TRANSFERRING A GIS-BASED SPECIES DISTRIBUTION MODEL: FROM ONE HOT SPOT TO ANOTHER HOT SPOT

by

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ABSTRACT

Species distribution models (SDMs) are efficient simulations of the distribution of species across geographical space and help to understand the spatial patterns of biological diversity. However, they are not designed to provide a description of species habitats. Geographic information systems (GIS) combined with SDMs have been used to illustrate the distribution and infer the sustainability and capability of habitats, to explore ecological relationships, serve as selection of vegetation types, avoidance of habitat disturbed by humans, establishing factors like predation, and to identify landscapes favorable for establishment of a new population. Despite the large number of SDMs papers published within the last decade, the practical utility of these models in the conservation management field remain sparse. The main objective of this research was to develop techniques for habitat modelling based on presence/availability data depicted by illustrative habitat maps and to test the new model on different landscapes. Resource selection function was used to develop a new model for the Yellowstone bison herd from published habitat maps. The predictor variables within the new model were elevation, ruggedness, profile curvature, percent of tree cove, Horizontal and vertical distance to water. The new model was then transferred and tested with field data from the National Bison Range and Grand Teton bison herds. The top predictive model performed better for the Yellowstone and Grand Teton herds than for National Bison Range herd. The output of this research indicated that habitat maps could work as source of land use by wildlife through transference to new areas of interest especially when local use data is not available.

CHAPTER ONE – INTRODUCTION

Introduction

Species distribution models (SDM) using correlations between species presence and environmental variables are valuable and increasingly used for environmental management and conservation. These predictive models are often developed for areas of interest surrounding the original study population. Conservation studies conducted in areas with no available species data, often use models developed with data from a different population location (Barbosa et al., 2009). That effort is called model transference in space.

In spite of broad use SDMs developed with data from one area could be considered to have a lower predictability elsewhere due to local variation in species responses (Torres et al., 2015). Usually model development and its transference is done in the same study, but those models are rarely exported by other research groups (Acevedo et al., 2014). Nonetheless, the possibility of using previously published habitat maps for a particular species to identify new conservation areas, indicates that spatial transference becomes particularly important in countries such as Brazil, where the resources for habitat studies are scarce (Acevedo et al., 2014).

The necessity of a standardized and periodic wildlife population distribution assessment has been recognized by the Brazilian conservationist community for a long time (Ayres & Best, 1979). However, Torres and Vercillo (2012) indicated that from 192 endangered vertebrate species, only 45 (23%) are protected and 33 (17%) are lacking specific areas for protection within the Brazilian National Conservation System (SNUC). Understanding the technique of model development based on previously published maps and its limitations would stimulate the use of previously developed maps to predict new scenarios (Acevedo et al., 2014). Although, the current study addresses the American bison (*Bison bison*), generalizing and transferring techniques developed in this study are applicable for species, elsewhere.

Using Habitat Transference to Address a Conservation Problem

A modelling study, based on bison range expansion driven by population growth, suggested that bison herds were close to carrying capacity at YNP (Coughenour, 2005). When the population relatively small, Meagher (1989) predicted migration towards lower elevation sites as the population increased, because the traditional winter habitat could not support the higher bison numbers. In agreement with Meagher (1989), Keigley (2018) argued that vegetation condition showed signs of overgrazing on the northern range of YNP. Both reports indicate that the carrying capacity for bison has been reached or even exceeded, making it impossible to maintain a herd of 5,000 animals within the park.

To maintain such a large herd, YNP managers suggested that the state of Montana tolerate free-roaming bison outside the park (USDI, 2000; Plumb et al., 2009). Four bison habitat maps developed by YNP were used by non-governmental organizations to persuade the Montana government into allowing some bison to remain outside park boundaries throughout the year, which was accomplished when a bison tolerance zone was enacted by Montana State Government in 2015 (Appendices B1 and B2; Jones

2017). The tolerance zone encompasses the maps developed by YNP (Appendices B1, B2, B3, B4, B5, and B6; Montana Fish, Wildlife and Parks, 2014; Jones, 2017).

The goal of this study was evaluate the potential utility of post-hoc analyses of habitat maps for conservation action (Appendices B3, B4, B5, and B6; Montana Fish, Wildlife and Parks, 2014). The objectives were 1) develop the necessary methodology for habitat modelling based on presence/availability data depicted by the habitat maps previously created by YNP for its bison herd, 2) test the model in a different environment by transferring predictive model attributes and comparing the outcome against field location data from the new area. Because of access to existing bison locations, Grand Teton National Park and the National Bison Range were used as test localities. As the study advanced, other objectives emerged: 3) calculate the area of potential bison habitat delineated by YNP biologists because it could not be done using the original maps because of overlap (Figure 1); and 4) compare the transference model outcome with the original bison habitat depicted by YNP. The outcome of these various objectives would address the feasibility of SDM transference in species conservation efforts.

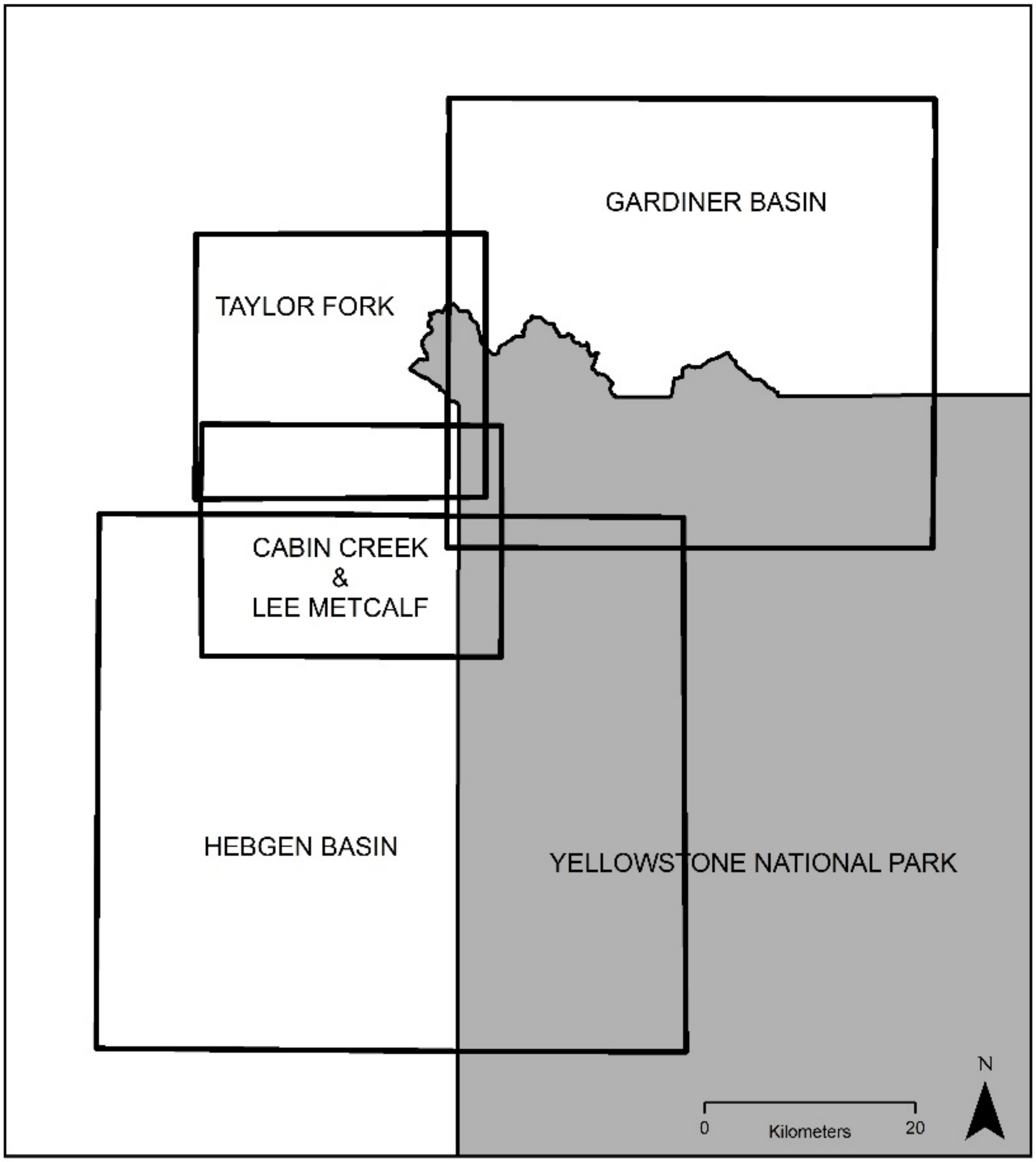

Figure 1. Boundaries of the four original bison habitat maps developed by Yellowstone National Park (Montana Fish, Wildlife and Park, 2014).

CHAPTER TWO – LITERATURE REVIEW

Literature Review

Biodiversity can simply be described as the variety of life. It expresses the variation among species, and ultimately the variations of populations, communities, ecosystems and gene complexes (Giannini et al., 2012). However, biodiversity is more commonly used to describe the number of species in a certain geographic area (Swingland, 2001). In this vein, biodiversity conservation rarely targets single species distribution, instead focusing on species' richness and community structure. Interest in the conservation of individual species aims to maintain organisms in their wild state thus preserving the diversity of species populations as well as the processes that enhance conservation of system-wide biodiversity (Swingland, 2001). Species distribution models (SDM) are important tools for biodiversity conservation efforts.

Species Distribution Model

Species distribution models (SDMs), also referred to as ecological niche models, predictive habitat distribution models, and predictive species distribution models, analyze species occurrence or abundance in relation to environmental variables (Elith & Leathwick, 2009). These models are frequently used to address issues related to ecology, biodiversity, biogeography, and conservation of species (Jiménez-Valverde et al., 2008; Costa et al., 2010; Zhang et al., 2012; Guisan et al., 2013). Galluzzi et al. (2017) compared two models, weighted linear combination (WLC) and logistic regression, to enhance the ecological knowledge of the alpine marmot (*Marmota marmot*) occupying the Italian Alps. In this study, the authors used the area under the curve (AUC) to assess the models and found that both methods had similar performance in predicting the land use by alpine marmot. Importantly, the study contradicted the previous knowledge that aspect was the most determining factor for habitat selection by alpine marmot. This disparity suggests that the relative importance of environmental factors might not be readily generalized from one study area to another (Galluzzi et al., 2017). A predictive spatial model based on logistic regression was used to estimate the amount and spatial configuration of potential gray wolf (*Canis lupus*) habitat in the upper Midwestern United States (Mladenoff et al., 1999). This study indicated that favorable areas are much smaller and more fragmented within Wisconsin than areas within Michigan or Minnesota, and that road density is a robust predictor of wolf habitat (Mladenoff et al., 1999). In addition, SDMs have been used to forecast anthropogenic effects on patterns of biodiversity at different spatial scales, assess climate change impacts, define species migration patterns, population dynamics, and biotic interactions (Guisan & Thuiller, 2005). Using projection of species distribution under climate-warming scenarios, Thomas and colleagues (2004) alarmed the ecological community by predicting that 15-37% of sampled species would be extinct by 2050. Collingham and Huntley (2000) used a spatially explicit model to study the ability of a wind-dispersed tree species to migrate in response to habitat loss and fragmentation caused by climate change. A joint species distribution model was used to examine the pattern of co-occurrence of frogs and trees in Australia (Pollock et al., 2014). A correlative SDM rather than a mechanistic model reveals the environmental variables associated with the presence of the studied species. These models rely on computer algorithms to predict the distribution of species throughout a geographical space based on spatial environmental data. Based on SDMs, the species distribution predictions improve understanding of the spatial patterns of biological diversity (Jiménez-Valverde et al., 2008; Kearney et al., 2010).

Therefore, SDMs have potential to improve understanding of the relationship between species distribution and the physical environment, becoming powerful tools for biodiversity conservation and management (Elith & Leathwick, 2009; Barbosa et al., 2009; Guisan et al., 2013).

Modeling methods are used to study wildlife distributions at different spatial scales. Resource selection functions (RSF) are a suite of correlative model commonly used to model relative selection or avoidance of resources by individuals on either local or regional scales (Morris et al., 2016). The concept of RSF has its origin within the theory of natural selection, which addresses species fitness but also characterizes the selection of resources by a specific species of animal. The process of natural selection occurs when resource selectivity promotes the success of an individual (Manly et al., 2002, Boyce et al., 2002). A RSF can be defined as any function that is proportional to the probability of use by an organism, relating field observations to a set of environmental variables, supposedly linked to key factors of the niche, like climate, topography, geology or land-cover (Manly et al., 2002; Hirzel et al., 2006). Resource selection probability model (RSPF) is a specific RSF with sampling design based on presence and absence data. Consequently, the probability of use can be inferred from site-specific environmental conditions. However, when absence data is lacking, non-used areas can be considered as available habitat. This approach facilitates use of the RSF as an estimation of the relative probability (Manly et al., 2002; Boyce et al., 2002). In the case of used/available data the most common statistical model is a generalized linear model (GLM) using a logistic regression to estimate the function rather than statistical inference (Boyce et al., 2002). With a logistic regression approach, RSF predicts the relative probability values solving the equation:

$$\text{Relative Selection} = \exp(\beta_1 X_1 + \beta_2 X_2 \ldots \beta_i X_i)$$

where β_1 is the estimated coefficient for variable X_1.

Applications in conservation and management, the most important consideration for evaluating RSF models is predictive capacity (Boyce et al., 2002; Hirzel et al., 2006). Boyce and colleagues (2002) developed an evaluation methodology to assess RSF model output. A critique by Keating and Cherry (2004) pointed that the contamination of available samples by used data because available locations were not surveyed extensively. This contamination would biases RSF estimates, and that RSF would not be proportional to the real probabilities. In response to Keating and Cherry (2004), Johnson et al. (2006) modified the evaluation k-fold cross validation developed by Boyce et al. (2002) and demonstrated that RSFs are robust enough to sample overlapping habitats and can be proportional to the true probability described by RSPF for the resource unit. In the study conducted by Johnson and colleagues (2006) it became clear that the RSF model used to predict caribou habitat achieved poor predictive capability but the authors made an important contribution to the modelling community with the modified validation of model output. The modification proposed by Johnson et al. (2006), instead of relying on rank correlations between RSF bins and animal-use frequencies described by Boyce et al. (2002), consists of dividing the data into training (usually 80%) and testing (usually 20%) subsets. The RSF for each group of data (train and test) values is categorized into bins representing increasing likelihood of land use. Then the observed proportions of used locations in each bin of the test data set are regressed against the proportion of used locations in each bin for the training data set, indicating how powerful the model predictive capacity is (Johnson et al., 2006; McNew et al., 2013). Morris and colleagues (2016) conducted a literature review in mapping RSF results finding that the quantile method with five bins was the most common. The authors also suggested that the mapping criteria should match the mapping display. Animal locations derived from telemetry data or GPS collar data combined with geographic information systems (GIS) are increasing in popularity.

The use of geographic information systems (GIS) has facilitated landscape planning oriented to conservation and sustainable development. Importantly, GIS combined with SDMs have been used to:

1) illustrate the distribution and infer the sustainability of habitats

2) explore ecological relationships, based on such variables as selection of vegetation types, as avoidance of habitat disturbed by humans or establishing factors like predation avoidance.

3) identify landscapes favorable for re-introduction or colonization of a new population (Johnson et al., 2006; Zabel et al., 2003; Niemuth, 2003; Brewer et al., 2005;

Hough and Dieter, 2009; Torres and Vercillo 2012). For example, GIS capabilities were combined with classification and regression tree (CART) analysis as well as Bayesian probability analysis to identify biophysical differences between areas of bison overutilization and underutilization within a ranch in southwestern Montana. Phillips (2000) found that from 14 considered variables, only four were significantly important on both methods of bison resource selection. GIS-based evaluations were reported as an efficient tool in preliminary and quantitative evaluation of big horn sheep habitat (Locke et al., 2005). Debeljak and colleagues (2001) used a GIS based habitat suitability model to determine unoccupied habitat for red deer (*Cervus elaphus*) in Slovenia. The results indicated elevation, proximity to settlements, presence of forest, percent of conifers in the forest, and wood stock as important predictors for red deer occupation but also pointed to the necessity of high quality GIS data (Debeljak et al., 2001). Importantly, GIS have been applied in studies of a variety of species (Table 1; Belda et al., 2011).

Table 1. Some examples of GIS-based species distribution models.

LOCAL	**SCIENTIFIC NAME**	**STUDY DETAIL**	**AUTHOR**
Hokkaido - Japan	*Cervus nipon*	habitat selection	(Kaji et al., 2000)
Mediterranean – Spain	*Sus scrofa*	anthropogenic impact	(Belda et al., 2011)
Central Africa	*Loxodonta Africana*	habitat selection	(Roever et al., 2012)
Canada	*Equus caballus*	habitat selection	(Girard et al., 2013)
Slovenia	*Cervus elaphus*	habitat connectivity	(Debeljak et al., 2001)
Wisconsin – USA	*Tympanuchus spp*	potential habitat	(Niemuth, 2003)
Austria	*Castor fiber*	species distribution	(Maringer and Slotta-Bachmayr, 2006)
Texas – USA	*Ovis canadensis*	potential habitat	(Locke et al., 2005)
East Antarctica	*Pagodroma nivea*	nest distribution	(Olivier and Wotherspoon, 2005)
Spain	*Meles meles*	cattle disease reservoir	(Acevedo et al., 2014)
Brazil	*Speothos venaticus*	endangers species	(Jorge et al., 2013)
Brazil	*Panthera onca*	anthropogenic threat	(Silveira et al., 2014)
Arkansas – USA	*Ursus americanus*	habitat selection	(Clark et al., 1993)
Portugal & Spain	*Galemys pyrenaicus*	model transferability	(Barbosa et al., 2009)
South Dakota – USA	*Glaucomys sabrinus*	habitat selection	(Hough and Dieter, 2009)

Geographic information systems (GIS) based SDMs assess the distribution for the species of interest as a function of different environmental predictor variables. These environmental predictors, extracted from carefully selected data from recognized agencies, might be sufficient to describe the species distribution (Maringer & Slotta-Bachmayr, 2006). However, these predictors variables often come from different sources and may have different scales making the task more complex ultimately requiring large data volumes (Store & Jokimäki, 2003). GIS tools can be used to deal with this problem by assimilating data with different spatial scales and then transforming the spatial information to conduct an analysis at the desirable scale for the project (Olivier & Wotherspoon, 2005). Consequently, GIS-based species distribution models (SDMs) are currently the main tools used to predict habitat suitability (Guisan et al., 2013).

Species Distribution Model Transference

Despite the large number of SDM papers published in the first decade of the current century, the practical utility of these models in the conservation management field has been sparse (Torres & Vercillo, 2012; Guisan et al., 2013). However, recent interest in SDMs has expanded beyond the field of ecology, e.g. spatial epidemiology, due to the apparent transferability of GIS-based SDM, and its capacity to predict species response in new scenarios (Werkowska et al., 2016). Spatial model transference can be defined as applying models to different areas of interest than the region from where the model was created (Barbosa et al., 2009). A model can be transferred if it describes biologically meaningful environmental relationships that generally determine the species distribution and at the same time, avoids local-specific relationships that cannot be generalized (Guisan & Thuiller, 2005). The development of spatial transference technique and a better understanding of its limitations appear to have overcome initial unwillingness to apply local models to outlying territories. Most SDMs contain valuable information that could be applied for more efficient research and to support decision making for conservation management (Acevedo et al., 2014). However, several researchers indicated factors that can obstruct the transference or lead to a poor transferability results, such as (Randin et al., 2006; Barbosa et al., 2009; Werkowska et al., 2016):

1. **Environmental differences between geographic regions**. The interpretation of ecological patterns and processes is scale dependent and varying the spatial extent, or the study area, affects patterns and processes that can be modeled. The choice of the study area boundaries is often a convenient rectangle drawn from geopolitical units that enclose the area of interest. In fact, the identification of the study boundaries is not objective (Boyce 2006; Barve et al., 2011; Merow et al., 2014). If boundaries are meant to circumscribe the area of interest, the appropriate extent depends on the specific study question. In case the researcher wants to map the distribution of a species across a large area, locations to be modeled should be drawn from a large area (Boyce, 2006). However, a large study area may include areas with lower suitability levels where species observations are rare or missing and consequently makes the model achieve higher predictive accuracy than warranted (Barve et al., 2011).

Additional bias may arise from differences between spatial extensions of the area where the model was developed to the size of the area where the model will be transferred. Studying the Iberian desman (*Galemys pyrenaicus*), Barbosa et al. (2009) converted a Portuguese distribution model for application in areas in Spain. As Portugal is remarkably smaller than Spain, the Portuguese model included some details that were not captured by the model in Spain.

2. **Spatial resolution of predictor variable**. Usually, the selection of spatial resolution of predictor variables is done opportunistically, guided by what is available for the study area, even knowing that spatial resolution is a factor that significantly affects modelling outcomes (Boyce, 2006). SDMs at both fine and coarse spatial resolution do not necessarily explain the same species distribution; consequently, the same spatial resolution should be used in the new scenario when proceeding with transference (Werkowska et al., 2016; Manzoor et al., 2018).
3. **Model complexity**. The number of predictors and the algorithm used in the model are the two components defining model complexity. Fewer predictors within a model, make it simpler. However, a model with insufficient predictors can bias selection of resources driving species distribution, while complex models, with an excessive number of variables can unintentionally identify local variations or noise as habitat patterns. Furthermore, models with too many predictors increase the risk of

overfitting to local conditions which decreases the predictive capacity of the model and its transferability (Randin et al., 2006; Werkowska et al., 2016). The complex algorithm is related to the shape of the inferred occurrence-environment relationships that are closely linked to the number of parameters used in the model (Elith et al., 2006; Werkowska et al., 2016). Environmental envelopes (e.g., BIOCLIM and DOMAIN) and distance-based approaches in multivariate environmental spaces (e.g., ENFA, Malahanobis) are considered to be the simplest SDMs, Generalized linear models (GLMs) are considered to be simple, and GARP and MAXENT are considered to be complex algorithms (Werkowska et al., 2016).

4. **Species' intrinsic traits, type of predictor variables and their collinearity**. Poor transferability can be caused by species specific traits that are not captured by the environmental predictors. Studying butterflies Vanreusel et al. (2006) found that models for species with smaller space use achieve better transferability than models for species with large home ranges. Werkowska et al. (2016) emphasized the need for more intense research that relates species functional traits to transferability. Therefore, the selection of predictor variables for the study influences directly the predictive performance of the model and its transferability. The majority of the physical environmental variables used as predictors when modelling wildlife habitat have an indirect relationship with ecological functional

resources, e.g. aspect and forage production. Indirect variables are those that would shape the primary variable or have no physiological effect on animal development, e.g. elevation dictates tree-cover. The use of only indirect predictors might increase the chance of errors during the model transference because the relation between those indirect variables and the environmental resources vary in space and time (Austin, 2002; Werkowska et al., 2016). Therefore, predictions derived from model transference must be considered with immense caution due to all the uncertainties raised from the transference process per se and the selected model (Werkowska et al., 2016).

Usually spatial transference is conducted by the same research group that developed the original model (Barbosa et al., 2009; Acevedo et al., 2014). However, when studying badgers (*Meles meles*), Acevedo and colleagues (2014) demonstrated that spatial transference can be done using a habitat map developed by other researchers. Acevedo and colleagues (2014) could not use the original badger habitat models developed by Reid et al. (2011) and Etherington (2009) because those models were developed using local fine scale predictor variables not available in Spain. However, Acevedo et al. (2014) used habitat areas in Northern Ireland (Reid et al., 2011) and England (Etherington et al., 2009), as the training region for a set of new models that was then, applied in Spain. This effort started by generalizing new models using broad-scale environmental predictors that were available for the training region, and the application region, Spain. The resulting model's assessment (Spearman's rank correlation, $rho>0.9$)

indicated that it was a useful predictor of badger abundance in the evaluation region in Spain (Acevedo et al., 2014).

