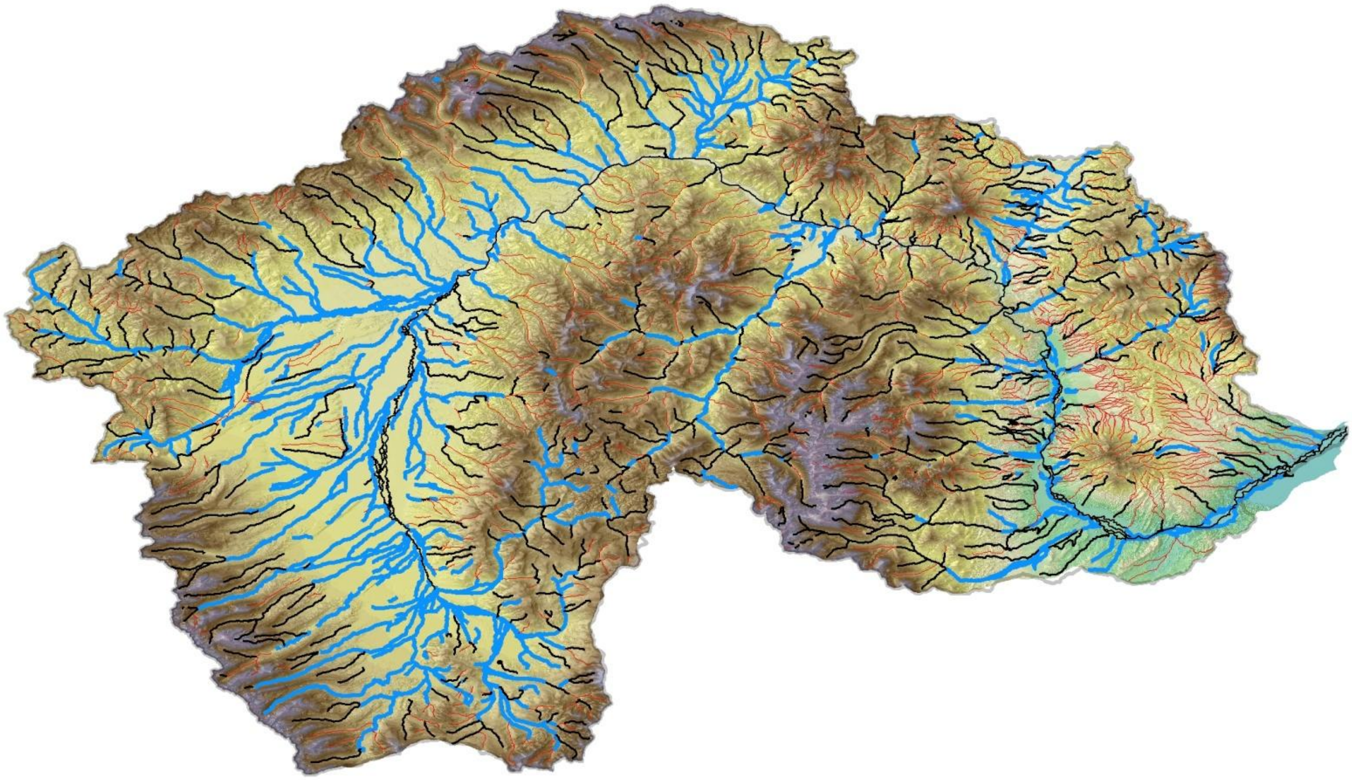
Beaver Habitat Suitability Model
Big Hole Watershed, Montana



Funding provided by: US Environmental Protection Agency
Wetland Pilot Demonstration Grant WL97831401

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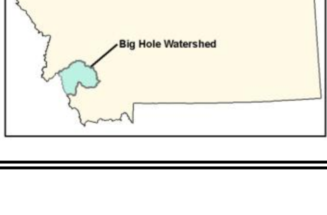
August 2011



Recommended Citation: Carpenedo, S.M. 2011. Beaver habitat suitability model: Big Hole watershed, Montana. Montana Department of Environmental Quality Wetland Program, Helena, MT. 33 pp.

Funding provided by: US Environmental Protection Agency. Wetland Pilot Demonstration Grant WL97831401

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Acknowledgements

This project was funded by the Environmental Protection Agency through a Wetland Pilot Demonstration Grant awarded to the Montana Department of Environmental Quality. I would like to thank Jim Magee (MT FWP), Jim Olsen (MT FWP), Dan Dowling (USFS) and Craig Fager (MT FWP) for providing information on the presence and absence of beaver in the Big Hole Watershed and taking the time to review the final beaver habitat suitability model. Lynda Saul (MT DEQ), Joe Meek (MT DEQ), and Bryce Maxell (MT NHP) for providing review on the various iterations of this report. Dr. John Weaver (WCS) for helping to refine the HSI variables within the model and providing review of this report. And, Chris Stump and Nat Carter (MT DEQ) for their assistance with the spatial analysis and model scripting during the development of the beaver habitat suitability model. Any errors or omissions in the report are entirely the responsibility of the author.