Bison as Target Species

The American bison (*Bison bison*) is a migratory ungulate that once lived in high densities throughout the Great Plains and in lower densities in meadows and shrub-steppe communities in the Rocky Mountains (Van Vuren, 1987). After the near extinction of bison during the 19th century, a population surviving on the Yellowstone Plateau became the cornerstone of species recovery serving as a source of animals for new herds throughout the nation. Prior to the establishment of Yellowstone National Park (YNP), historical estimates of the Yellowstone Plateau bison herd size were approximately 800 animals (Meagher, 1973; Dary, 1974). The population remained under 1,500 between the time of park creation in 1872 and 1954 because the herd was managed through culling (Coughenour, 2005; Fuller et al; 2007). After the Natural Regulation Policy, that stopped human interference, was adopted in 1968, the herd rapidly increased to 3,000 animals by the end of 20th century. In an effort to address the issues associated with an expanding herd, a multidisciplinary collaboration was formed, the Interagency Bison Management Plan (IBMP; USDI, 2000). The preferred management alternative of the IBMP focuses on maintaining the Yellowstone bison herd below 2,500 individuals (USDI, 2000). However, park managers were not able to control the herd size, which later peaked at 5,500 animals in 2016 and through a culling effort, the population declined to 4,200 according to the YNP estimation in February of 2018 (Wright, 2018). Despite recent culling, the Yellowstone bison herd has been managed as free roaming. In contrast, another population at the National Bison Range (NBR) is constricted by fences and managed in a rotation grazing system (Borgreen, 2010). The NBR was established as a US Fish and Wildlife Service (USFWS) refuge in 1909 to restore and conserve the remaining local herd of 37 animals. The population has been stable at 250 - 300 animals since the early 1950's through annual culling (Borgreen, 2010; Garcia Neto, 2014). A third, regional population, in Grand Teton National Park started from 11 animals that escaped from a wildlife park in 1968 growing to 1,100 in 2005. Since then, a population reduction plan has been in place lowering the herd to 600, in 2017, through a long annual hunting season that lasts from August to January (D. Reinhart, personal communication, May 6, 2016). Unlike the NBR population, bison at Grand Teton National Park (GTNP) are free-roaming animals like the Yellowstone herd. Developing a model based on maps of bison land use within the GYE and transferring it to GT and NBR enrich the understanding of the transfer processes itself and the general bison resource selection.

Bison Resource Selection

Several studies indicated that bison are highly mobile. Norland (1984) studying the herd fenced within the Theodore Roosevelt National Park, observed a constant movement of bison into new areas. Bison moved an average of 1.6 km per day, reaching a n annual home range of 56.1 km^2 (Norland, 1984). In Utah's Henry Mountains the summer home range of bison cows was 98 km^2 (Van Vuren, 1983). In the more mesic conditions of Yellowstone National Park, Wyoming, McHugh (1958) reported summer home ranges of 31 km² and winter home range of 93 km², and daily movement between 2.7 and 9.3 km within several other refuges and parks that he studied. However, Geremia et al. (2014) reported the movement of a single bison reached 40 km during the winter migration out of YNP. The home range of bison cows on Santa Catalina Island, California (Lott and Minta, 1983) was equivalent to the area reported by Norland (1984). These home range sizes fit the observations of Later and Gates (1994) and Van Vuren (1983) that home range is related to forage availability, animals that have access to a richer environment developed smaller home ranges.

Several researchers report that bison select for grasslands (Table 2). In the Konza Prairie environment, comparison between bison and domestic cattle emphasized that bison strongly prefer open grassland to wooded habitats (Knapp et al., 1999). In contrast, Shult (1972) studying bison in the Ponderosa pine mixed grass, reported a strong selection for grasslands except during the spring when bison also selected for woodlands. In Prince Albert National Park, Canada, a forested landscape with wolves, Fortin et al. (2009) reported that large groups of bison select for larger meadows in a clear effort to lower predation risk (Fuller, 1960). In another study of Prince Albert National Park bison, Dancose et al. (2011) described meadow selection and found that bison were more likely to transit to meadows that were closer to their current location, using forest canopy gaps rather than dense forest. Norland (1984) interpreted North Dakota bison avoidance of forest habitats as diet based, 90% graminoide (Peden et al., 1974; Van Vuren & Bray, 1983).

Table 2. Summary of reported bison habitat selection.

ECOREGION	HABITAT PREDICTORS	SEASON	AUTHOR
Badlands	Grassland	Year	Norland, 1984
Boreal forest	Forage availability	Year	Larter & Gates, 1994
Tallgrass Prairie	Grassland	Year	Knapp et al., 1999
Ponderosa mix-grass	Grassland	Summer	Shult, 1992
Northern Rockies	Meadows	Year	Fortin et al. 2009
Northern Rockies	Meadows	Year	Dancose et al. 2011
Northern Rockies	Low elevation, gentle slopes	Year	Phillips, 2000
Northern Rockies	Low elevation, ruggedness, distance to water, gentle slope	Year	Fisher & Gates, 2005
Northern Great Plains	High elevation, distance to water, gentle slope	Summer	Kohl et al., 2013
Palouse Prairie	Gentle slope	Yearly	Rutberg, 1984
Yellowstone Plateau	Gentle slope	Yearly	Rutberg, 1984
Yellowstone Plateau	Gentle slopes	Year	Coughenour, 2005
Tallgrass Prairie	Gentle slope	Year	Allred et al. 2016
Tallgrass Prairie	Gentle slope	Year	Raynor et al., 2016
Pinon-juniper	Steep slope, vertical distance to water	Summer	Van Vuren, 2001

Bison are able to cope with deep snow easier than any other gregarious species of large animal within YNP (Meagher, 1973). McHugh (1958) observed bison grazing in snow up to 4 feet deep; however, Meagher (1973) reported that the location of the most used sites by bison within YNP would rarely face that condition. Snow is a highly local variable (Geremia et al., 2014) and within mountainous areas, the elevation impacts snow depth. Therefore, elevation might work as an indirect measure of snow depth. Two studies conducted in mountainous environments, Phillips (2000) in southwestern Montana and Fisher and Gates (2005) in Yukon, Canada found that bison selected locations that were lower in elevation. However, Van Vuren (1979, 1983) reported that elevation was not significant on bison habitat selection. A study conducted in the prairie of eastern Montana and Saskatchewan during summer, Kohl et al. (2013) reported that bison selected higher elevation and the authors suggested that the selection is related to the selection of upland vegetation communities.

Large groups of bison were found on more gentle slopes (Rutberg, 1984). Phillips (2000), Coughenour (2005), Fisher and Gates (2005), Allred et al. (2011), Kohl et al. (2013), and Raynor et al. (2016), confirmed bison selection for less steep areas. In YNP Coughenour found that bison do make use of slope up to 25% (14°). Apparently, the only disagreement comes from the Henry Mountains, Utah where Van Vuren (1979, 2001) and Ranglack and Toit (2015) conducted studies comparing domestic cattle with bison. These last authors found slope being not relevant on their bison model selection but Van Vuren (1979, 2001) reported bison selection for steep areas and found that bison exhibited a peak of use at slopes of 30°. In contrast to Phillips (2000), Fisher and Gates (2005), Allred et al. (2011), Kohl et al. (2013), and Raynor et al. (2016) used digital elevation model (DEM) to calculate slope, Van Vuren (1979, 2001) calculated slope using a clinometer which raises the question if slope values measured with different methods support different conclusions.

Ruggedness, also called roughness, can be defined as topographically uneven or broken terrain (Sappington et al., 2007). There is no consensus in how to calculate ruggedness, but this terrain characteristic is closely related to slope. Ruggedness calculated as the standard deviation of elevation correctly identifies smooth sloping areas and terrain breaks (Grohmann et al., 2011). Another terrain descriptor, profile curvature, is also related to the breaks of slope but not as strongly as ruggedness (Grohmann et al., 2011). Ruggedness is frequently considered in bighorn sheep habitat studies, especially related to escape terrain (McKinney et al., 2003, Mooring et al., 2004, Bangs et al., 2005, Sappington et al., 2007). However, Fisher and Gates (2005) used this terrain variable as a predictor in bison resource selection because it explained bison occupancy better than slope (Fisher & Gates, 2007).

In a study conducted in the Tallgrass Prairie of Oklahoma, distance to water did not influence bison habitat selection (Allred et al., 2011). Within the North Dakota badlands, Norland (1984) reported that the distance between water sources and bison locations averaged 1 km, which was shorter than the average distance of randomly placed locations (1.8 km). He also pointed out the ability of bison to use different water sources each day including ephemeral creeks, potholes and snow. Both the Phillips (2000) and Van Vuren (2001) studies were in a mountainous environment, and found horizontal distance to water irrelevant regarding bison utilization. However, Phillips (2000) suggested that all foraging areas on the studied ranch might have water sources close enough for bison drinking requirements. The Van Vuren (2001) study was conducted within a small pasture (375 ha) and showed that bison occurrence declines as vertical distance to water increases. In a study comparing bison against caribou in Yukon, Canada, within a mountainous environment bison were found close to water bodies (Fisher & Gates, 2005). In agreement with that, Kohl et al. (2013) studying bison on the prairie in north central Montana and Saskatchewan, Canada, observed selection of water resources; however, bison still used areas more than 10 km from these sources. In summary, there is a strong agreement of bison selection of grassland and that vertical distance to water negatively affects bison land use. On the other hand, horizontal distance to water and elevation depend on the particular study area. In addition, ruggedness, profile and planimetric curvature, slope, and horizontal distance to water were also considered possible predictors on the current bison resource selection study.

CHAPTER THREE – METHODOLOGY

Study Area and Bison Management

The current study used habitat information from 3 different locations. The Greater Yellowstone Ecosystem (GYE) the study area was delimited by the four maps previously developed by YNP. In Grand Teton (GT) the study area was delimited by the watersheds that contain at least one record of the bison telemetry data (Boyce, 2006). The National Bison Range (NBR) study area was delimited by fences within the range.

Greater Yellowstone Ecosystem

The study area is located in the northwestern GYE encompassing part of the Yellowstone National Park (YNP), the Gardiner Basin, the Taylor Fork, the Cabin Creek Recreation & Management Area, the Lee Metcalf Wilderness Area, and the Hebgen Basin, Montana (Figure 2). Outside YNP, there are some private properties, some land owned by the Bureau of Land Management (BLM), and Montana State; however, the US Forest Service (USFS) owns the majority of the land within this area. The YNP bison are one of the few free roaming herds in the US, and the migration toward lower elevation sites has increased as the population size increased (Coughenour, 2005). The migration increased because the traditional winter habitat is not large enough to sustain the excessive number of animals (Meagher 1989, Coughenour 2005). Historically bison have been forced by Montana Fish, Wildlife and Parks to go back to the park in the spring when the animals have access to replenished grazing sites within the YNP. However, recently Montana State Government established a tolerance zone where bison are allowed to stay outside the park yearly (Appendices B1 and B2). It became clear that the tolerance zone was based on the four original maps created by the YNP biologists in 2014.

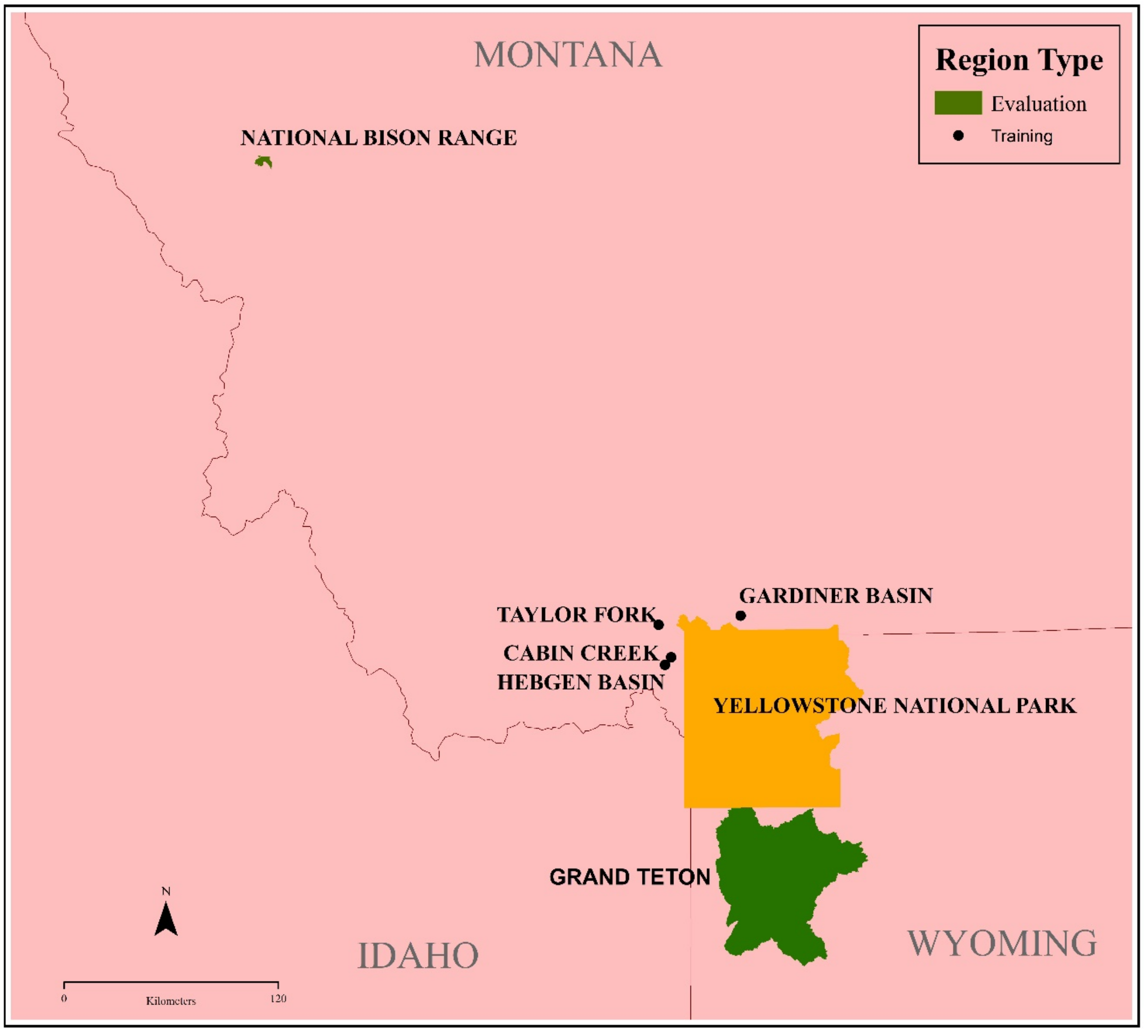

Figure 2. Study area including training regions where the top predictive model was developed and the evaluation regions where the top predictive model was transferred for evaluation.

Grand Teton and National Bison Range

Grand Teton National Park (GTNP) is located on the western border of Wyoming, only 16 kilometers south of Yellowstone National Park (YNP). The GT study area presents a highly diverse landform from the high elevation of the Grand Teton peaks (4,199 meters) to the Absaroka and Wind River Ranges to the east. Between these mountain ranges lies the Jackson Hole Basin (1,860 meters). The Grand Teton mountain range became a national park in 1929 and was extended in 1950 incorporating some portions of Snake River Valley. The GT study area includes the Grand Teton National Park (GTNP), a large portion of US National Forest (USNF) land, the National Elk Refuge and the John D. Rockefeller Junior Memorial Parkway because all these administrative units are fenceless areas contiguous to GTNP and are accessible to the bison herd (Figure 3). As outlined for this evaluation, the GT study area sums 41,145.2 ha. The local bison population is managed through hunting to stay around 500 animals, a size that is accepted by all the agencies involved and the private sector (D. Reinhart, personal communication, May 6, 2016).

The National Bison Range (NBR) was established as a US Fish and Wildlife Service (USFWS) refuge in 1909 with the objective to restore and conserve the remaining herd of bison. It lies in the Flathead Valley with rolling hill formation where elevation varies from 763 to 1490 meters (Garcia Neto, 2014). The study area encompassed four pastures of NBR, Alexander Basin, Mission Creek, Headquarter, and Upper Pauline, reaching 3,686.1 ha (Figure 4). The NBR herd contains approximately 250-300 animals managed through the pastures in a deferred rotation during the summer. The pastures vary in landform and vegetation from lowlands in Alexander Basin and river bottoms in Mission Creek to steep slopes within Upper Pauline (Guffey et al., 2011).

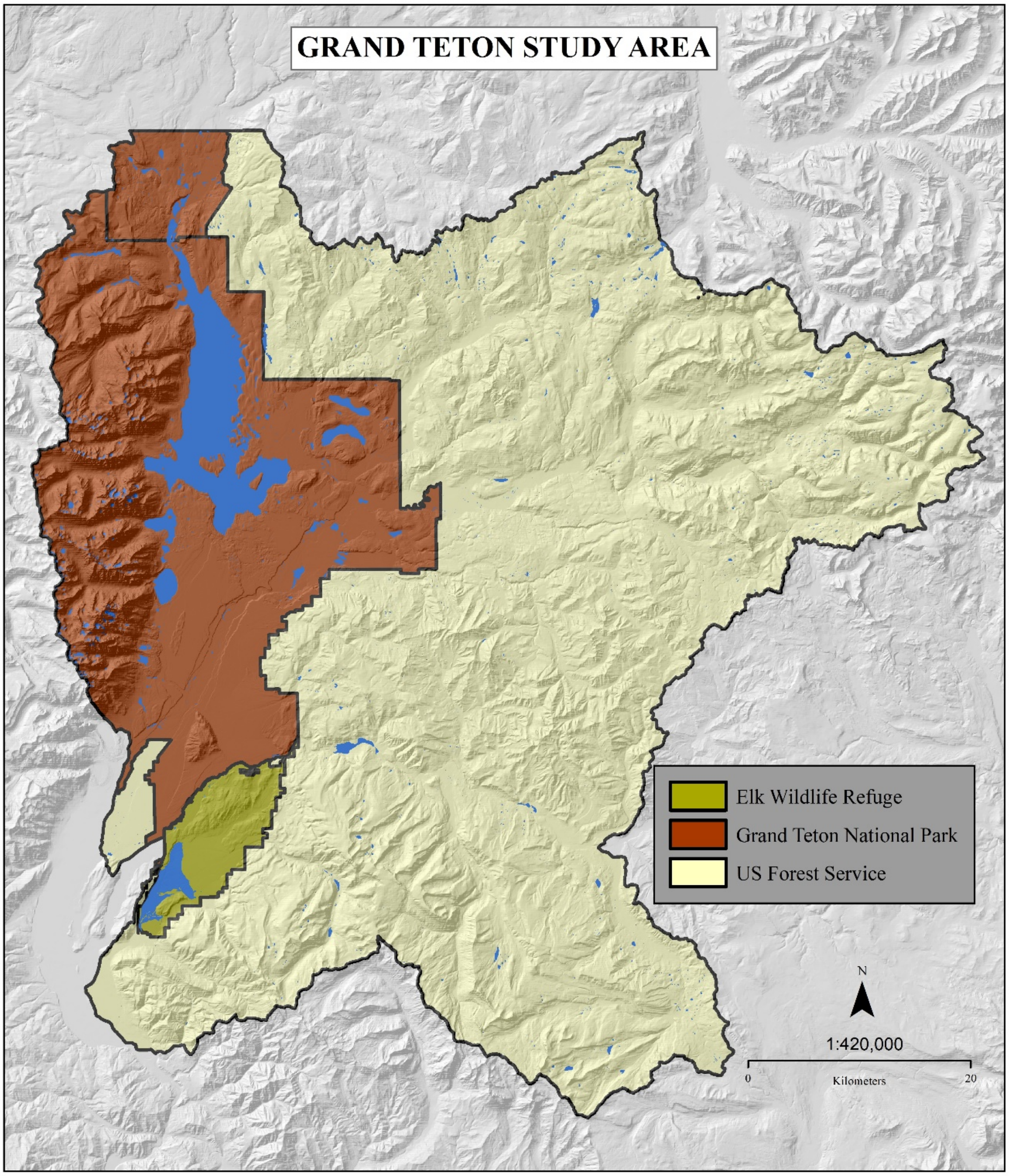

Figure 3. Grand Teton study area encompasses the Grand Teton National Park, the National Elk Wildlife Refuge and land owned by US Forest Service.

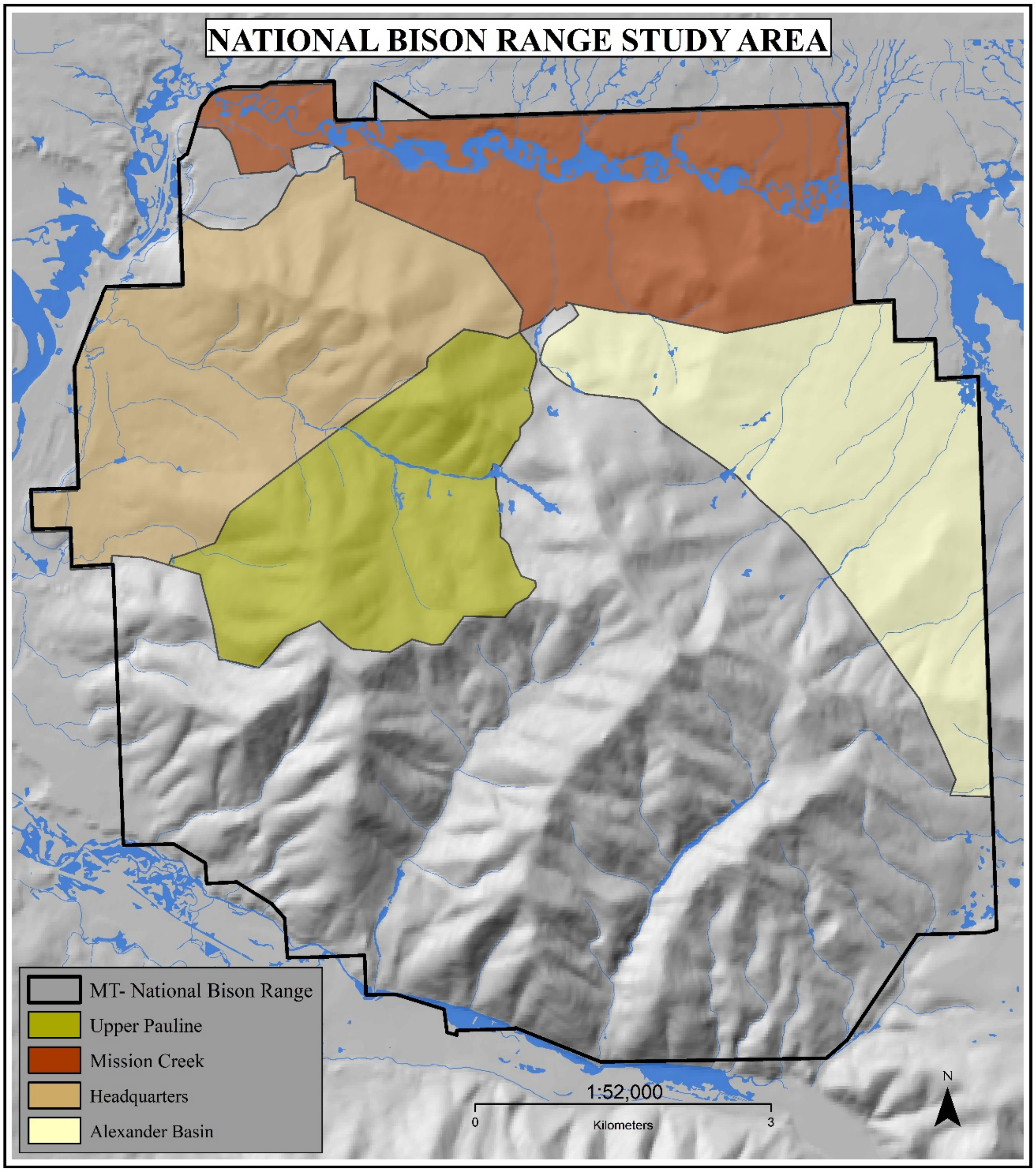

Figure 4. Study area is at the northern portion of National Bison Range encompassing the Upper Pauline, Mission Creek, Headquarters, and Alexander Basin pasture units.

Map Acquisition

When discussing the availability of areas outside YNP boundaries for yearlong bison occupation, YNP biologists developed four maps as accessory information meetings of the Interagency Bison Management Group. Three maps encompassing the areas around Gardiner Basin, Taylor Fork, and Hebgen Basin were downloaded from the Montana Fish, Wildlife and Parks website (2014). The fourth map, encompassing the Cabin Creek Recreation & Management Area and Lee Metcalf Wilderness was acquired from USFS (J. Canfield, personal communication September 4, 2014). These original maps became the base for a new bison habitat model. The original maps (Appendices B3, B4, B5, and B6) were downloaded in a pdf format and were opened with Adobe Acrobat Pro 11 then saved as high quality graphic format (.tif) making it possible to use ArcGIS 10 (ESRI, 2011), to conduct spatial analysis within each mapped environment. The unit of measurement for the YNP on the original maps was acres, so areas within the new maps were calculated as acres to make direct comparison. The study area encompassed 1.3 million acres of the northwestern portion of the Greater Yellowstone Ecosystem (GYE) and overlapped the YNP boundaries. The four original maps contain five areas of interest: 1) Gardiner Basin, 2) Taylor Fork, 3) Cabin Creek Recreation & Management Area, 4) Lee Metcalf Wilderness, and 5) Hebgen Basin (Figure 1 and 2). The four original maps were created in 2014 by YNP biologists to depict both the current and predicted bison habitat in the northwestern GYE. However, the maps did not encompass the entire bison range of the YNP herd.

I assumed that current habitat are the areas delineated by the original maps to be used by bison, predicted habitat are those areas, delineated by the original maps, that the park biologists believe fit bison requirements, but were not inhabited yet, and no-habitat are those remaining areas depicted by the original maps expected to be unused by bison. In most SDM studies, habitat classification is based on fieldwork defining map cells or polygons as used by the designated species. Both classes, used and not used, are generally or not determined from direct observation of space use patterns (Manly et al., 2002, p.4). For the current study, the habitat classes were defined by the mapped predictions of bison use extracted from the four original maps developed by YNP biologists and used by IBMP.

Georeferencing

Georeferencing is the process that aligns an image to a known coordinate system, so it can be viewed and analyzed with other geographic data (ESRI, 2018). A key step in georeferencing is the identification of reference points on the map that can be linked with other layers that already have embedded a coordinate system. In other words, points on the figure must be linked with other layers that are already georeferenced. Therefore, the georeference procedure, available on the ArcMap 10 software package (ESRI, 2011), was used to digitize all four original maps individually (Figure 2, Appendices B3, B4, B5, and B6).

The YNP boundary layer (NPS, 2015) was used as the base for the georeference procedure because all four original maps include the YNP boundary (Appendices B3, B4, B5, and B6). In addition, I used other source layers to achieve accuracy on the georeference process. For the Gardiner Basin map I used the Hydrological Units boundaries (HUC12; NHD, 2014) layer as the georeference source. For the Taylor Fork map, the Lee Metcalf Wilderness boundaries (USDA, 2015), and the public land survey system (PLSS; Montana State Government, 2015) layers were used. For the Cabin Creek Recreation & Management Area and Lee Metcalf Wilderness map, the US Forest Service (USDA, 2015) wilderness boundaries layer and the PLSS layer (Montana State Government, 2015) were used as a reference. Finally, the Hydrological Units boundaries layer (HUC10; NHD, 2014) and the Cabin Creek Recreation & Management Area boundaries layer (USDA, 2015) were used to georeference the Hebgen Basin original map.

I georeferenced each original map one at a time. A minimum of four control points were established on each original map, spreading the control points over the entire map area in a way to have at least one control point in each corner, if needed, one in the center to achieve accurate georeference. I established a link at each control point to connect the original map point with associated reference layers. The final georeferenced map is only as accurate as the data with which it was aligned. For each established link, the ArcGIS georeference tool calculates the root-mean-square error (RMSE). This error describes how consistent the georeference process is, but it should not be interpreted as an absolute accurate georeference per se (Klinger, 2102). With this information, I erased links with RMSE higher than 100 meters, and tried to link a different control point. Using this trial-and-error process, I worked to achieve the best possible accuracy (Table A1, Hayes, 2013). Additionally, the United States National Map Accuracy Standards (USGS, 1947) determine that, not more than 10% of the points tested should have error larger than 1/50 of an inch. Because there is no ground tested points in the current study, the highest RSME (98.3 meters) was set as the value to define the scale.

Classification

The four original maps contain both predicted and no-habitat. However, current-habitat was depicted in the original Gardiner and the Hebgen Basin maps. One challenge that may occur in other effort similar to this one is that the original maps had poor color contrast between current, predicted and no-habitat classes (Appendices B3, B4, B5, and B6). Two or more similar colors can represent the same class due to the high amount of superimposed layers contained in those habitat maps. The YNP biologists drew ownership and habitat classes over a topographical map that already had several colors depicting different features. The result is a color complex map, which makes segregation of the habitat classes difficult (Figure 5a). Therefore, I created a new raster depicting areas of different habitat classes using the tools within ArcGIS 10 (ESRI, 2011): classification, cleanup and mosaic.

After testing a couple of classification methods, “unsupervised maximum likelihood”, and “principal components”, I selected the “interactive supervised classification” where the operator draws samples over the polygons of interest over the original map, assigning them to the new raster classes: current habitat, predicted habitat, and no-habitat. Therefore, based on the information from the four original maps, the first classification process was used to create new rasters depicting areas of two classes, predicted habitat and no-habitat. The same classification process, described above, was repeated to define the current habitat within the Gardiner and the Hebgen basin maps resulting in two other rasters. There are no tools to assess the resulting classification raster, therefore the classification was subjectively assessed by a visual inspection. Using the high degree of transparence on the raster resulted from the classification process I checked the cell classification against the original map.

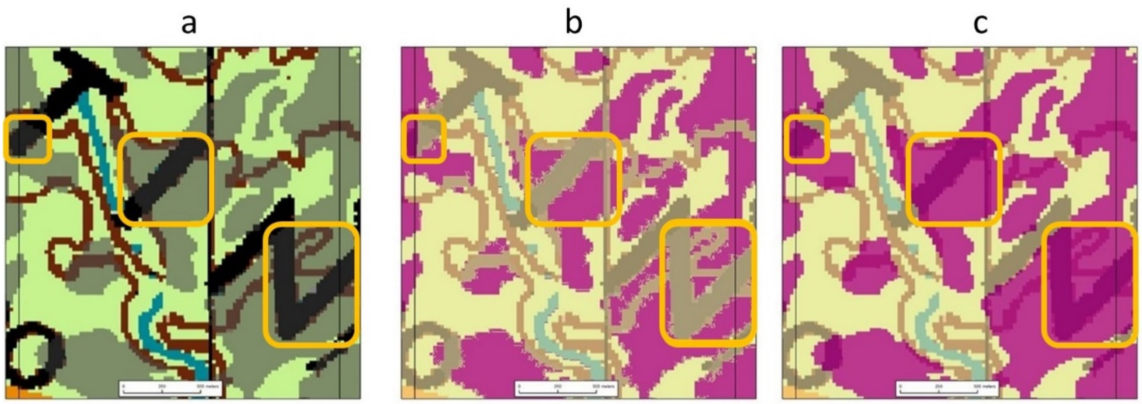

Figure 5. Classification process example. The yellow boxes depict cells with low color contrast within the original map (a). The classification process misclassified those cells (b), which were correctly re-classified through the cleanup procedure (c).

Clean Up

I conducted the cleanup procedure on the four predicted habitat maps and the two current habitat maps. Using the original map as a background and the classification outcome new raster with high transparency, I identified erroneously classified cells, and with the editor tool, corrected the classification of those cells. A significant zoom was needed to see the exact border of the different habitat class areas (current habitat, predicted habitat, or no-habitat). The procedure was conducted by moving the window over the entire area covered by the map, certifying that all the cells were corrected according to the original map. This visual inspection required 40-60% of transparency on the newly classified raster. The original Hebgen basin map is extremely color complex resulting in a very poor classification (Figures 5b, and 5c) consequently considerable time was devoted to the cleanup procedure (Table 3).

Table 3. Time spent on the geographic information system (GIS) procedures of the four maps developed Yellowstone National Park biologists.

Training Area	Procedure	Hours
Gardiner Basin	Georeference	5
Gardiner Basin	Classification	6
Gardiner Basin	Cleanup	85
Taylor Fork	Georeference	4
Taylor Fork	Classification	5
Taylor Fork	Cleanup	95
Cabin Creek	Georeference	4
Cabin Creek	Classification	9
Cabin Creek	Cleanup	65
Hebgen Basin	Georeference	5
Hebgen Basin	Classification	9
Hebgen Basin	Cleanup	255
Gardiner Basin	Classification	4
Gardiner Basin	Cleanup	55
Hebgen Basin	Classification	5
Hebgen Basin	Cleanup	85

Mosaic

After classification and clean up procedures on the four maps depicting predicted habitat and the two maps showing current habitat, I used the mosaic tool of ArcGIS 10.5.1 (ESRI, 2017) on those maps to compile in a new raster (Figure 6) that contained the habitat class classification for the entire study area.

Sampling

Presence/absence information is preferred over presence-only data when modelling spatial distribution (Boyce et al. 2002; Hirzel et al., 2006). However, presence/absence data are not often available (Royle et al., 2012). The four original maps depict both bison habitat and no-habitat; therefore, I assumed that areas described as no-habitat and predicted-habitat were unused by bison. Additionally, I had to assume that the original space-use analyses used to generate the habitat classification were conducted without error, or at least that any classification error was random. Although there is no information available on how YNP biologists defined the bison current habitat areas, it is reasonable to assume they used YNP bison location data generated with global positioning system (GPS) collars (Bruggeman et al., 2007). To account for errors in bison space use that may influence predicted map error, I used the GPS error values defined by Hulbert and French (2001). However, GPS errors are not the only errors we should consider when developing habitat maps.

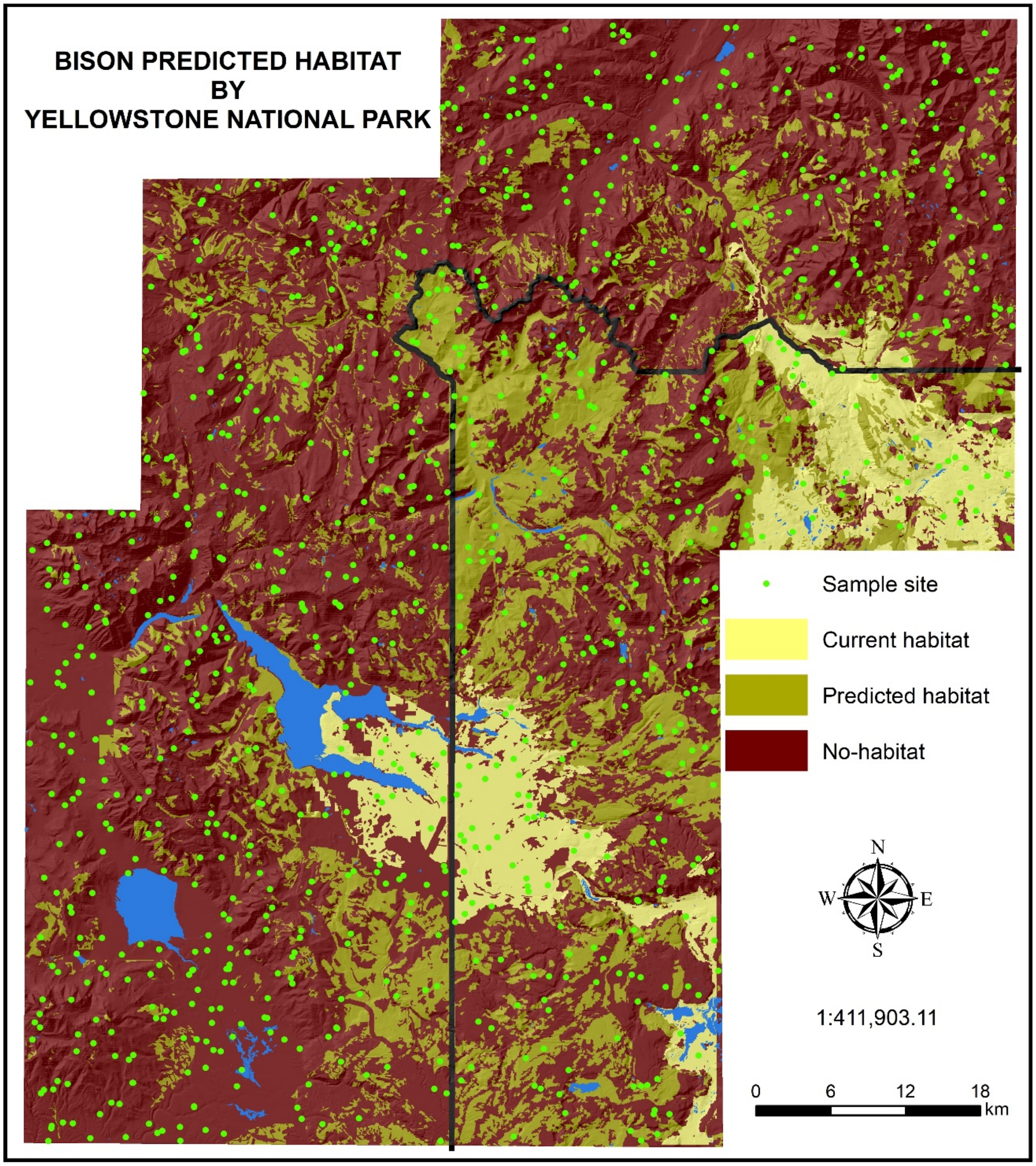

Figure 6. The 959 randomly assigned sample points over the different habitat classes developed by Yellowstone National Park, digitized and mosaic by the authors.

Georeferencing also introduces uncertainties into the map, further diluting map accuracy. Therefore, I summed the largest root-mean square error (RSME) from the georeferencing process (98.3 meters; Appendix A1) with the possible GPS error on roving GPS collared animals (25 meters; Hulbert & French, 2001) and developed a buffer of 124 meters on the boundaries of all polygons to compensate for both types of errors (Figure 7). Thus, the study area minus the buffer of 124 meters, defined the sampling area. In other words, sampling was not done within the 124 meter buffer.

The spatial analyst extraction tool in ArcGIS Desktop 10.6 (ESRI, 2018) was used to extract the predictor variables for each sample point. A set of one thousand sample points was randomly assigned within the sampling area. Those points that fell within water bodies were discarded as well as those falling on polygon boundaries because we were not able to classify those cells.

Environmental Predictors

Using ArcGIS Desktop 10.6 (ESRI, 2018), an overlay of the following 12 rasters, representing the environmental candidate variables was used to transfer the value of each covariate for the sample points, and then transferred to “R” package 3.4.4 analyses (R Developing Core Team, 2013). All the selected environmental predictor variables for the entire US are available for download, making it possible to extrapolate the model to the entire country.

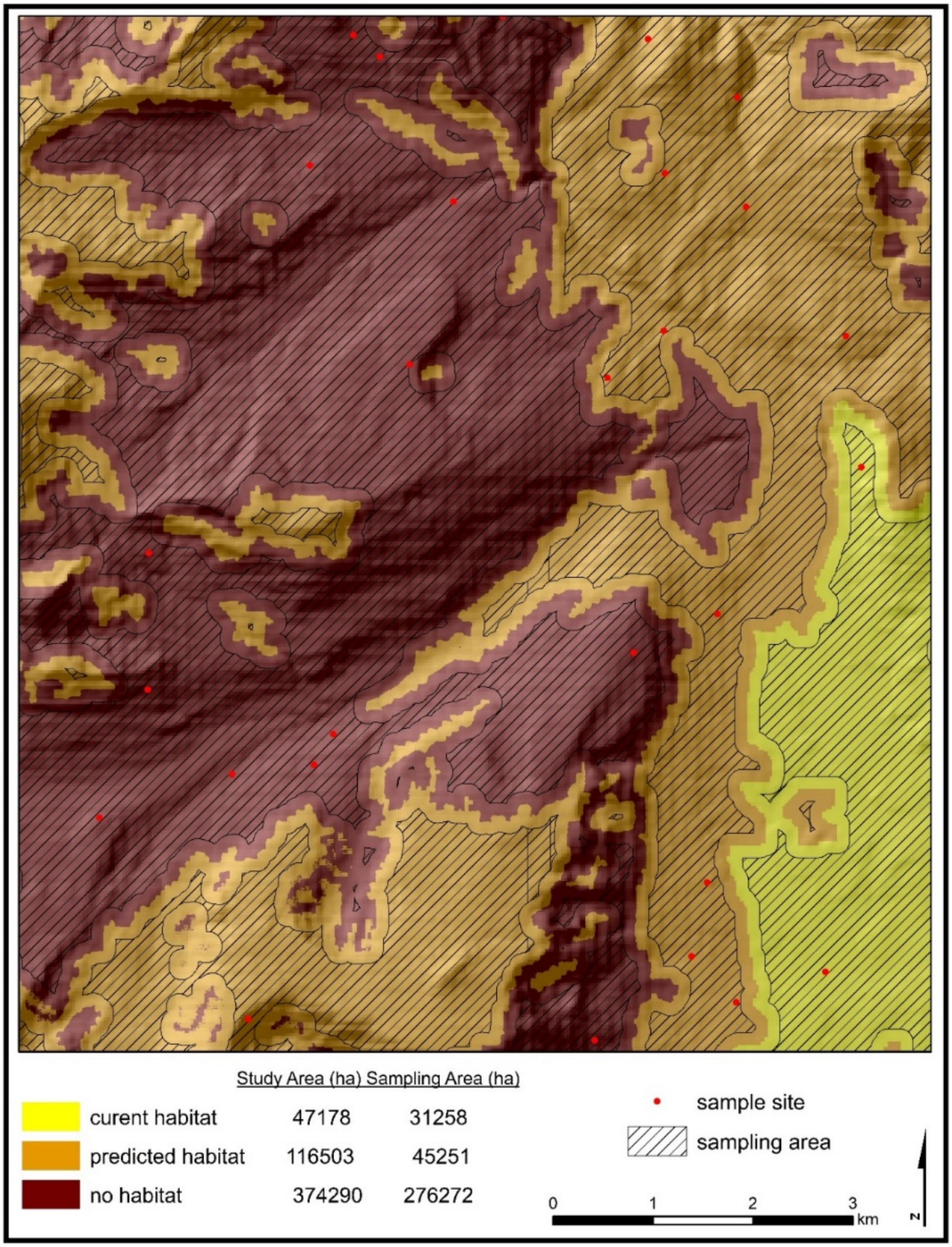

Figure 7. A detail of different habitat classes from original maps classified and mosaicked by the author. The buffer zone was excluded from sample site assignment to compensate for possible errors from the georeferencing procedure and bison position data.

Relative Elevation

Digital Elevation Model (DEM) is a numerical dataset that contains the elevation of the topography data for a specified area, usually as a fixed grid interval over a surface of the earth (Erdogan, 2009). The United States Geological Survey (USGS, 2017) website site has the 1 arcsec, DEM from the National Elevation Dataset (NED) with a spatial resolution of 27 meters. After downloaded, I clipped the tile to the study area extent and projected the layer to UTM, Zone 12 North, on North American Datum of 1983 (NAD 83). Because I intended to transfer the model to other regions and the elevation range of other areas might be different from the current study area, I scaled the elevation by dividing DEM cell value by the average of the DEM values of the entire study area, creating a new raster of the relative elevation named 'elrati'. I hypothesized that the probability of bison use would decline with increasing elevation (Phillips, 2000; Fisher & Gates, 2005).

Slope

Slope is the measure of steepness and may be a major determinant of ungulate distribution across the landscape (Ganskopp & Vavra, 1987). The DEM from USGS was used to create a unique value raster representing the slope in degrees with the previous spatial resolution of 27 meters. I hypothesized that bison land use will decline as the slope increases (Phillips, 2000; Coughenour, 2005; Fisher & Gates, 2005).

Curvature

The curvature tool from ArcGIS was used to measure change in slope and aspect by calculating second derivatives from the DEM (Kennely, 2008). The tool also produces a profile curvature and a planform curvature. The profile curvature is the curvature of the surface parallel to the slope direction. A positive value depicts that the surface is upwardly concave. A negative value means that the surface is upwardly convex. The profile curvature can help identify marked changes of slope and ruggedness (Grohmann et al., 2011). I am pioneering the relationship of curvature to bison habitat selection and I hypothesize that convex curvatures will lead to relatively greater use by bison compared to concave profile because a lower runoff speed and consequently more stable soils that ultimately favors forage production. Planimetric curvature is perpendicular to the direction of the slope, a positive value means that the surface has convex sides and negative value indicates the surface has concave sides. Because the convex planimetric curvature might show higher vegetation productivity, I hypothesized that bison would select for the convex planimetric curvature. The curvature is measured in centimeters.

Ruggedness

Terrain ruggedness or roughness can be defined as how the terrain is broken, or how drastically the elevation changes over a short distance. It is a feature that can be an important driver of land use by terrestrial animals (Riley et al., 1999). In the GIS field of study, there is no consensus on how terrain ruggedness can be represented or calculated, so I tested four methods as possible parameters (Grohmann et al., 2011):

1) The vector ruggedness (VRM) is the result of a tool added to the ArcGIS software (ESRI, 2018) that was developed by Sappington and others (2007).

2) In an attempt to capture how the slope changes through the landscape, we used the regular slope tool within ArcGIS 10.6 (ESRI, 2018) to calculate the slope of the previously calculated slope raster.

3) The standard deviation of elevation in a 10 x 10 window (sddem; Grohmann et al., 2011).

4) The standard deviation of slope in a 10 x 10 window (sdslo; Grohmann et al., 2011). I hypothesized that as the ruggedness of the terrain increases the probability of bison use decreases. In addition, I anticipate that these indexes will be collinear with slope (Fisher & Gates, 2005).

Percent Tree Canopy

The National Land Cover Database (NLC2011; NLCD, 2014) is a source of vegetation data that covers the entire United States. The NLCD2011, US Forest Service Remote Sensing Applications Center (RSAC) developed the "Percent Tree Canopy" as a cartographic product. This Landsat based layer (percov) with spatial resolution of 30 meters was used to represent the tree canopy. I hypothesized that land use by bison will decrease as the percent tree canopy increases (Fortin et al., 2009; Dancose et al., 2011).

Horizontal Distance to Water

The Euclidean distance tool was used to calculate the distance to the closest water source (hordis). The water source layer is a combination of the perennial features on the "NHDFlowline" from the National Hydrological Dataset (NHD, 2014), the streams from US National Atlas Water Features Lines (USANAWFL, 2016), and wetlands from the US Fish and Wildlife Service (2017). I hypothesized that land use increases as the distance to water increases until it reaches a specific value above which the use declines (Norland, 1984; Allred et al., 2011).

Vertical Distance to Water

The same layer combination used to calculate horizontal distance was transformed into a raster, and then the tool Euclidean allocation was used to assign elevation values from the closest water source to a grid representing the entire study area. Then those values were subtracted from the elevation raster (DEM). The resulting raster contains the vertical distance to the closest water source (verdis). I hypothesized that the land use declines as the vertical distance increases (Fisher & Gates, 2005; Kohl et al., 2013).

Generalized Model

The search for a highly predictive model was the main objective of the current study however, the need to keep it simple was also pursued because simplicity increases the likelihood of model success elsewhere. This means spatial transference had to be another objective of the current study (Barbosa et al., 2009; Werkowska et al., 2016). Because, there is uncertainty that areas classified as no-habitat on the original maps were never used by bison. I used a resource selection function (RSF) to evaluate bison selection for habitat features in a use/available design (Manly et al., 2002). This approach meant no-habitat and predicted habitat had to be considered as available because bison did probably not occupy both classes when the YNP biologists developed the original maps. I used a logistic regression (R Development Core Team, 2013) to model the land use by bison comparing available (predicted habitat and no-habitat) against current-habitat (Manly et al., 2002). The predicted response from a RSF does not represent the real probability of use, but is proportional to the true probabilities of use calculated from logistic regression. Thus the sampling probabilities and the intercept term (β_0) cannot be estimated (Manly et al., 2002).

The first step in defining which predictor variables (Table 4) to include in candidate models was to assess multi-collinearity using Pearson correlation coefficient (Zuur et al., 2009). If the correlation was less than 0.5, I kept both variables as candidates for modelling. I considered collinear variables those with correlation larger than 0.5 (Appendix B7). Two models containing one of the collinear predictor variables each were created and compared using Akaike Information Criterion (AIC; Zuur et al., 2009). The predictor variable present in the model with lower AIC was retained and considered more important in explaining bison land use. Before selecting models, AIC was used to decide if a predictor variable should be included as a linear term or as a quadratic term. To determine the most parsimonious model a backward stepwise regression was used starting with a full model containing all the non-collinear variables, each appearing as linear or quadratic function according to the preliminary screenings. The model with lowest AIC was selected as the one that provided the most parsimonious model of bison habitat use (Burnham & Anderson, 2002; Arnold, 2010). I then used the raster calculator of ArcGIS (ESRI, 2018) to create a raster of bison land use relative probability.

Table 4. Summary of candidate predictor variables.

Predictor Variables	**Descripiton**	**Raster Names**
Elevation ratio	Elevation ratio from DEM	elrati
Slope	First derivative from DEM	slopd
Curvature	Second derivative from DEM	curvat
Planimetric curvature	Second derivative from DEM	placur
Profile curvature	Second derivative from DEM	procur
Ruggedness 1	Vector ruggdness measure (VRM)	rugd1
Ruggedness 2	Slope of slope	rugd2
Standard deviation of elevation	Ruggedness index from dem	sddem
Standard deviation of slope	Ruggedness index from slope	sdslo
Tree cover	Percent of trees (USGS)	percov
Horizontal distance to water	Euclidean distance	hordis
Vertical distance to water	Diference in elevation	verdis

*Digital elevation model

A cross validation assessment was conducted to evaluate the predictive accuracy of the top model. Using a k-fold cross-validation approach, the data were randomly split into training data (80%) and test data (20%) (Johnson et al., 2006; McNew et al., 2013) First, the top model was fitted to the train data. Then, the coefficient estimates obtained from the training data were used to calculate RSF values for the test data. The test data was binned according to RSF values into five bins; the first bin contained the lowest 20% RSF values and the fifth bin the highest 20%. The proportion of locations used by bison and the median RSF values (RSF bin mid-points) were calculated for each bin. This process was repeated ten times and averaged. Lastly, I regressed the averaged proportion of used locations against the averaged RSF mid-points of each bin. A highly predictive model would yield R^2 and the regression slope values close to 1, and an intercept value close to zero (Johnson et al., 2006; McNew et al., 2013).

Mosaic of Original Maps

Summing the predicted habitat would be inflated because the original maps overlap in some areas (Figure 8). Therefore, the original maps were combined into a mosaic using ArcGIS 10.5.1 (ESRI, 2017) with UTM-zone 12 NAD83 coordinate system. The final product of the mosaic procedure depicts current and predicted habitat for the entire study area. It is important to mention that the GIS procedures maintain the same habitat polygons defined by YNP biologists. The mosaic tool (ArcGIS) just put the four maps together based on georeferenced points.

Land Ownership

The cadastral of Park, Gallatin and Madison counties within Montana, were downloaded from Montana State Library website (Montana State Government, 2015) and the cadastral file for Fremont County from Idaho State tax commission website (Idaho State Tax Commission, 2018). The US Forest Service (USFS) owns the majority of the land within this area and the YNP biologists considered all the land owned by USFS available to bison. However, some of the original maps depict private properties as bison predicted habitat. For the top predictive model mapping, we considered all USFS land available to bison, ownerships other than USFS, including Montana or Idaho private or state land were considered not available to bison.

Top Predictive Model and Map

The current habitat depicted from the mosaic of the original maps (Figure 4) is the area bison use, based on GPS collar data. However, it is unclear what the predictor variables were that park biologists considered to predict habitat. The top predictive model describes bison land use as a relative probability range, in other words, it depicts a gradient of relative probability values. Therefore, the minimum RSF value of top predictive model within the current habitat established the threshold between bison habitat and no-habitat. Consequently, the other polygons throughout the study area that have the same relative probability range as the current habitat polygons would then be classified as habitat. Therefore, inputting the specific relative probability value in the top predictive model produced a map depicting bison habitat that can be compared against the predicted habitat in the original maps. The output of top predictive model depicts the current habitat layer drawn from the mosaic of the YNP to make visualization easier. The Jaccard similarity coefficient was used to assess the similarity between the predicted habitat depicted within the original maps and the predicted habitat outlined the top predictive model. Jaccard similarity coefficient is a ratio between the calculated areas of the intersection between two polygons, divided by the polygon area resulted from the union of the two polygons (Levandowsky & Winter, 1971).

Model Transference

The top predictive model developed with data from GYE was used to predict bison habitat in the GT study area and NBR. The predictor variables were downloaded from the same sources as for GYE. The bison herd at NBR is managed in a rotational system in a way that the resource availability is constrained by the pasture fences. Therefore, the predictors' raster were created for each individual pasture independently and only then mosaicked to calculate the RSF. With this process, it is guaranteed that the RSF had taken into account when bison are within a specific pasture they do not have access to other pastures' resources.

The ability of the top predictive model to predict bison habitat in GT and NBR, was tested using two approaches. First, I calibrated the top RSF from GYE using habitat data generated from studies in GT and NBR, in which predictors were the same ones selected by the GYE model but the coefficients were re-estimated using site-specific presence /availability data. The 10 years (1997-2007) telemetry dataset from GT bison herd (S. Dewey, personal communication, December 6, 2016) was used to calibrate the top predictive model.

At NBR, bison-selected grazing areas were delimited in an observational study conducted during the summers between 2010 and 2012 using methodology adapted from Plumb and Dodd (1993). Each summer five 3 days sampling periods with a minimum of 10 observations per sampling period were used to define bison selection at NBR. Ocular pastures observations were made between sunrise and 10:00 am and again from 2:00pm to sunset to match diurnal activity peaks of bison. Herds were located by traveling all

NBR roads and further searching on foot. Pastures were extensively surveyed to maximize the possibility of encountering bison. When a group of 15 or more bison was encountered, observations commenced. A minimum distance of 260 meters was kept from the bison group to minimize disturbance. Distance to various landmarks was estimated and manual sketches or photographs were taken for accurate re-location of the central position of the group. A total herd count was obtained with binoculars at 15-minute interval. Within the same observation interval, a single animal was systematically selected and behavior (grazing, resting, ruminating…) was classified and recorded. Observations continued for two hours, or until the group left the site. Valid observation required a minimum of 30 minutes herd occupancy at the site. Locations from all four NBR pastures were used to calibrate the top predictive model. The assessment of RSF model transference was done using the k-fold cross-validation used for the GYE (Johnson et al., 2006; McNew et al., 2013). The second approach, using the uncalibrated model, was drawn from the top RSF using GYE coefficients.

Another model assessment was done comparing training and test data as the percentage of used locations within each bin. Similar proportions are expected from a high predictive model (McNew et al., 2013).

CHAPTER FOUR – RESULTS

Top Predictive Model

Georeference

The largest RMSE came from the Cabin Creek map, 98.3 meters (Appendix G). This value dictates the cartographic scale that the model must use to objectively assess all four original maps. Therefore, to comply with the United States National Map Accuracy Standards the most detailed scale should be applied to this model is 1:198,000.

Sampling

After discarding 41 samples points falling on waterbodies and boundary lines, a total of 959 points covered the bison habitat map, with 93 occurring in areas classified by YNP as current habitat. One hundred thirty three points were within the predicted habitat class, and 733 were within the no-habitat class. The sampling area was reduced from 537,971 ha to 352,781 ha due to 124 meters buffer used to control the uncertainties from georeferencing and GPS collar errors (Figure 7). The number of points in each habitat class was approximately proportional to the area of the class (Table 5).

Table 5. Distribution of habitat classes through sampling area and sampling points among bison habitat classes.

	Sampling Area		**Sample Points**	
Habitat classes	**ha**	**%**	**quantity**	**%**
Current	31,258	8.9	93	9.7
Predicted	45,251	12.8	133	13.8
No habitat	276,272	78.3	733	76.4

Collinearity

Two sets of variables were collinear. The curvature methodology takes into account the two derived curvatures: planimetric curvature (placur) and profile curvature (procur). As expected curvature (curvat) and planimetric curvature were correlated (r = 0.8) and curvature was correlated to profile curvature (r = - 0.9; Appendix H). The lower AIC supported the model containing planimetric curvature (placur) and profile curvature (procur) over the model with only curvature (Table 6). So, planimetric curvature and profile curvature were retained in full resource selection modelling.

Table 6. Collinear variable selected by Akaike Information Criteria (AIC). The lower IAC values within the set of models indicated the model that represent better the data.

Collinear variables set 1	k*	AIC
procur +(procur)²+placur+(placur)²	4	604.08
curvat+(curvat)²	2	607.1
Collinear variables set 2		
slopd+(slopd)²	2	535.29
rugd1+(rugd1)²	2	552.15
rugd2+(rugd2)²	2	551.12
sddem+(sddem)²	2	524.59
sdslo+(sdslo)²	2	526.82

*k is the number of co-variates.

Slope (slopd) was collinear with all ruggedness indices. Standard deviation of elevation (sddem) were more influential in the model for terrain ruggedness, thus I eliminated slope and all other ruggedness indices from further consideration (Table 6).

Model

The four models were fitted to the dataset derived from the habitat map developed by YNP and ranked by AIC values (Table 7). The resulting AIC values for models 1, 2 and 4 were substantially higher than that of model 3. Therefore, model 3 had the most support (ω_i = 0.67) and was selected as the best model for bison habitat selection.

Table 7. Models for bison habitat selection based on current (1) and no-habitat (0) plus predicted (0) data.

	Model	k	AIC	Δ AIC	AIC weight
3	elrati+(elrati)²+sddem+(sddem)²+procur+(procur)²+percov+hordis+ verdis	10	431.84	0.00	0.67
4	elrati+(elrati)²+procur+(procur)²+percov+hordis+ verdis	8	433.94	2.10	0.23
2	elrati+(elrati)²+sddem+(sddem)²+placur+(placur)²+procur+procur²+percov+hordis+ verdis	12	435.8	3.96	0.09
1	Null	1	612.67	176.87	0.00

Notes: Each model are presented with the number of parameters (k), the AIC value, the delta AIC (Δ AIC) and the Akaike weight (Weight).
elrati = relative elevation
sddem= standard deviation of elevation
placur= planimetric curvature
procur= profile curvature
percov= tree percent cover
hordis= horizontal distance to water
verdis= vertical distance to water

Model 3 was the most parsimonious model and indicated that bison habitat selection in the study area was associated with elevation, standard deviation of elevation, representing ruggedness, profile curvature, percent of tree cover, horizontal distance to water, and vertical distance to water (Table 8).

Table 8. Estimated resource selection function coefficients of the model 3 for bison.

parameter	**estimate coef**	**std.error**	**z value**	**p - value**
intercept	-26.1600	9.159	-2.856	0.0043
relative elevation	68.0200	21.860	3.111	0.0019
(relative elevation)²	-44.8700	13.080	-3.431	0.0006
ruggedness	-0.0362	0.036	-1.006	0.3145
(ruggedness)²	-0.0002	0.001	-0.207	0.8362
profile curvature	-0.5958	0.376	-1.585	0.1129
(profile curvature)²	-0.0525	0.160	-0.329	0.7424
percent tree	-0.0282	0.007	-4.225	0.0000
horizontal dist. to water	0.0007	0.000	2.516	0.0119
vertical dist. to water	-0.0013	0.003	-0.398	0.6910

The plot of elevation (Figure 8a) and its quadratic term indicated that bison use increased until elevation reaches 1,750 meters, decreasing after that, and becoming almost non-existent when elevation reached 2,500 meters. The estimated relative probability of use by bison decreases as the standard ruggedness increases, becoming almost non-existent when standard deviation of elevation is about 55 meters (Figure 8b).

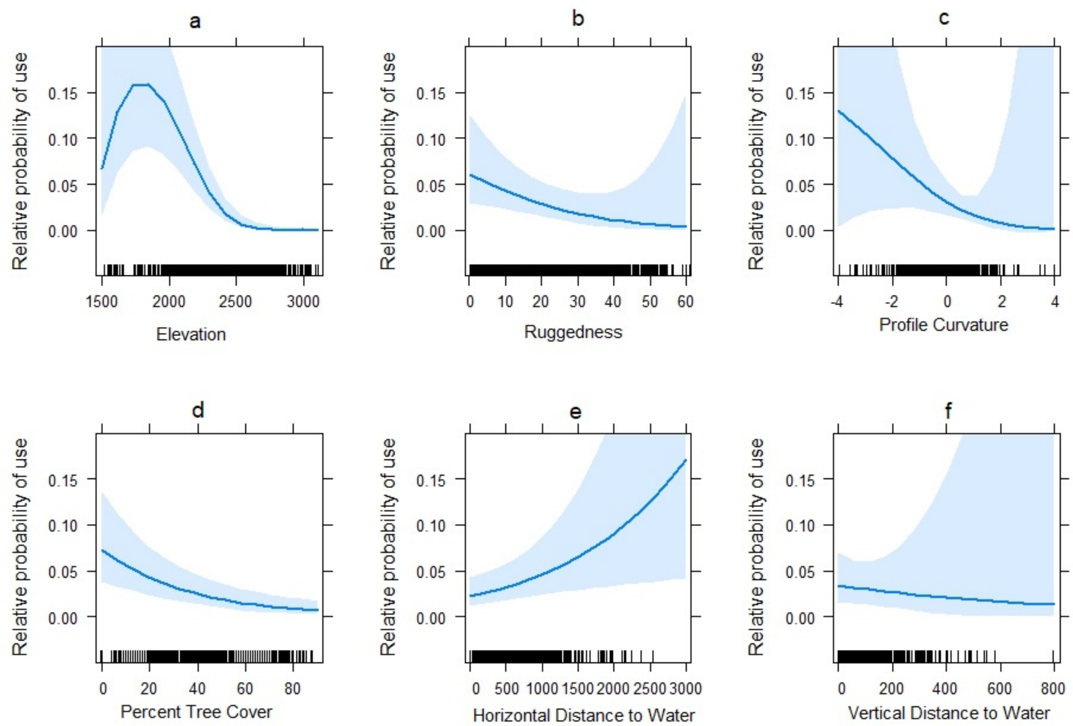

Figure 8. Estimated effects with 95% confidence bands of (a) elevation, (b) standard deviation of slope, (c) profile curvature, (d) percent tree cover, (e) horizontal distance to water, and (f) vertical distance to water. These curves were designed using logistic regression values from a dataset of bison land use.

The estimated relative probability of bison use decreased abruptly as profile curvature departed from negative values, demonstrating bison selection of convex profile (Figure 8c). Relative use by bison declined as tree cover increased, and this relative probability become very low when tree cover reaches 40% (Figure 8d).

The estimated relative probability of bison use increased as horizontal distance to water increased. However, the results indicate that the great majority of bison occurrence is closer than 2,000 meters to water (Figure 8e). The estimated relative probability of use by bison decreased as vertical distance to water increased (Figure 8f). The results indicate that the great majority of land use occurs when values of vertical distance to water are lower than 400 meters.

Model Assessment

Cross validation of the top model indicated high coefficient of determination (R^2= 0.98), an intercept of 0.02, overlapping zero (95% CI: -0.06 to 0.09), and a slope close to 1.0 (β=0.92, 95% CI: 0.7 to 1.13; Figure 9) suggesting good fit to the data and high predictive accuracy (Johnson et al., 2006; Figure 8). From the comparison between train and test data, the top predictive model classified the great majority of RSF values on the top two bins for both datasets (Figure 9). Similarly, the Spearman Rank Correlation (r_s = 0.97) confirmed that the top predictive model achieved a good overall fit. Thus, the RSF was used to generate a new map depicting five classes, in line with the accuracy assessment (Figure 10; Morris et al., 2016).

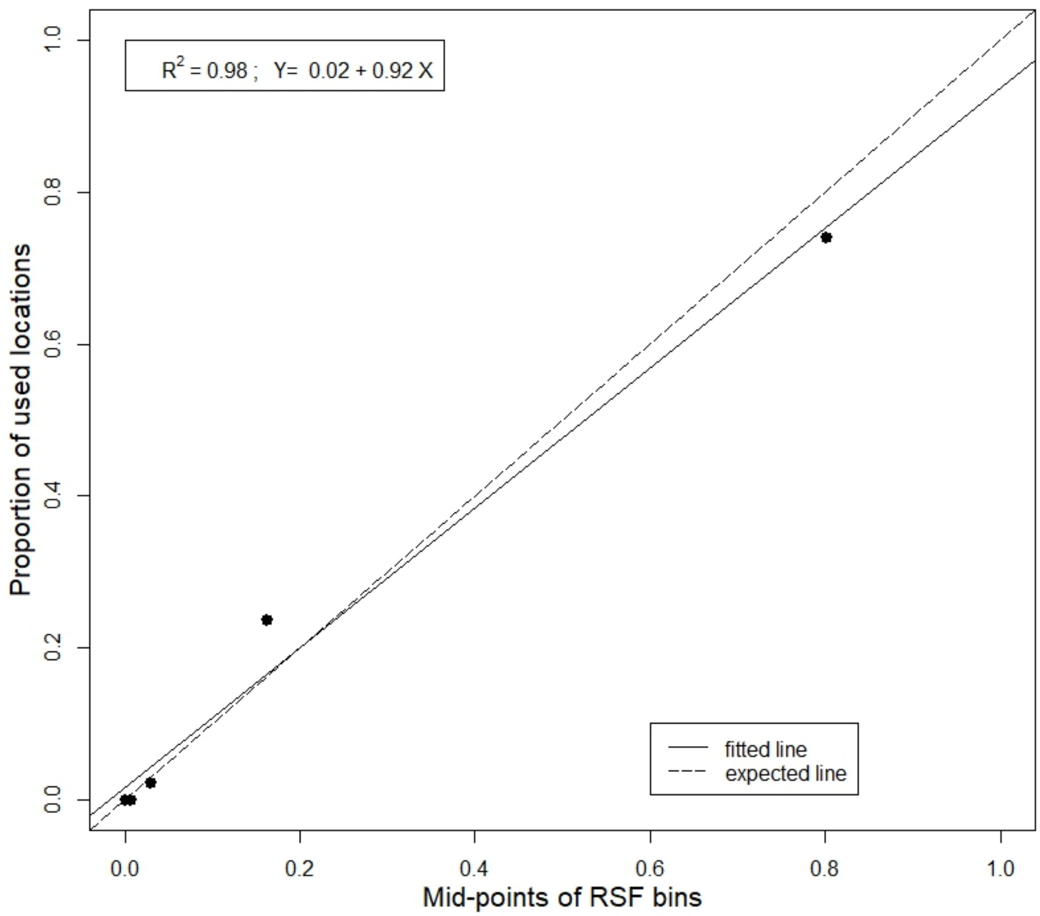

Figure 9. The proportion of resource selection function (RSF) values of used locations versus the proportion of RSF bin values. The perfect fit (train-test) would occur along a line with slope of 1 and intercept of zero (dashed line). The fitted regression is shown as dark line, while points are the observations. Regression coefficient of determination (R^2) equal to 0.98 indicates that the top predictive model accurately classified used points in the test data set used for model validation.

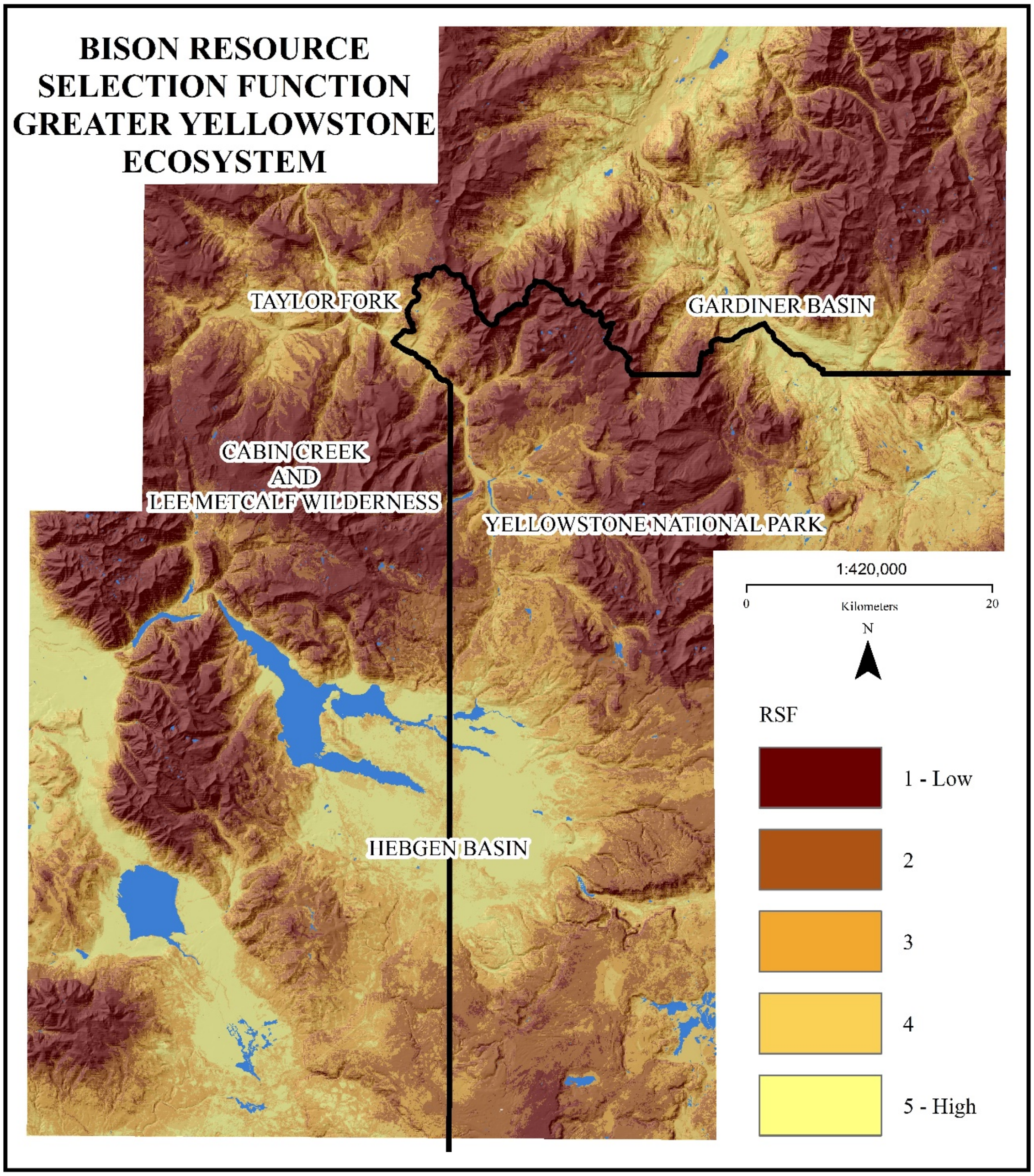

Figure 10. Bison resource selection function (RSF) at Greater Yellowstone Ecosystem. RSF results were mapped using quantile classification with 5 bins in line with the validation binning.

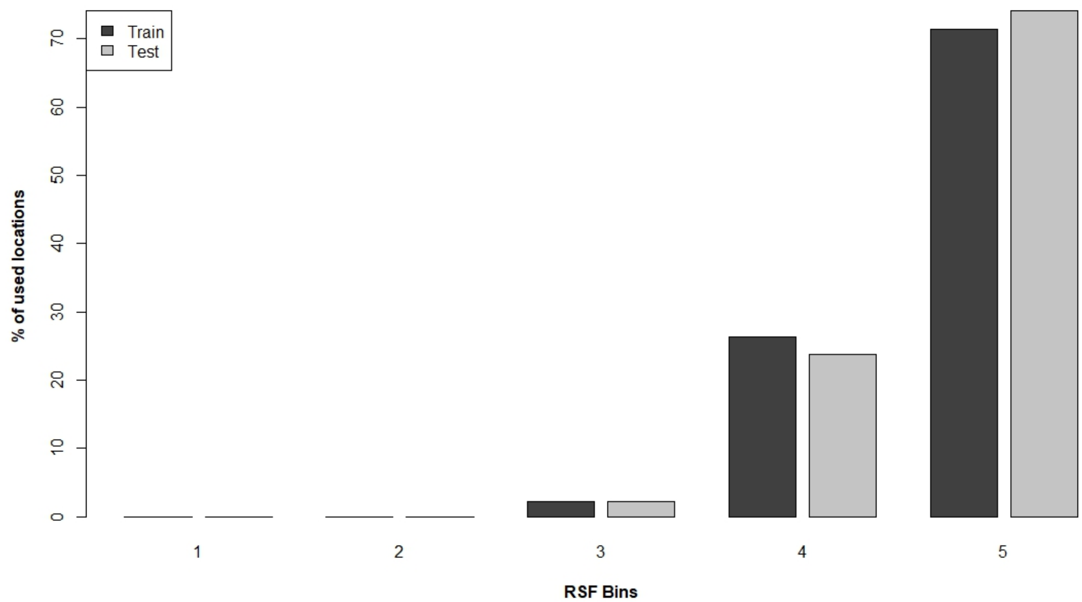

Figure 11. Percentage used locations in 5 bins of increasing resource selection function (RSF) values used to train (black bars, n = 767) and test (gray bars, n = 192) the top predictive resource selection function model for bison in Greater Yellowstone Ecosystem. The matching proportions indicated that the top predictive model (model 3) accurately classified used locations in the test data set.

Model Comparison

I used the minimum RSF value within the current habitat polygons depicted in the original maps as a threshold to segregate bison habitat. Within the GYE study area, any cell that had a RSF value larger than 4.3 e+12 was considered bison habitat (Figure 12 b). To calculate the Jaccard similarity coefficient, I overlaid the bison habitat depicted by the top predicted model (model 3) with the mosaicked original maps. The intersection of both polygons that predict habitat was 49,648 acres. The union of both raster that predict habitat (the mosaic of original maps, and the top predictive model) is 390,794 acres. Calculation of Jaccard similarity coefficient (dividing 49,648 acres by 390,794 acres) produced a value of 0.127. A perfect match would have a coefficient of one, in other words only 12.7 % of bison habitat predicted by the top predictive model coincide with the predictions of YNP. In addition, 32.5% of the predicted habitat by the top predictive model is in agreement with the original maps. On the other hand, 17.2% of the predicted habitat by the original maps agrees with the top predicted map (Figure 12).

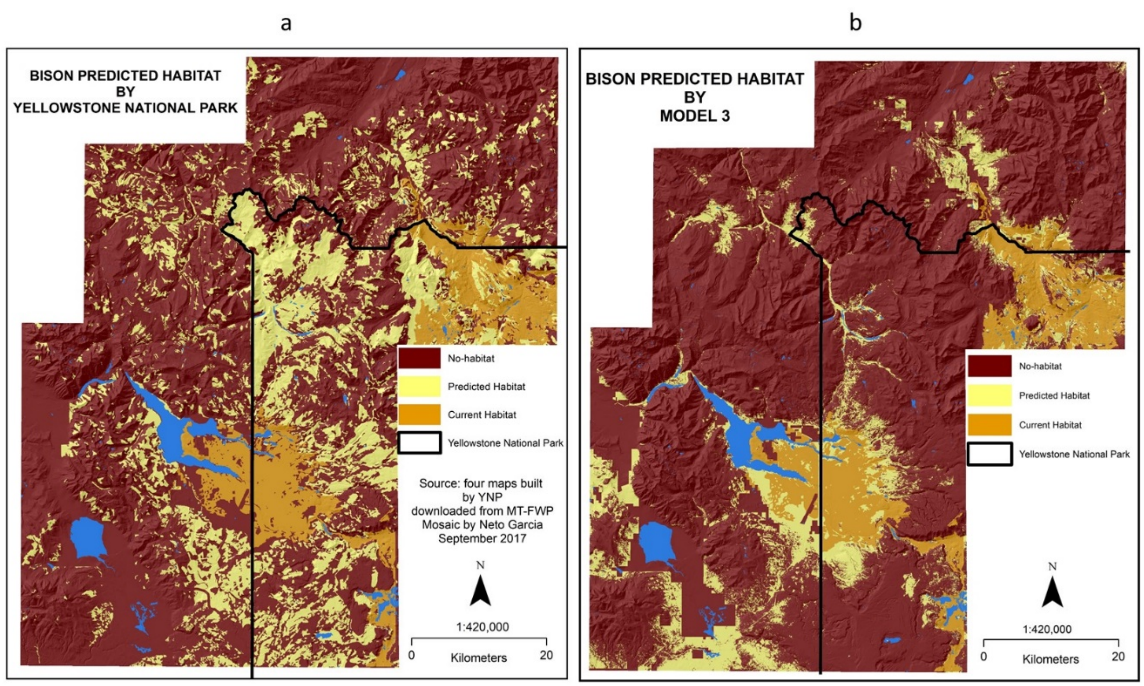

Figure 12. The mosaic of maps originally built by Yellowstone National Park biologists (Montana Fish, Wildlife and Parks 2014; a) and top predictive model (b).

The mosaic of the four original maps delimited 1,329,355 acres with 116,581 acres of current habitat and 287,885 acres of predicted habitat, and the remaining area as no habitat (Figure 12, Table 8). Importantly, 160,986 acres of predicted habitat are inside the northwestern portion of YNP (Figure 12a). In contrast, the top predicted model depicts 152,558 acres of predicted habitat, with 47,889 acres within the northwestern portion of the park (Figure 12b, Table 9).

Table 9. Summary of differences in size between the mosaic of maps originally built by Yellowstone National Park (YNP) biologists (Montana Fish, Wildlife and Parks 2014) and the top predictive model.

	Bison Habitat by Mosaic YNP (ac)	**Bison Habitat by Top Predictive Model (ac)**	**Difference Between Models (ac)**
Predicted total	287,885	152,558	135,327
Predicted inside YNP	160,986	47,889	113,097

The original Gardiner Basin map depicts 13,707 acres of current habitat while map 3 depicts 13,179. The original Gardiner Basin map depicts 55,727 acres of predicted habitat, of which 37,816 acres are outside the park (Figure 13a, Table 10). Top predictive model depicts 31,279 acres with 22,453 acres outside the park boundaries (Figure 13b, Table 10).

Table 10. Summary of differences in size between the mosaic of maps originally built by Yellowstone National Park (YNP) biologists for Gardiner Basin (Montana Fish, Wildlife and Parks 2014) and top predictive model.

	Bison Habitat by Mosaic YNP (ac)	**Bison Habitat by Top Predictive Model (ac)**	**Difference Between Models (ac)**
Current	13,707	13,179	528*
Predicted total	55,727	31,279	24,448
Predicted outside YNP	37,816	22,453	15,363

*Difference might be attributed to geographic information system (GIS) procedures to develop the top predictive model.

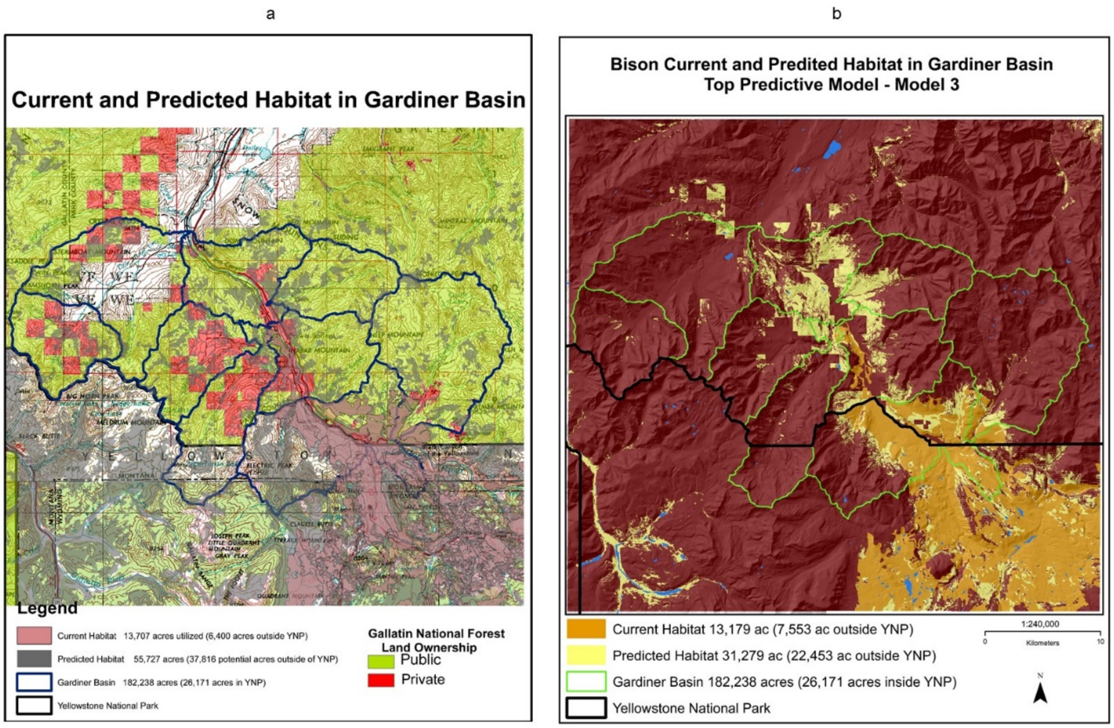

Figure 13. The mosaic map built by Yellowstone National Park biologists for the Gardiner Basin (Montana Fish, Wildlife and Parks 2014; a), and top predictive model (b).

The original map of the Taylor Fork area, depicts 14,894 acres of predicted habitat (Figure 14a, Table 11) and my top predictive model (model 3) depicts 9,050 acres of predicted habitat, primarily riparian areas (Figure 14b, Table 11).

Table 11. Summary of differences in size between the mosaic of maps originally built by Yellowstone National Park (YNP) biologists for Taylor Fork (Montana Fish, Wildlife and Parks 2014) and top predictive model.

	Bison Habitat by Mosaic YNP (ac)	**Bison Habitat by Top Predictive Model (ac)**	**Difference Between Models (ac)**
Taylor Fork area	61,032	62,124	1,092*
Predicted	14,894	9,050	5,844

*Difference might be attributed to geographic information system (GIS) procedures to develop the top predictive model.

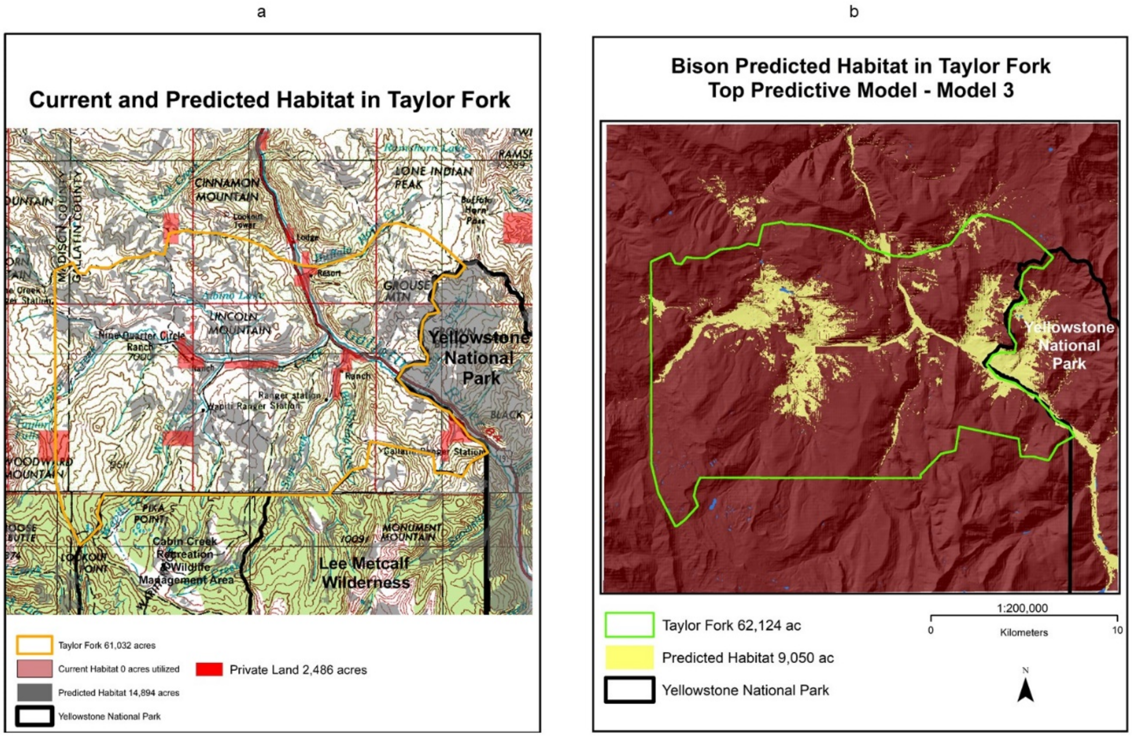

Figure 14. The Taylor Fork map built by Yellowstone National Park biologists (Montana Fish, Wildlife and Parks 2014; a), and top predictive model (b).

Within Cabin Creek, the original map depicts 4,641 acres of predicted habitat on Cabin Creek Recreation & Management Area and 6,808 acres within Lee Metcalf Wilderness (Figure 15a, Table 12). Top predictive model depicts 21.5 acres of predicted habitat within the Cabin Creek Recreation & Management Area, and 27.9 acres in the Lee Metcalf Wilderness (Figure 15b, Table 12).

Table 12. Summary of differences in size between the mosaic of maps originally built by Yellowstone National Park (YNP) biologists for Cabin Creek Recreational & Management Area and Lee Metcalf Wilderness (Montana Fish, Wildlife and Parks 2014) and top predictive model.

	Bison Habitat by Mosaic YNP (ac)	**Bison Habitat by Top Predictive Model (ac)**	**Difference Between Models (ac)**
Cabin Creek	4,641	21.5	4,619.5
Lee Metcalf	6,808	27.9	6,780.1

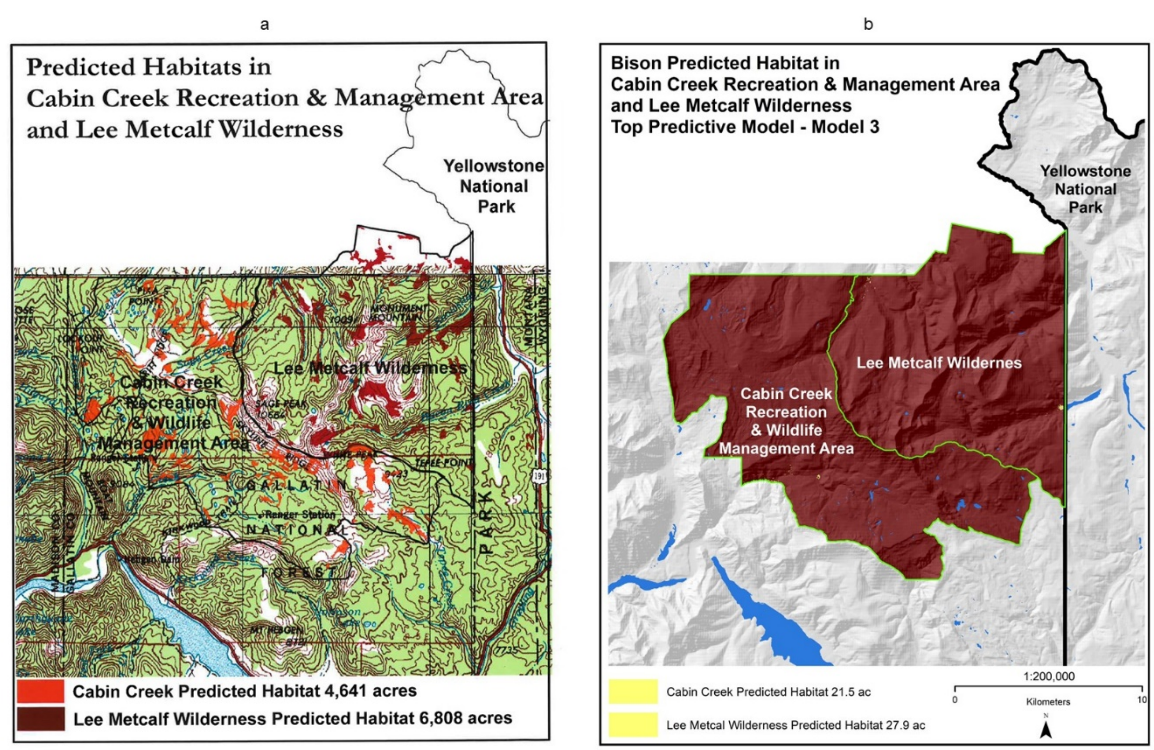

Figure 15. The Cabin Creek original map built by Yellowstone National Park biologists (Montana Fish, Wildlife and Parks 2014; a), and top predictive model (b).

The Hebgen Basin encompasses 146,625 acres shown in the YNP original map and 149,534 acres in the map based on top predictive model. In the YNP original map, there are 21,795 acres of current habitat, and 43,602 acres of predicted habitat within Hebgen Basin (Figure 16a, Table 13). Top predictive model depicts 17,702 acres of current habitat and 24,677 acres of predicted habitat within Hebgen Basin (Figure 16b, Table 13).

Table 13. Summary of differences in size between the mosaic of maps originally built by Yellowstone National Park (YNP) biologists for Hebgen Basin (Montana Fish, Wildlife and Parks 2014) and top predictive model.

	Bison Habitat by Mosaic YNP (ac)	**Bison Habitat by Top Predictive Model (ac)**	**Difference Between Models (ac)**
Basin	146,625	149,534	2,909 **
Current	21,795	17,702	4,093*
Predicted	43,602	24,677	18,925

*Difference might be attributed to geographic information system (GIS) procedures used to develop map3 and to geographic coordinate system variations between two methods.
**Difference might be attributed to geographic coordinate system variations between two methods.

a b

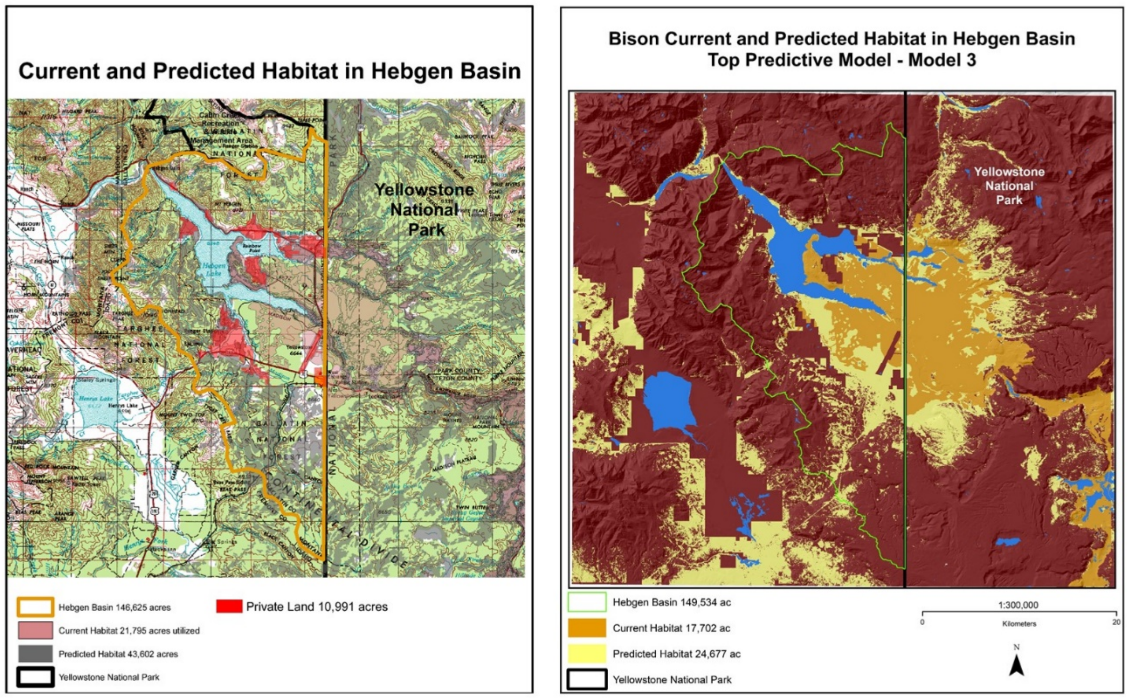

Figure 16. The Hebgen Basin original map built by Yellowstone National Park biologists (Montana Fish, Wildlife and Parks 2014; a), and top predictive model (b).

In summary, within the four original maps are five areas of interest, Gardiner Basin, Taylor Fork, Cabin Creek Recreation & Management Area, Lee Metcalf Wilderness, and Hebgen Basin, which provide 107,761 acres of bison habitat in the northwestern GYE (Table 14). However, the top predicted model depicts 56,229 acres within the five areas of interest (Table 14).

Table 14. Summary of bison predicted habitat within the area of interest depicted on the original maps built by Yellowstone National Park biologists (Montana Fish, Wildlife and Parks 2014) and top predicted model.

Area of Interest	Bison Habitat by Mosaic YNP (ac)	Bison Habitat by Top Predictive Model (ac)	Difference Between Models (ac)
Gardiner Basin	37,816	22,453	15,363
Taylor Fork	14,894	9,050	5,844
Cabin Creek	4,641	21.5	4,619.5
Lee Metcalf	6,808	27.9	6,780.1
Hebgen Basin	43,602	24,677	18,925
Total	107,761	56,229	51,532

Model Transference

Grand Teton

Results for the calibrated model, which uses GT coefficients (Appendix I) were evaluated with the cross-validation, generated a high coefficient of determination (R^2=0.99), an intercept overlapping zero (95% CI: -0.03 to 0.17), and a slope close to 1.0 (β=0.93, 95% CI: 0.6 to 1.01; Figure 17). The uncalibrated model, which uses the coefficients from GYE, had a slightly lower coefficient of determination (R^2=0.94), an intercept overlapping zero (95% CI: -0.24 to 0.08), and a slope coefficient close to 1.0 (β=1.42, 95% CI: 0.86 to 1.98; Figure 17). Using the withheld telemetry data and local coefficients, the calibrated model classified 585 of 622 (94%) bison locations into highest relative probability bin, with a performance close to perfection (Figure 18). The Spearman rank correlation (r_s =0.99) is in agreement with these results. The uncalibrated model also performed well for GT segregating the RSF values in bins in the same proportion as at GYE (Figure 19). In addition, Spearman rank correlation (r_s =0.99) also supports those results.

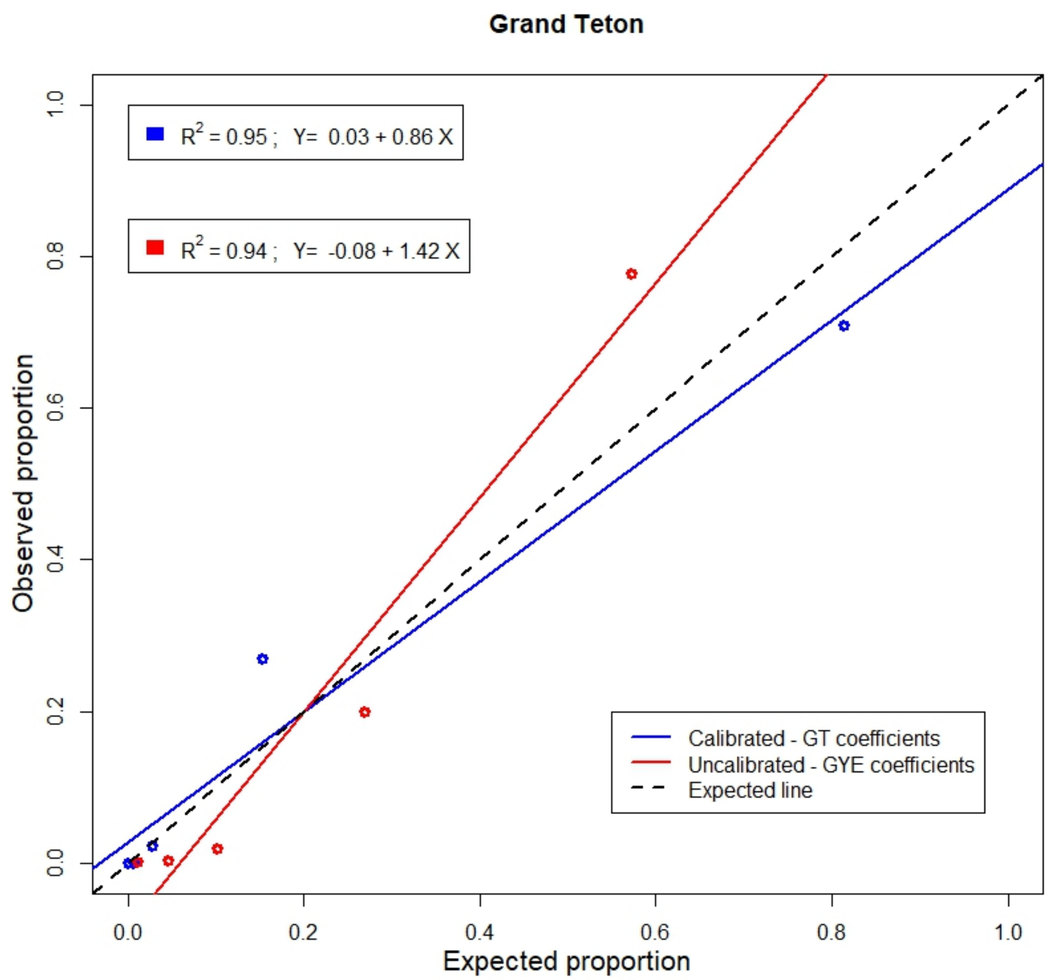

Figure 17. The proportion of used locations versus median resource selection function (RSF) values within bins (n=3,138). The perfect fit would occur along a line with slope of 1 and intercept of zero (dashed line). The fitted regression for the calibrated model that uses local coefficients shown as blue line, while points are the bins observations (blue dots). The fitted regression for the uncalibrated model carrying the coefficients from Greater Yellowstone Ecosystem is shown as a red line, while points are the bins observations (red dots). Regression coefficient of determination (R^2) close to 1.0 indicates that the top predictive model accurately classified radio collar data set used for model validation in both cases.

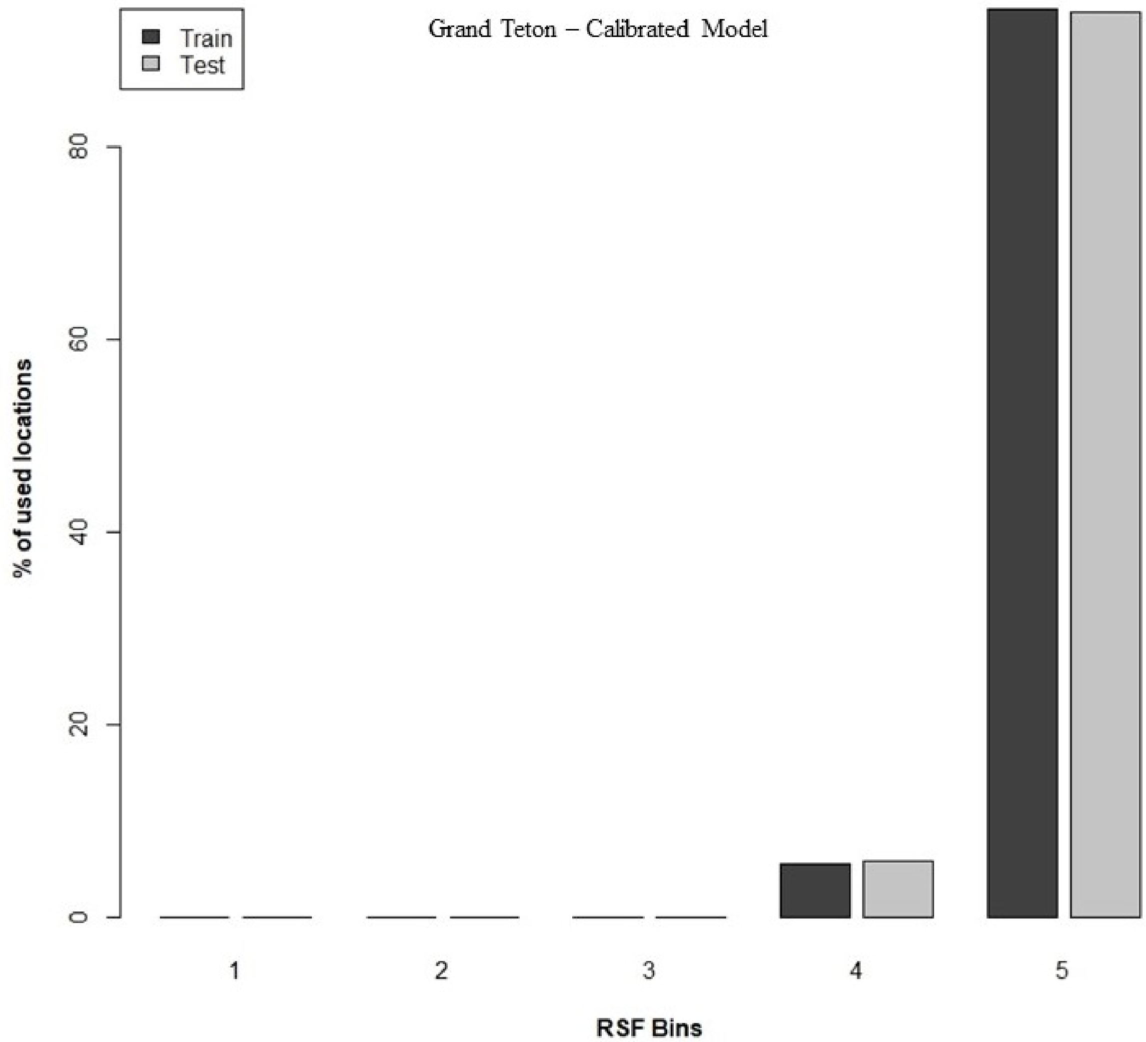

Figure 18. Percentage of radio collar locations in 5 bins of increasing resource selection function (RSF) values used to train (black bars, n = 2,488) and test (gray bars, n = 622) of the top predictive resource selection function model for bison at Grand Teton. The matching proportions indicated that the calibrated top predictive model accurately classified radio collar sites in the holdout data set used for model validation.

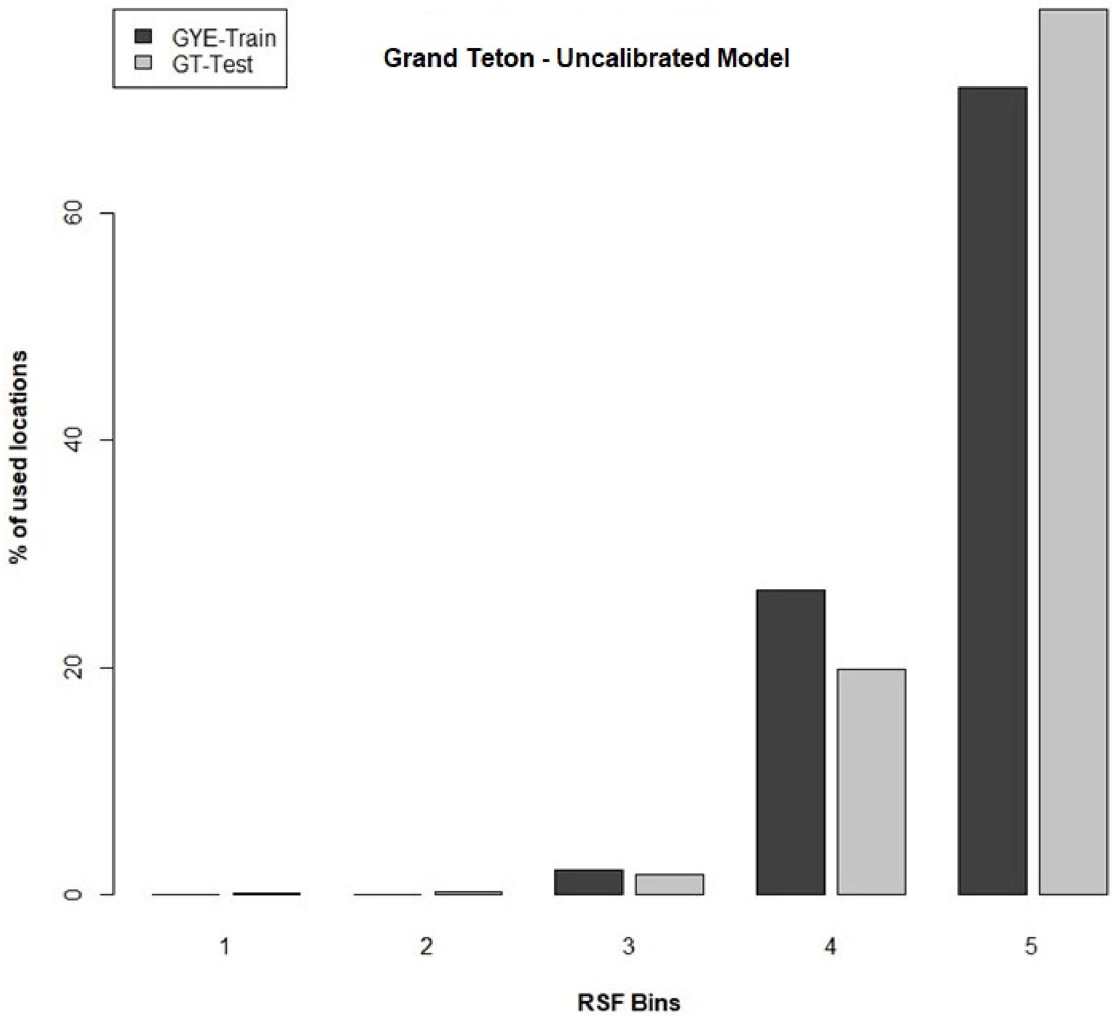

Figure 19. Percentage of radio collar locations, within Grand Teton (GT), in 5 bins of increasing resource selection function (RSF) values that were used to train the model at Greater Yellowstone Ecosystem (black bars) and tested at GT (gray bars). The increasing percentage of used locations towards the higher bins indicated that the uncalibrated model classifies the used locations with high values of RSF in both locations.

The high predictive power of the uncalibrated model, which carries the coefficient from GYE, is corroborated by the map of RSF at Grand Teton where the great majority of used locations are within the highest RSF class (Figure 20).

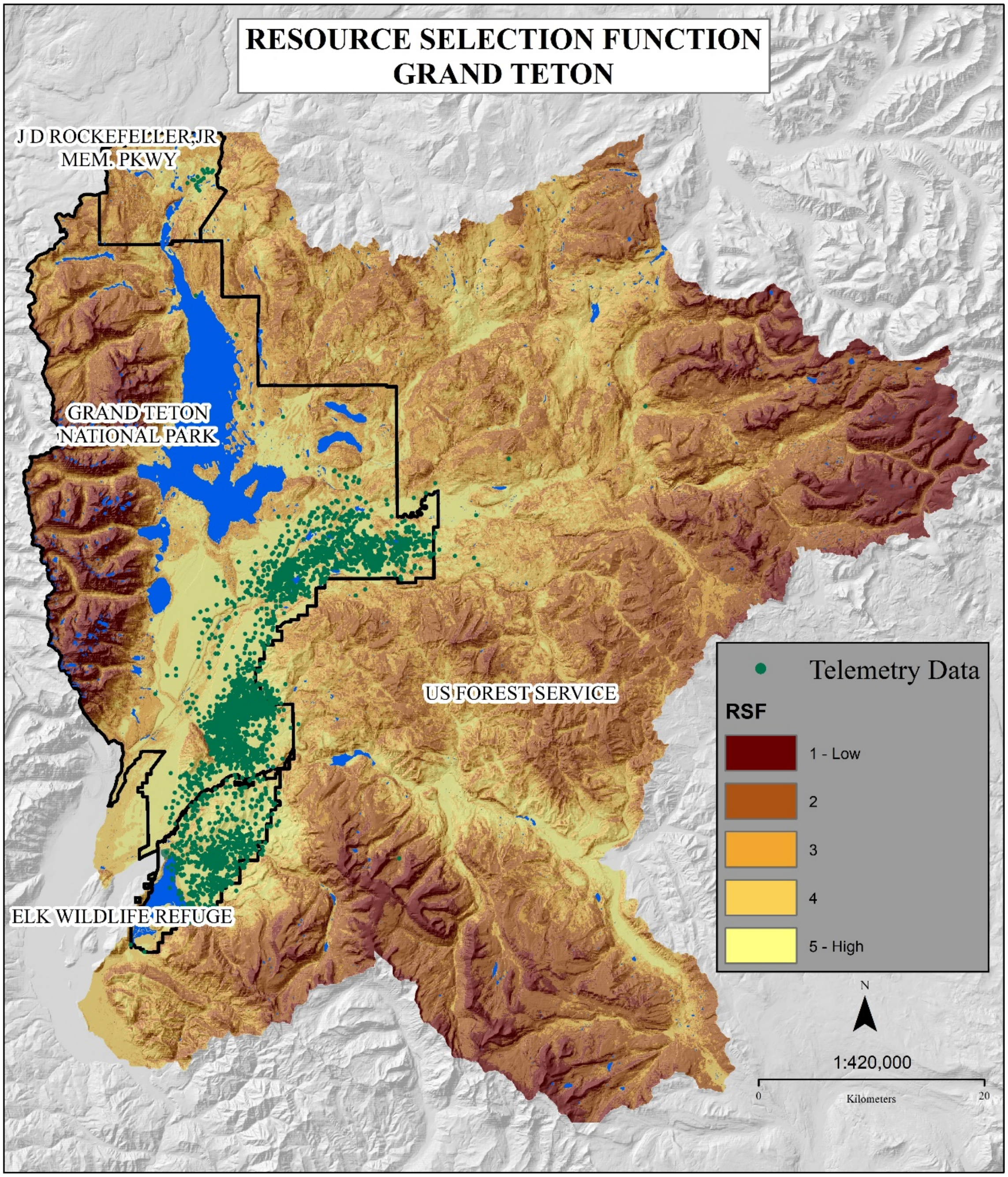

Figure 20. The uncalibrated model, which carries coefficients from Greater Yellowstone Ecosystem (GYE), applied in Grand Teton (GT) study area, and bison telemetry data collected from 1997 to 2007. The resource selection function (RSF) results were mapped using quantile classification with 5 bins in line with the validation binning.

National Bison Range

The transference of the calibrated model, which uses the local coefficients was assessed through the model validation by withholding 20% of the preferred grazing observation data, including a proportional number of observation data and random points (Appendix J). For the calibrated model, regression validation showed a high coefficient of determination (R^2=0.88), an intercept of 0.07 (95% CI: -0.03 to 0.17), and a slope close to 1.0 (β=0.64, 95% CI: 0.27 to 1.04; Figure 21). Conversely, the uncalibrated model had low predictive accuracy. Regression showed a low coefficient of determination value (R^2= -0.1), although the intercept overlaps zero (5% CI: -0.04 to 0.36), the slope coefficient is low (β=0.2, 95% CI: 0.6 to 1.01; Figure 21). From the test observation data of grazing selection, the calibrated model classified 54 of 72 (75%) points into the top 2 relative probability bins (Figure 22) indicating that this model is reasonable overall. Similarly, the Spearman rank correlation (r_s =0.9) confirms the reasonable strength of the model. The uncalibrated model did not segregate the RSF values accordingly to the training at GYE, indicating that the uncalibrated model is close to random (Figure 23). The Spearman rank correlation (r_s =0.1) confirms the overall poor performance of the uncalibrated model at NBR. The distribution of the selected grazing locations over the RSF also supports the poor performance of the uncalibrated model at NBR (Figure 24).

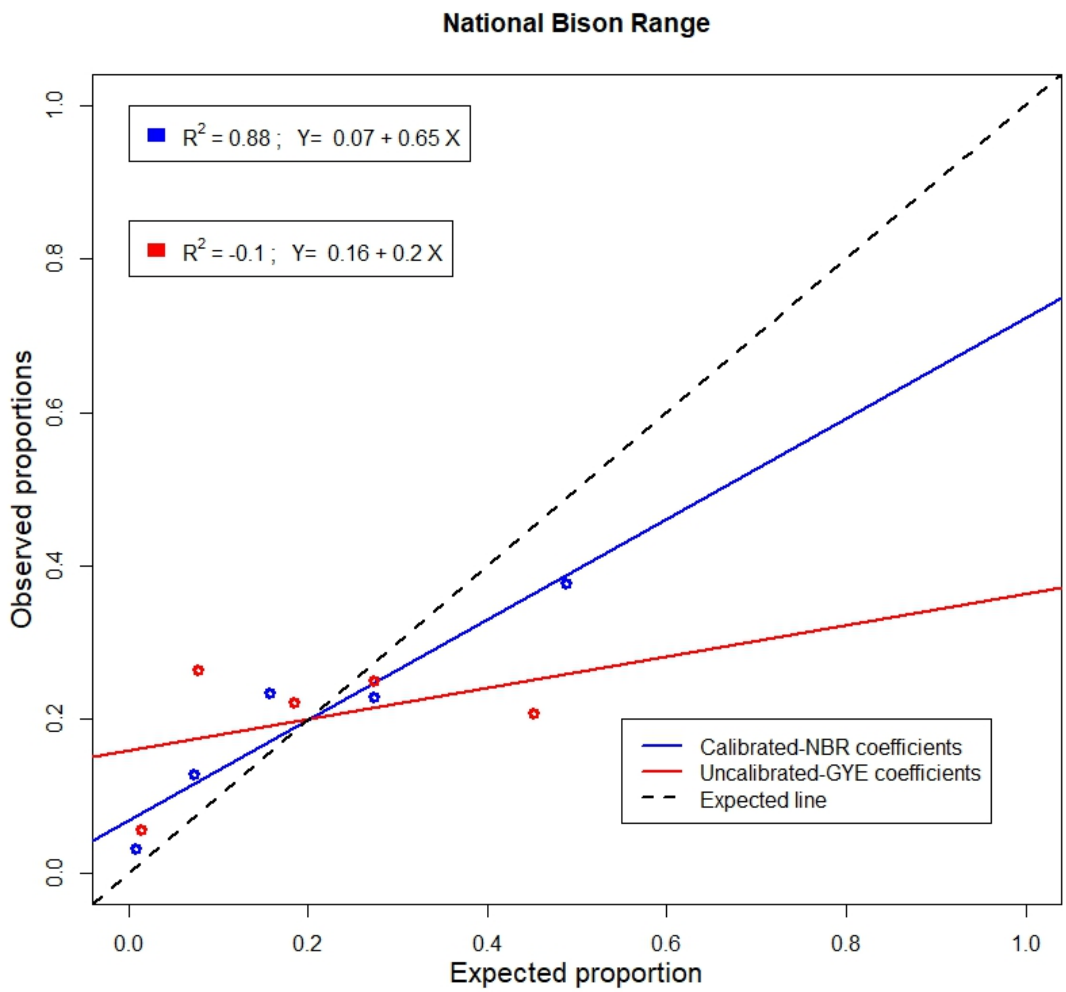

Figure 21. The proportion of used locations versus median resource selection function (RSF) values within bins (n=72). The perfect fit would occur along a line with slope of 1 and intercept of zero (dashed line). The fitted regression for the calibrated model that uses local coefficients is shown as a blue line, while points are the bins observations (blue dots). The fitted regression for the uncalibrated model carrying the coefficients from Greater Yellowstone Ecosystem (GYE) is shown as a red line, while points are the bins observations (red dots). Regression coefficient of determination (R^2) equal to 0.88 indicates that the calibrated top predictive model, using the local coefficients, classified grazing selected site data used for model validation. Conversely, the uncalibrated model carrying the GYE coefficients poorly classified preferred grazing sites.

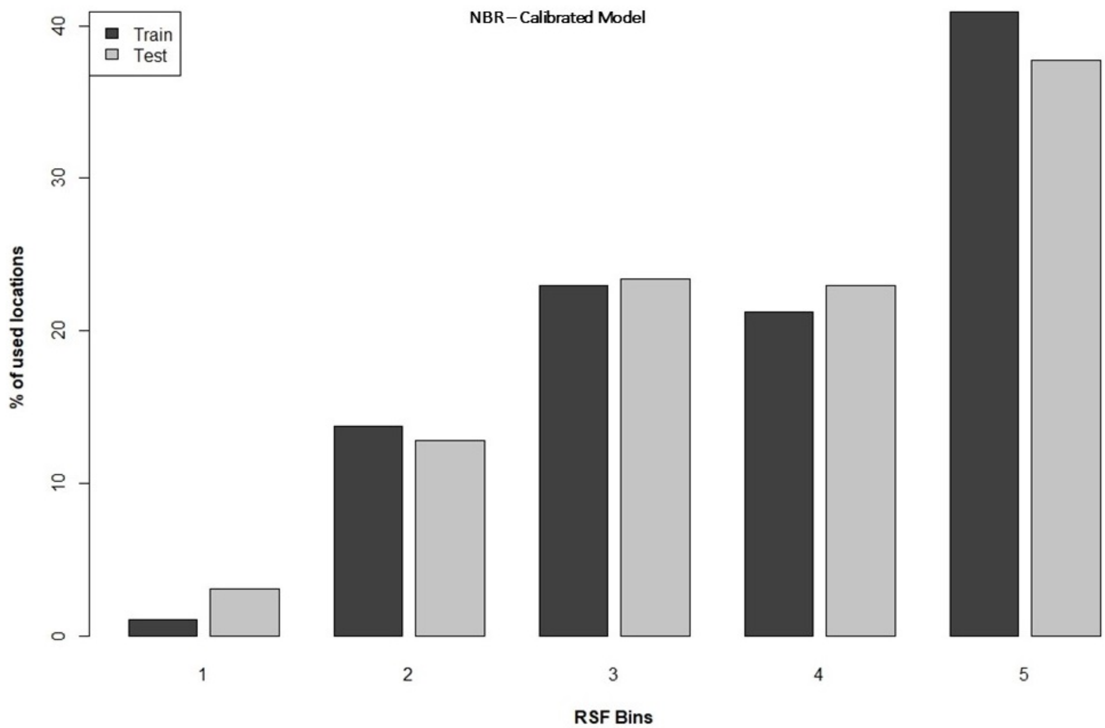

Figure 22. Percentage of selected grazing locations in 5 bins of increasing resource selection function (RSF) values used to train (black bars, n = 57) and test (gray bars, n = 15) of the top predictive resource selection function model for bison at National Bison Range. The results indicate that the calibrated predictive model (model 3) classified grazing preferred observation sites relatively accurately.

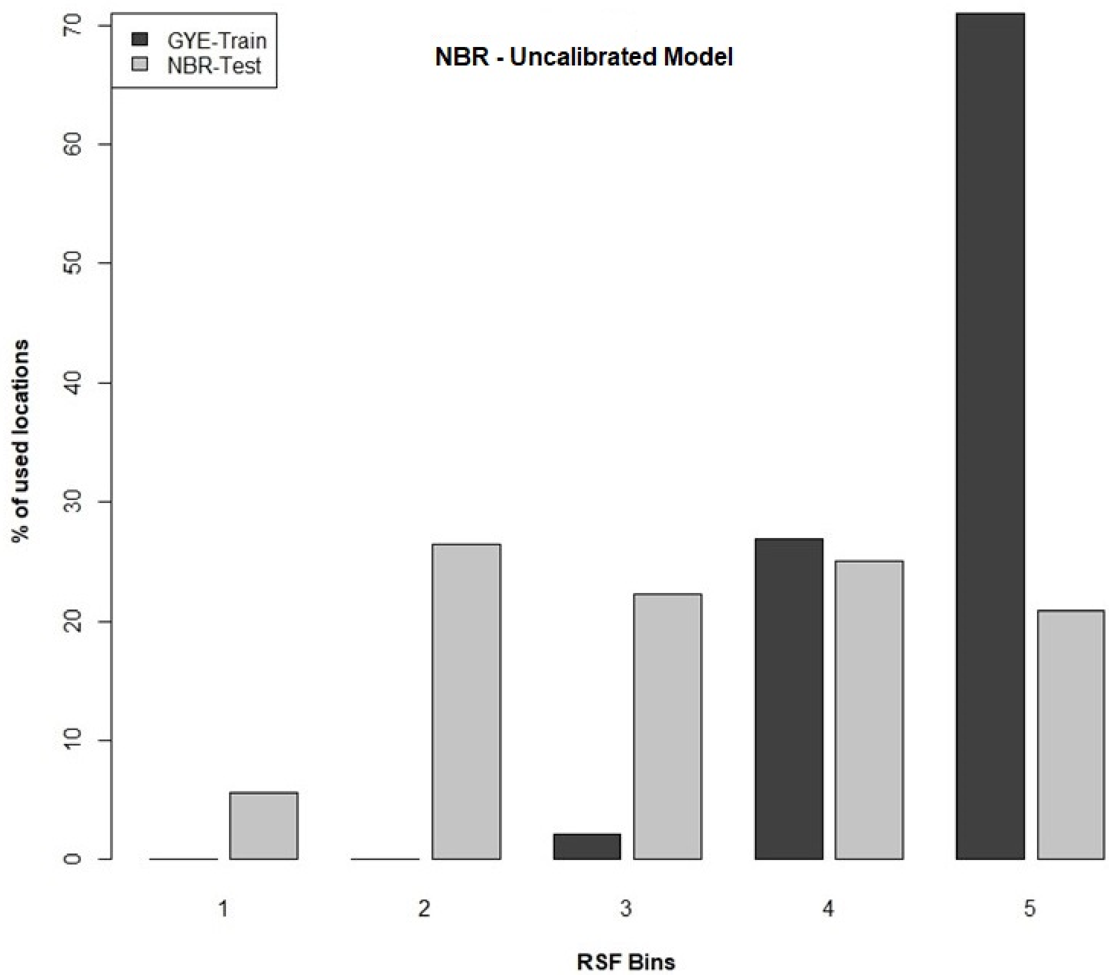

Figure 23. Percentage of selected grazing observations locations, within National Bison Range (NBR), in 5 bins of increasing resource selection function (RSF) values that were used to train the model at Greater Yellowstone Ecosystem (GYE, black bars) and tested at NBR (gray bars). The increasing percentage of used locations towards the higher bins indicated that the top predictive model classifies the used locations with higher values of RSF at the GYE. But performed poorly at NBR.

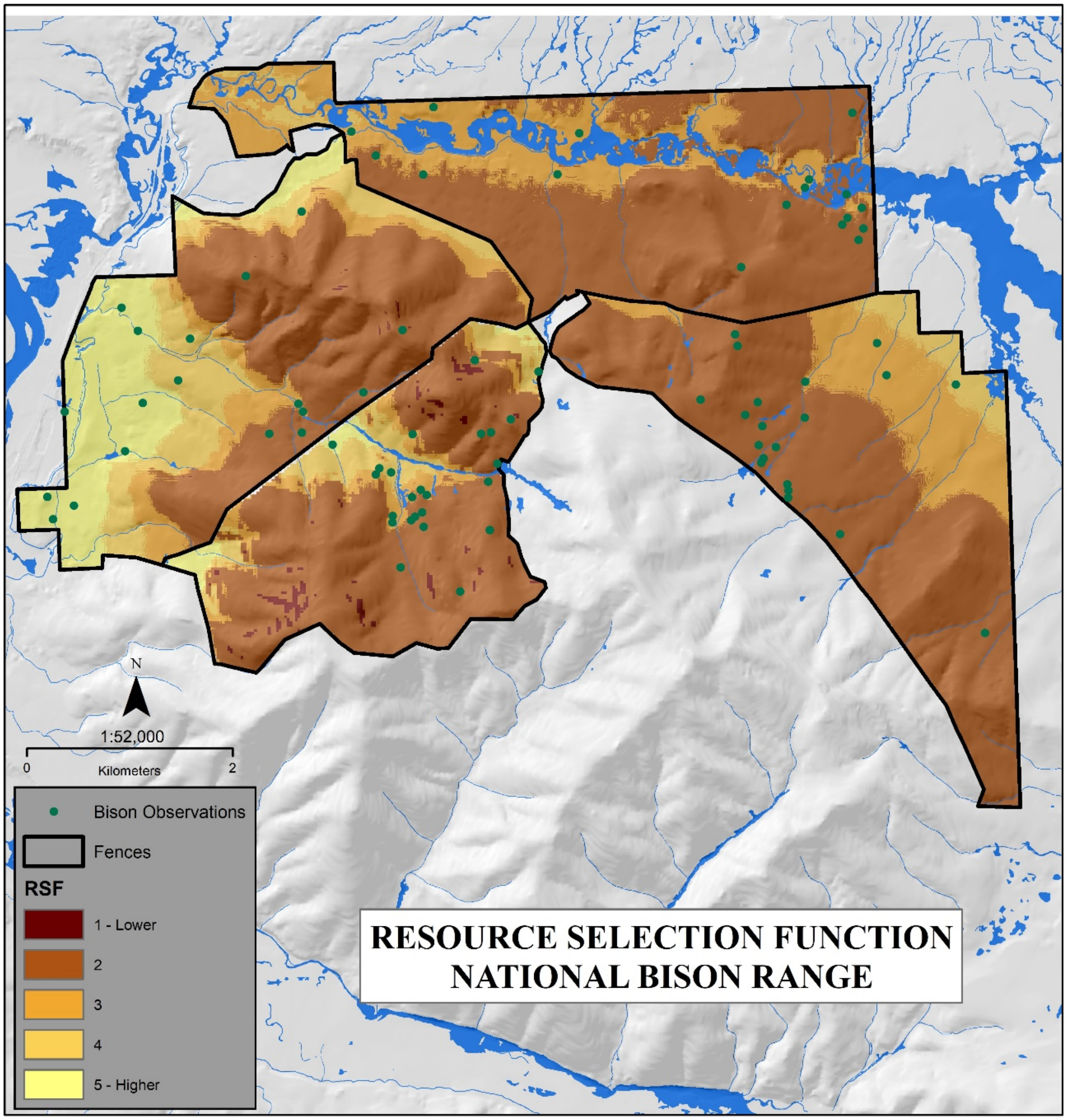

Figure 24. The uncalibrated model, which carries coefficients from Greater Yellowstone Ecosystem applied at four pastures within the northern section of National Bison Range, Moiese, MT, in demonstrated bison sites. The resource selection function values (RSF) were classified by quantile in 5 bins. Bin 1 has the 20% lowest values and bin 5 the 20% highest values.

CHAPTER FIVE – DISCUSSION

Discussion

The purpose of this study was to test the feasibility of habitat model transference by developing a bison SDM using only the maps previously created by researchers from YNP. The top predictive model assessment, through K-fold evaluation, achieved accuracy equal to or higher than reported by other researchers (Johnson et al., 2006; Fortin et al., 2009; McNew et al., 2013; Acevedo et al., 2014) indicating that this approach can be useful as a predictor of habitat suitability for bison. The results also indicated that it is possible to develop a SDM based on maps previously created by a different group of researchers through combination of GIS tools and ecological knowledge of the designated species.

Georeferencing is a very useful tool in conservation studies because it opens the opportunity to use relic maps to previous compare information with newly acquired data. However, it is important to know that georeferencing accuracy depends on the identification of reference sites on the relic maps to be used as links in the georeferencing procedure. This dictates the appropriate scale for new maps. In this study, the largest RMSE, 98.3 meters, came from the Cabin Creek map (Appendix B1). Therefore, based on the United States National Map Accuracy Standards (USGS, 1947) the georeference accuracy of this study is adequate to use maps at a scale not more detailed than 1:198,000. In addition, one must keep in mind that original map errors are always inherited by the georeferenced map and not all original map errors may be apparent.

The maps created by the researchers from YNP contain information (GIS layers) easily downloaded from other agency websites, which facilitated the georeferencing procedure. However, in some cases, the shapefile borderlines were so thick, that the lines covered the target layer (bison habitat) which may have created uncertainties about the cell classification. Additionally, in this study, the major problem with classification was the color complexity that decreased the ability of ArcGIS to segregate the polygons accurately, which in turn increased time expended on the cleanup procedure. On the original maps created by the YNP biologists, the color complexity resulted from using a topographic map as background. Topographic maps have features with different colors, complicating the habitat class identification when overlaid with multiple layers of ownership or habitat. Therefore, to improve the classification efficiency one should select base maps with high contrast and fewer layers. In spite of these challenges, we learned the following:

Within the mountainous environment of YNP, elevation is the main driver of bison habitat selection, sites used by bison were below 2,500 meters, which was consistent with use patterns of bison in a mountainous landscape in southwestern Yukon, Canada (Fisher and Gates, 2005). Additionally, Phillips (2000) studied bison in a similar environment and reported bison most often used sites below 2,162 meters. This pattern may result from the animals' efforts to avoid rugged terrain. Terrain ruggedness can be an important landform parameter in habitat selection for large mammals, like bison (Debeljak et al., 2001; Fischer & Gates 2005; Sappington et al., 2007; Girardi et al., 2013). However, in our study ruggedness was highly collinear with slope (Appendix A7).

Thus, my top predictive model indicated that terrain ruggedness was more influential than slope, which is similar to outcomes reported by Fischer and Gates (2005). Because there is no agreement in the literature on how to represent terrain ruggedness in SDMs, we tested four different formulas and selected the most parsimonious, the deviation of elevation within a 10 x 10 cell window. The fact that the formula used to calculate terrain ruggedness in the current study was different from the formula used by Fischer and Gates (2005) suggest that more than one index can capture how bison respond to terrain ruggedness. Regardless of the approach, slope serves as a proxy for ruggedness. Although, several authors reported bison selection for less steep slope (Coughenour, 2005; Fischer & Gates, 2005; Allred et al., 2011; Kohl et al., 2013; Raynor et al., 2016), others reported that slope did not influence site selection by bison (Phillips, 2000; Ranglack & Toit, 2015). Further disagreement is apparent in studies conducted by Van Vuren (1979, 1983) who reported bison selection for steeper areas. However, Van Vuren (1979, 1983) used a clinometer to measure the slope coefficient of the areas occupied by bison while the other authors used DEM. The discrepancy among slope selection reported by Van Vuren (1979, 1983) and the above mentioned authors could be due to different ways of measuring slopes; consequently, the disagreement may arise from methodology rather than animal selection.

Because of the disagreement among published sources, I choose a second measure of ruggedness, landform profile curvature. The results indicate selection for a convex profile leading to speculation that this profile will decelerate surface flow, therefore lowering sheet erosion. Less erosion favors organic matter accumulation and ultimately vegetation productivity (USDA 2018). The next habitat predictor was open or non-forested areas.

Several authors reported bison selection for open land (Shult, 1972; Knapp et al., 1999; Fischer & Gates, 2005; Fortin et al., 2009; Allred et al., 2011) not only because bison prefer graminoides species, but also due to avoidance of predators commonly associated with forest (Fortin et al., 2009). As described in the current literature, my top predictive model demonstrates the probability bison use declines as tree canopy increases becoming null when the tree canopy is higher than 40%.

Bison use related to the distance to water is a controversial topic due largely to comparisons between domestic cattle and bison (Knapp et al., 1999; Allred et al., 2011; Kohl et al., 2013). While this study does not discuss environmental benefits of bison, it is important to discuss how far from the water source bison will move. Some authors reported that distance to water is not important in determining space use by bison (Phillips, 2000; Van Vuren, 2001) but in several studies, distance to water is not included as a possible variable in bison habitat selection (Coughenour, 2005; Allred et al., 2011; Ranglack & Toit, 2015). Another possibility for disregarding distance to water as a driver of bison selection would be the wide availability of water sources in some study sites. Specially, bison have been reported to use ephemeral water sources like potholes, ephemeral creeks and snow (Shult, 1972; Norland, 1984). Capturing these ephemeral sources of water in a GIS layer would require complex use of remote sensing data with very fine spatial temporal scales, which becomes very expensive. Studying bison and cattle behavior in the prairie, Kohl and colleagues (2013) reported that bison selected landscapes near water but they appeared to use other areas more than 10 km from water source. Fischer and Gates (2005) described a strong bison selection for lakeshores however, it was not clear if the reason was the water source or emergent vegetation. Allred et al. (2011) reported water sources didn't influence bison selection when only streams were considered. However, when combining ponds and streams, bison were influenced by water source. I found that the relative probability of land use increases as the horizontal distance to water increases, but most use occurred within 1.5 kilometers and bison relative probability of use becomes null after 2.5 kilometers. The top predictive model may suggest closer affinity to water than Kohl et al. (2013) predicted because of the rugged GYE landscape. Studying bison in a mountainous environment, Van Vuren (2001) found that bison were unaffected by horizontal distance to water, but bison only used sites with vertical distance to water less than 270 meters. In my study, bison use declined with increasing vertical distance to water, with the higher relative probability of use being below 400 meters and becoming null after 600 meters.

To be objective, the current habitat mosaic from the original maps should have exactly the same area within the map derived from the top predictive model. However, there were differences in the current habitat maps for the Gardiner and Hebgen basins due to uncertainties generated during the process of georeferencing and classifying the map mosaic. Another possibility could be that the differences in size (area) came from the different coordinate systems used on the original maps and in the map derived from the top predictive model. This occurred because the original maps coordinate system is unknown while GIS specialists, for keeping shape and area integrity, recommend the coordinate system used in this current study, the UTM-zone 12 NAD 83.

When the four original maps depicting bison habitat were released, the YNP was in need of a SDM that could support the expanding bison herd for the areas surrounding the park because the Natural Regulation Policy avoids bison culling. However, the total amount of bison habitat was difficult to calculate using the original YNP maps as the way they were released, because of overlap among those maps. The composite mosaic of the four original maps allowed visualization and ultimately measurement of the predicted habitat. Measures from the mosaic map indicated 287,885 acres with 56% (160,986 acres) occurring inside the park (Table 10).

Another consideration is how predicted habitat is distributed through the GYE study area. Because elevation is an important predictor in the top predictive model, its derived map depicts bison habitat in a more continuous manner. Importantly, this map displays three pockets of habitat connecting the two current habitat areas by narrow travel corridors (Figure 8b). Bison habitat within the original maps depicts smaller polygons of habitat scattered throughout the study area, without connecting corridors and a large area on the northwest corner of the park which disagrees with the map derived from the top predictive model (Figure 8a). The Jaccard coefficient result (0.13) indicates that the map derived from the top predictive model only matches the original YNP predictions in a small proportion (49,647 ac) of the mapped habitat (390,794 ac). The low Jaccard coefficient suggests the YNP prediction were based on other set of predictors or inferred from other areas.

The area reviewed in this study is comparable in size with 60% of YNP and, still, does not encompasses the entire range of the Yellowstone bison herd. The top predictive model depicts 152,558 acres of habitat within the study area as a whole, encompassing areas inside and outside YNP (Figure 12, Table 8). A source of criticism may be that the Gardiner and Hebgen basins are recognized as important bison winter habitat while most of bison summer range is out of the study area, in the Lamar and Hayden Valleys of the park (Meagher, 1989; Coughenour, 2005). Thus, the top predictive model approach for developing the bison habitat model technically describes mostly winter habitat. However, in mountainous environments, like the GYE, winter range is often considered the limiting habitat element. In response, the top predictive model used generally available physical and biotic covariates to define bison habitat, so when local data, specifically summer range environmental characteristics are available, the model can be improved to make inferences that are more precise.

Within the Gardiner Basin, the difference between the original YNP biologists map and the map derived from the top predictive model is 15,363 acres (Figure 13, Table 9). What becomes clear with further investigation is that, within the original maps, some private property was excluded from the analysis, as on northwest corners of the basin, but private land was included at other localities (red layer, Figure 13a). The original map for Gardiner Basin, depicts predicted habitat scattered over the basin (Figure 13a) while the map derived from the top predictive model indicates continuous bison habitat broken by private property (Figure 13b).

Biologists from YNP created a generalized polygon that defined the Taylor Fork drainage boundaries consequently, georeferencing the original map for Taylor Fork made it possible to use the same boundary polygon on the map derived from the top predictive model. Therefore, the difference in size of the polygon that defines the Taylor Fork area, probably results from the GIS processes involved in the methods of the current study. That difference (1,092 acres, 1.8%) indicates that some of the differences in habitat size that we are experiencing could be caused by GIS processes and not just to the differences in criteria defining bison habitat used by YNP biologists and the top predictive model. Nonetheless, original map predicts 1.6 times more bison habitat in the Taylor Fork drainage than the map derived from the top predictive model. The original map developed by the YNP biologists depicts disconnected polygons scattered through the basin and tributaries. The top predictive model reveals clearly depicts the habitat polygons as in lowland meadows and riparian areas. Within the combined Cabin Creek Recreation & Management Area and Lee Metcalf Wilderness units, the original map predicts 11,449 acres, while, the top predictive model virtually predicts zero (49 acres) of bison habitat. This discrepancy arises because the unit is dominated by dense forest and located at elevations above the habitat criteria in the top predictive model.

The size of Hebgen Basin polygon described by the map derived from the top predictive model disagrees with the size outlined in the original map (Figure 16, Table 12) even though both methods used the same watershed layer downloaded from National Hydrographic Data (NHD, 2014). The only plausible explanation is differences in coordinate system between the two methods. However, the difference (18,925 acres, 43%) for predicted habitat is too large to be explained by coordinate system irregularities alone, so the larger portion of the difference between the two maps must be due to bison habitat criteria. The original map of Hebgen Basin displays the same pattern depicted in the other unit maps, specifically the predicted habitat is scattered over the basin. However, the top predictive model predicts more habitat around the current habitat mapped by the YNP biologists which, could be explained by the lower elevation of this areas. It is interesting to note that the top predictive model predicts additional habitat on the southwestern corner of the map well outside the Hebgen Basin. Even though the area outside Hebgen Basin belongs to USFS, YNP biologists predicted very little habitat outside that basin.

The top predictive model developed with data from the Greater Yellowstone Ecosystem was used to identify bison habitat in Grand Teton study area and National Bison Range. The transference was carried out in two ways: the calibrated model, which, used local variable coefficients, and the uncalibrated model that carried the variable coefficients from the development area, the GYE. As expected, the locally calibrated model performed better at both locations, GT and NBR. The dimension of the two study areas coupled with free-roaming herds in GYE study area and GT study area seems to positively affect the transference result. Noticeable in the model assessments for GT study area both approaches, the uncalibrated and the calibrated, achieved good accuracy (Boyce 2006; Merow et al., 2014). Despite the apparent good results, bison distribution within a small portion of the total available bison habitat (Figure 20) might be explained by supplemental feeding and State of Wyoming culling policies. The GT herd has access to hay on the Elk National Refuge during winter and emigration is curtailed by the hunting season, August to February. These two management tools might be constraining bison movement other areas of the prime habitat. In addition, the population might have being kept below the carrying capacity as GTNP objective to avoid conflict with other federal and state agencies (D. Reinhart, personal communication, May 6, 2016).

Contrary to GT study area outcomes, the calibrated model on NBR achieved a reasonable performance but the uncalibrated model did not perform well. This difference probably exists because the bison herd at NBR is managed intensively through fenced pastures in comparison to free roaming YNP herd. Furthermore, the environment is quite different, rolling hills fescue grasslands on the west side of continental divide at NBR in contrast to the mountainous environment on top of continental divide for the GYE. The location data for NBR bison where collected to explain where bison spent more time grazing and not just animal presence as the GYE maps depicted. In combination, these differences could explain the poor performance of the uncalibrated model at NBR as Guisan and Thuiller (2005), Barbosa et al. (2009), Werkowska et al. (2016), suggested it.

CHAPTER SIX – CONCLUSION

Conclusion

The purpose of this study was never to criticize habitat modelling but provide an alternative when local data is not available. The current approach makes it possible to develop a SDM when the only information available is habitat or land use maps. The methodology tested, proved useful in developing a new SDM that could be transferred among environmentally similar areas.

The modelling process based on a previously developed map will be more effective when following these guidelines: 1) select a map with features easily downloadable from a reliable agency to georeference. These features should include boundary lines, coordinate quadrangles, or PLSS section. 2) Select a map depicting high color contrast to improve the classification process. And 3) use environmental predictors ecologically meaningful to the species of interest.

In contrast to these recommendations, the four original maps created by the YNP biologists do not describe the criteria that were used to define bison habitat. Consequently, I had to assume that the YNP biologists accurately defined the current bison habitat, and then I used a GIS-based RSF to model bison habitat using tree cover and physical co-variates as predictors. The top predictive model was then used to make a different map of bison habitat, which was then compared to the original YNP maps. Based on that comparison I concluded that GIS processes of georeferencing, classification, and mosaic can introduce some uncertainties to the model but, these uncertainties were not so large as to preclude the possibility of objectively measuring the size of predicted habitat over the entire study area. Another outcome, from the comparison is the small Jaccard value, which suggests that the biologist from YNP used a different set of predictors or inferred values from a different area when developing the GYE bison habitat map.

The original YNP maps depict 107,761 acres of potential bison habitat within the five areas of interest (Table 14). This level is almost double, what the top predictive model predicts. The overestimation of potential bison habitat might lead to erroneous management actions in the authorization of how many bison could remain outside the park. If the habitat size was too large, the carrying capacity will be inflated leading to overgrazing with resulting environmental degradation, increasing weeds, bare ground and erosion. These changes would ultimately jeopardize the sustainability of the bison and other species in the GYE. Furthermore, over estimation of habitat would have a direct effect on bison competitors, like elk. If there are too many bison grazing in surrounding areas of the park, there would be less forage available for elk.

My model indicated that Cabin Creek and Lee Metcalf units have virtually no bison habitat (49.4 ac); therefore, Taylor Fork will be the only available area for expansion of the YNP herd. However, the great majority of the predicted bison habitat, within Taylor Fork, is located on riparian areas raising concerns about water quality and fishery conservation. Like the Hebgen and Gardiner units, predicted habitat within Taylor Fork is contiguous with private properties that are not prepared to cope with a large ungulate that can damage fences and facilities. In addition, a natural colonization of

Taylor Fork seems very unlikely because the narrow travel corridor is along the highway 191. Consequently, if IBMP members decide to have a bison herd inhabiting Taylor Fork, it would require an assisted introduction. The question that raises from the possibility of Taylor Fork bison herd is the ecological and political cost compared to the few bison the area can sustain during the winter.

This transference exercise clearly indicates that collecting wildlife land use data would be rewarded with a more accurate model. However, even the use of an uncalibrated model can be useful when use data for the area of interest is not available due to lack of resources or work force. In either case, higher predictive power can be achieved by taking into account differences in: 1) study area size, 2) environmental patterns, and 3) predictor variables resolution (Boyce, 2006; Werkowska et al., 2016; Manzoor et al., 2018).

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APPENDICES

APPENDIX A

TABLES

A1. Georeference process errors from each map.

Region Map	Link	Residual_x	Residual_y	RMSE
Gardiner Basin	1	32.0061	24.4355	40.2676
Gardiner Basin	2	-21.7509	-16.6809	27.4108
Gardiner Basin	3	-29.7522	-26.6344	39.9322
Gardiner Basin	4	15.398	-7.55377	17.151
Gardiner Basin	5	34.849	26.4335	43.7766
Taylor Fork	1	-13.3729	22.994	26.6006
Taylor Fork	2	13.2536	-22.7895	26.3632
Taylor Fork	3	9.88564	-16.9984	19.664
Taylor Fork	4	-9.76631	16.7932	19.4266
Cabin Creek	1	13.0234	-8.40597	15.5006
Cabin Creek	2	63.0768	-40.713	75.0748
Cabin Creek	3	-82.5897	53.3075	98.2993
Cabin Creek	4	6.48944	-4.18861	7.72381
Hebgen Basin	1	7.61939	-0.346973	7.62729
Hebgen Basin	2	76.2557	-60.3665	97.2576
Hebgen Basin	3	-72.7295	38.603	82.3394
Hebgen Basin	4	14.7262	-16472	22.095
Hebgen Basin	5	-25.8718	38.5825	46.4538

A2. Estimated resource selection function coefficients of the top predictive model calibrated to Grand Teton.

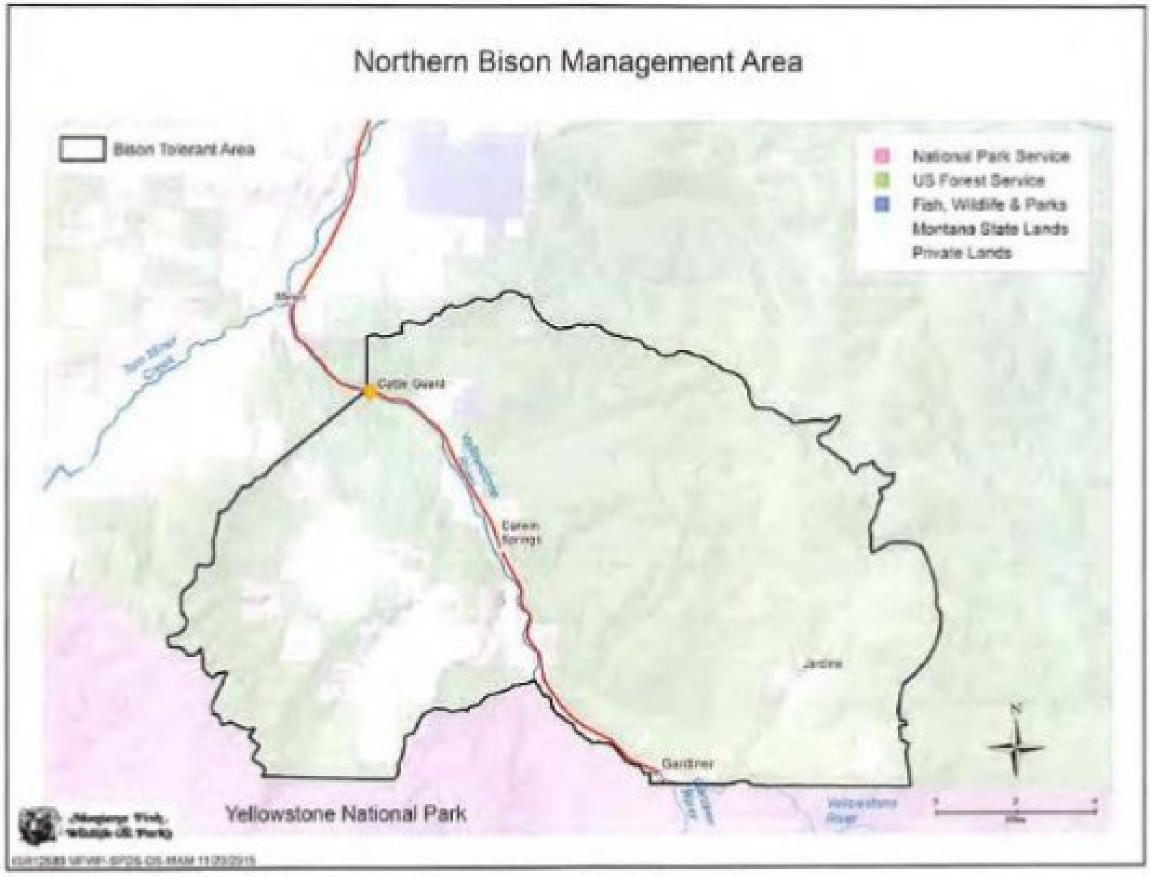
parameter	**estimate coef**	**std.error**	**z value**	**p - value**
intercept	-128.400	20.620	-6.228	< 0.001
relative elevation	411.000	58.280	7.051	< 0.001
(relative elevation)²	-324.200	41.190	-7.870	< 0.001
ruggedness	0.300	0.027	10.945	< 0.001
(ruggedness)²	-0.015	0.001	-10.766	< 0.001
profile curvature	-0.065	0.089	-0.723	0.470
(profile curvature)²	-0.010	0.051	-0.195	0.846
percent tree	-0.078	0.003	-25.072	< 0.001
horizontal dist. to water	0.002	0.000	6.688	< 0.001
vertical dist. to water	0.042	0.024	1.778	0.075

A3. Estimated resource selection function coefficients of the top predictive model calibrated for National Bison Range.

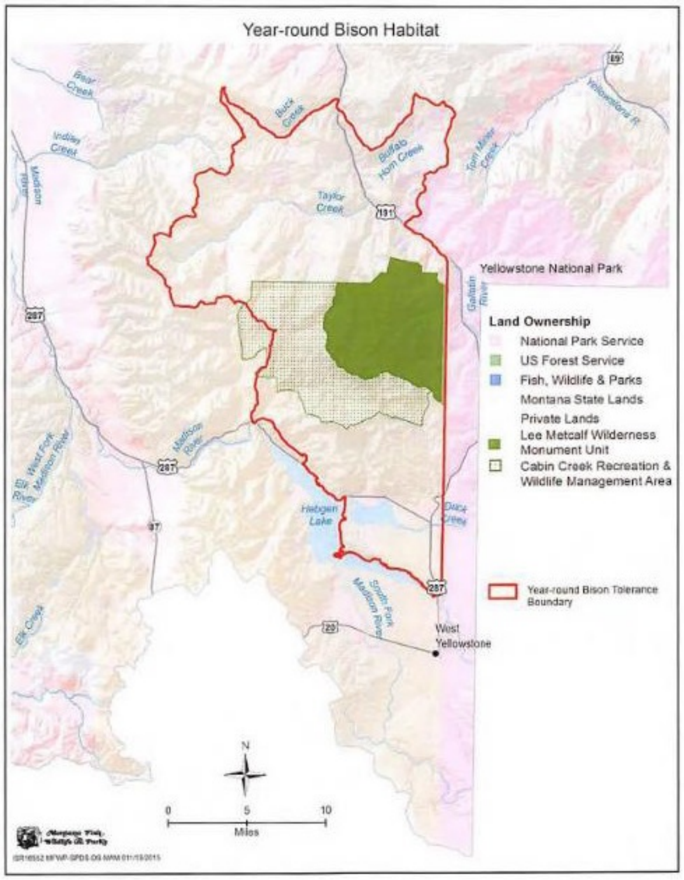
parameter	estimate coef	std.error	z value	p - value
intercept	-29.647	27.615	-1.074	0.283
relative elevation	63.629	58.621	1.085	0.278
(relative elevation)^2	-34.098	31.076	-1.097	0.273
ruggedness	0.717	0.304	2.356	0.018
(ruggedness)^2	-0.089	0.039	-2.255	0.024
profile curvature	0.211	1.545	0.137	0.891
(profile curvature)^2	-13.510	14.683	-0.920	0.358
percent tree	-0.147	0.068	-2.164	0.030
horizontal dist. to water	-0.005	0.002	-2.762	0.006
vertical dist. to water	0.003	0.010	0.247	0.805

APPENDIX B

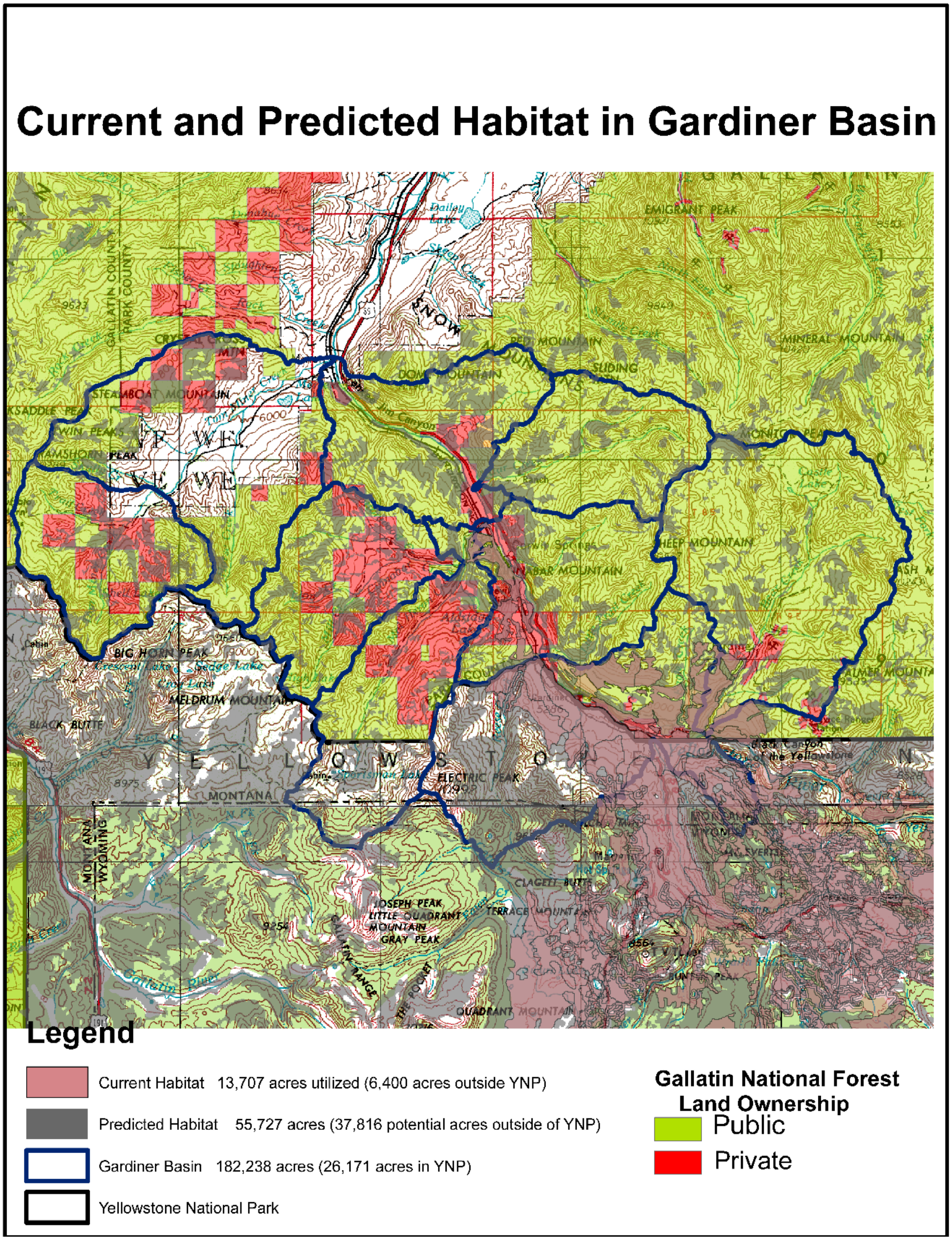
FIGURES



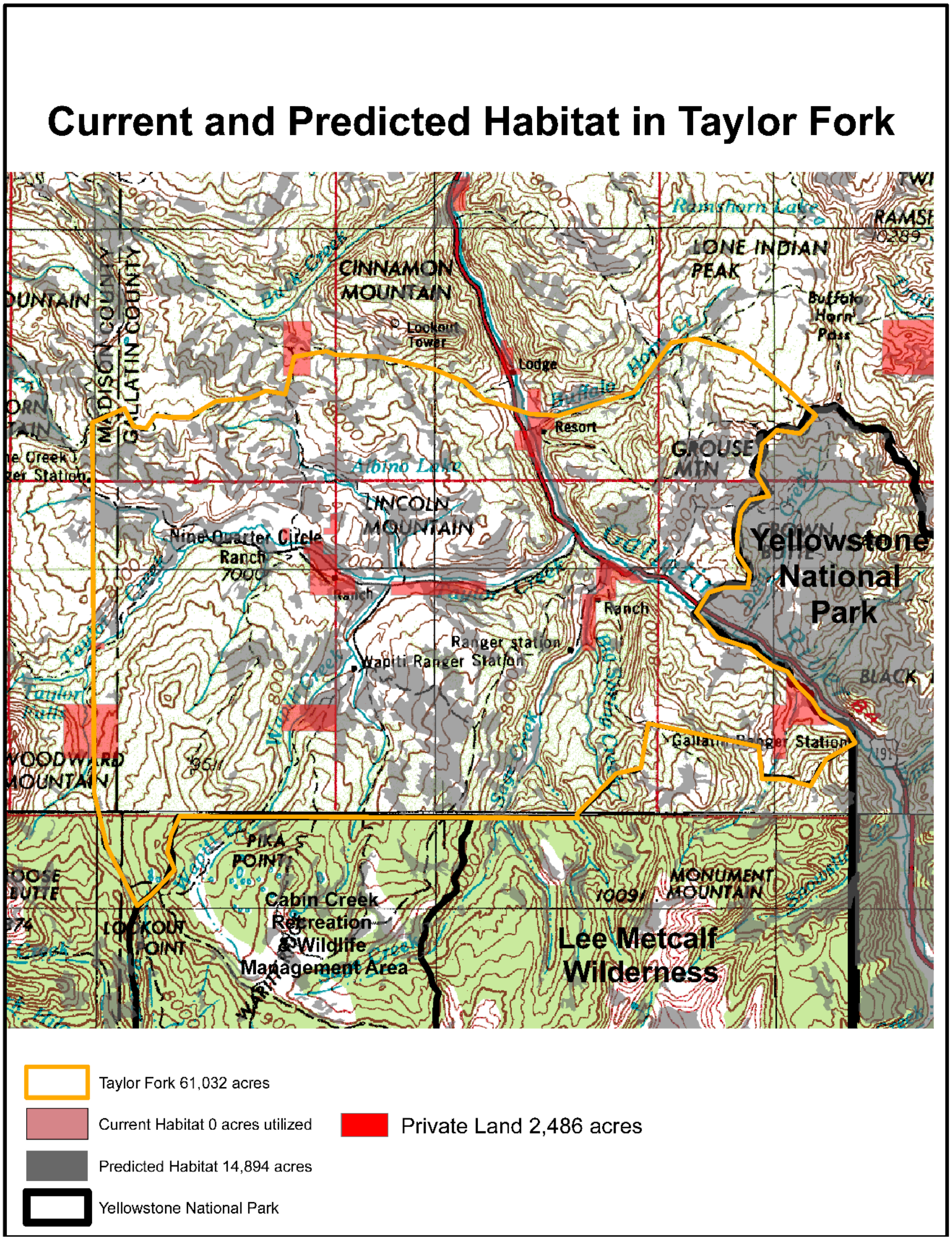
B1. Northern Bison tolerance zone enacted by Montana governor in December 2015



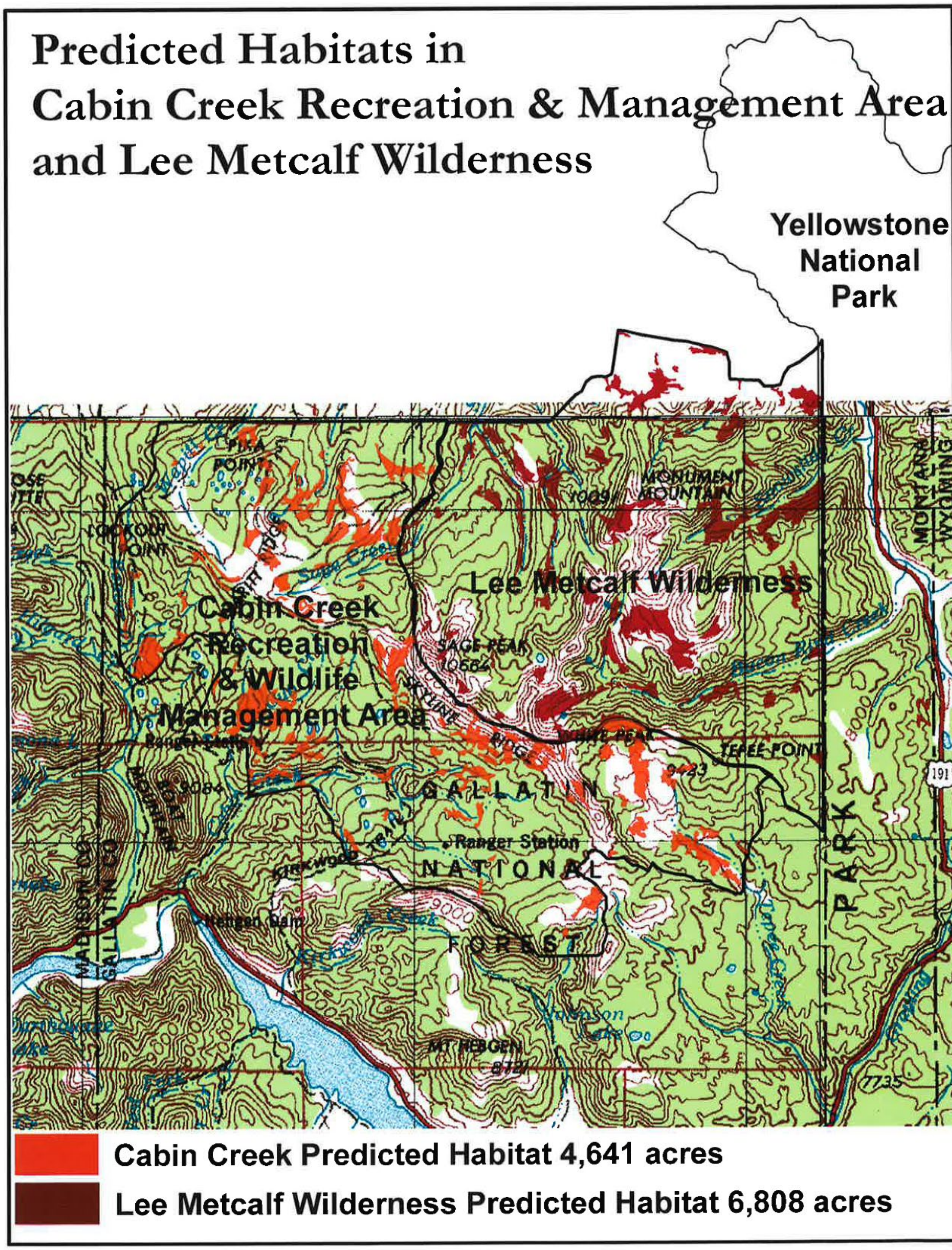
B2. Northern Bison tolerance zone enacted by Montana governor in December 2015



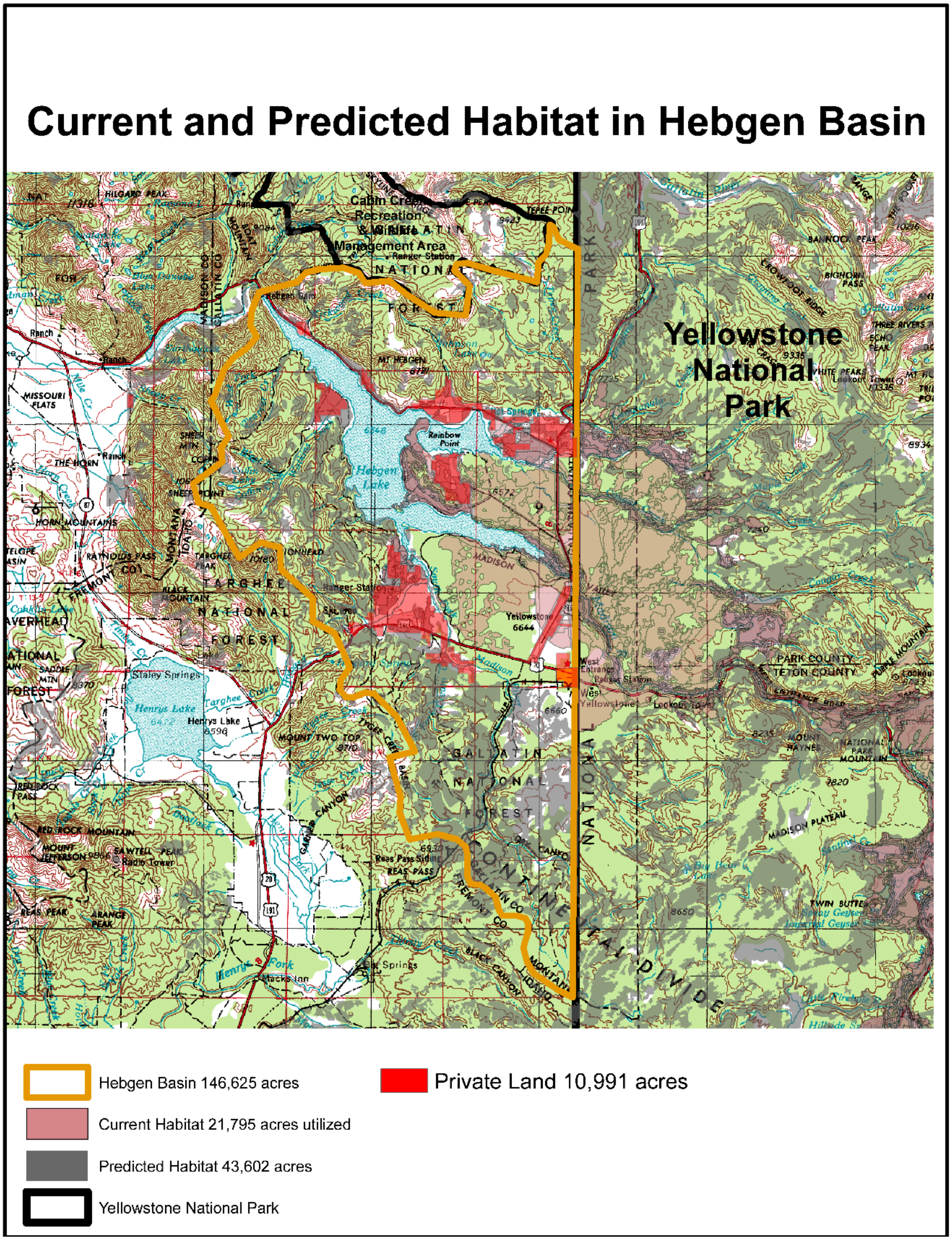
B3. Bison Habitat map developed by biologist of Yellowstone National Park and used by Interagency Bison Management Plan (Montana, fish, Wildlife and Parks, 2014).



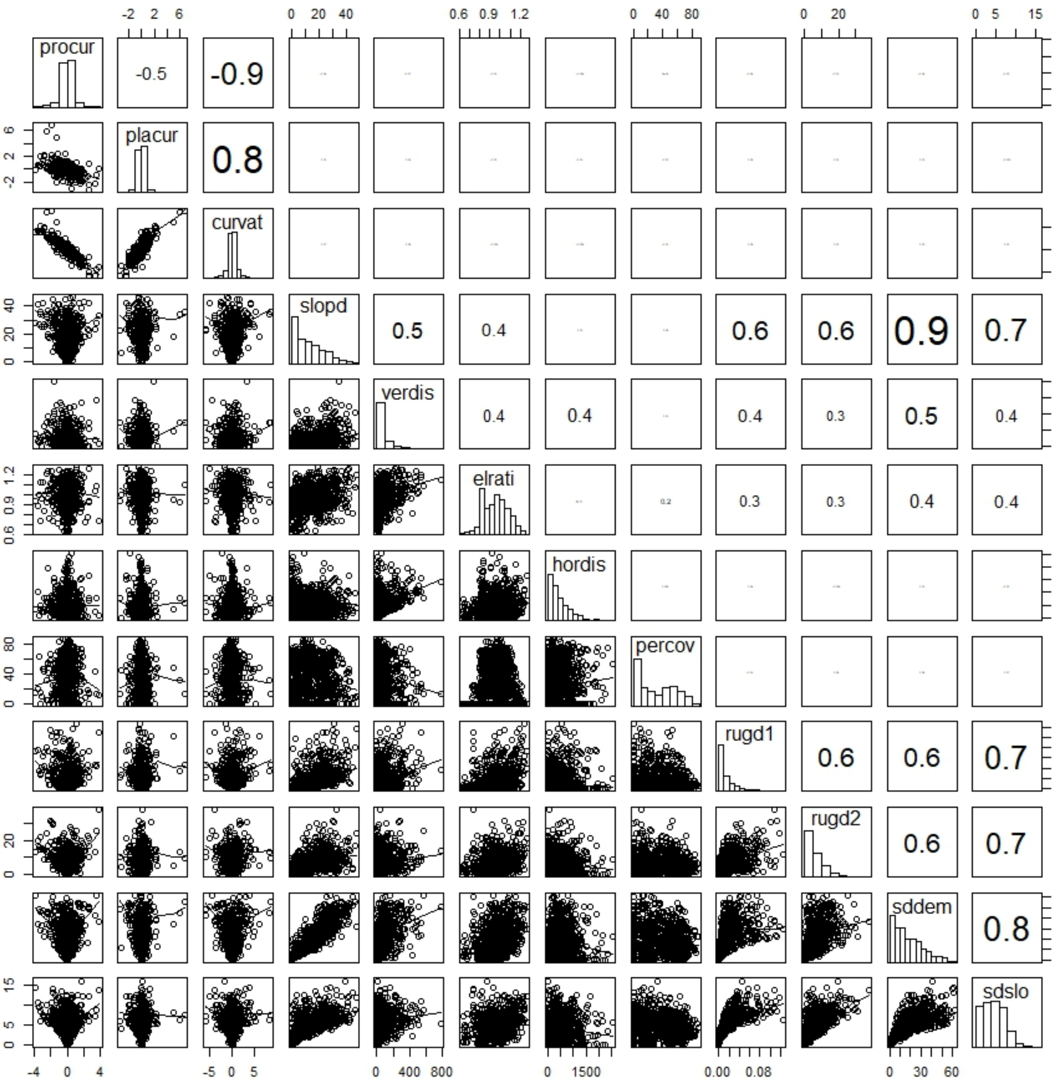
B4. Bison Habitat map developed by biologist of Yellowstone National Park and used by Interagency Bison Management Plan (Montana, fish, Wildlife and Parks, 2014).



B5. Bison Habitat map developed by biologist of Yellowstone National Park and used by Interagency Bison Management Plan (J. Canfield, personal communication September 4, 2014).



B6. Bison Habitat map developed by biologist of Yellowstone National Park and used by Interagency Bison Management Plan (Montana, fish, Wildlife and Parks, 2014).



B7. Relationship between the predictor candidates