Introduction

Beaver have long been known as ecosystem engineers that modify their environment to the benefit of both themselves and other species associated with the habitats they create. These benefits extend beyond fish and wildlife populations to the people living within the same watershed. Some of these benefits include the retention of sediment, nutrient cycling and decomposition of organic material, flood peak de-synchronization, water storage, and stream resiliency. One example of their benefit to people is their ability to store large amounts of sediment. Naiman et al. (1986) found that a small beaver dam could potentially retain up to 6500 cu. meters of sediment. In Montana a large number of our streams and rivers are on the 303d list of waters that do not meet water quality standards because they are impaired due to increased sediment loading. It has been suggested that using beaver relocation in combination with other watershed restoration activities may be an effective means to reduce certain pollutants in our streams and rivers and restore other benefits associated with beaver ponds.

Seton (1929), as reported in Naiman et al. (1986), estimated that pre European settlement there were upwards of 400 million beaver in North America and that they occupied most suitable aquatic habitats. After the arrival of Europeans and the large scale trapping efforts of the mid 1800's beaver populations declined dramatically. Beginning in 1900's, most states had enacted laws protecting beaver and began actively reintroducing them to their historic ranges. Naiman et. al (1988) estimated that the population is approximately 10% of its original size. The loss of the beaver population equates to a loss of the benefits that beavers provide through their dam building activities. For example, the loss of beaver dams in a watershed results in less water storage and a potential decrease in critical late season in-stream flows. The Big Hole Watershed Committee and Big Hole River Foundation commissioned a study to identify water storage capacity options to improve in-stream flows to sustain fluvial arctic grayling, maintain irrigation rights, and traditional uses in the Big Hole River Watershed. Of the 19 water management alternatives evaluated, beaver ponds were identified as one of the more important and cost effective water storage methods that could be used to improve in-stream flows for cold water fisheries (DTM Consulting 2005).

Several studies have looked at the influence of beaver habitat on cold water fisheries. While it is acknowledged that in marginal trout fisheries or locations with non-native species beaver dams and their hydrologic effects may be detrimental. In general their effect on cold water fisheries is positive. White and Rahel (2008) found that streams with complementary habitat (spawning areas and adult refuge habitat) contained a higher abundance and broader age class distribution of Bonneville cutthroat trout, *Oncorhynchus clarki utah*, when compared to streams that lacked the adult refuge habitat. Beaver ponds were the critical habitat feature that was used as refuge by adult trout (Harig and Fausch 2002). Contrary to popular thought, Gard (1961) found that beaver dams are not complete barriers to movement of trout species, and this may only be true during the fall when lower in-stream flows exist. White and Rahel (2008) also saw the effect of drought on trout populations. In their study area the presence of beaver ponds mitigated the effects of drought through maintaining in-stream flows necessary to support cutthroat trout fry in their preferred habitats and provide refuge for juveniles and adults. The resiliency of streams to perturbations with beaver ponds is further supported by research Naiman et. al (1986) conducted showing that streams with beaver ponds have a higher resistance and quicker recovery to perturbations such as drought. Similar resiliency can be expected from other perturbations such as climate change.

The beaver habitat suitability model is part of a larger project to relocate 'nuisance' beaver to suitable sites to promote resiliency of stream and riparian ecosystems during climate change (drought), including increasing important habitat for the rare arctic grayling in the Big Hole Watershed. The beaver habitat suitability model was developed as a landscape level management tool to identify unoccupied stream segments in the Big Hole River Watershed that can support a population of relocated beaver. The final product of the beaver habitat suitability model is a map for use by natural resource managers to identify potential beaver relocation sites for further evaluation. This project is being undertaken by Dr. John Weaver from the Wildlife Conservation Society and Stephen Carpenedo from the Montana Department of Environmental Quality's Wetland Program with support from US EPA Region 8 Wetland Pilot Grant WL97831401. Part of this project includes working with Montana Fish, Wildlife, and Parks to develop a process and understanding where a relocation option can be used as a management tool for 'nuisance' beaver. This report only outlines the development, testing, uses, and limitations of the beaver habitat suitability model and does not address the overall project and its goals.

Uses and limitations of the beaver habitat suitability model

The beaver habitat suitability model is a landscape level model looking at potential stream segments that can support and sustain a population of relocated beavers. The output of the model should be used as a "first cut" tool when determining potential sites for relocating beaver, Potential sites then should be field checked to ensure suitability before a final decision is made for any relocation. Appropriate use of this model is to use the information at a stream reach scale, based NHD ReachCode segments, and field verification should be used to determine the exact location on that stream reach to be targeted for relocation. While the model was developed to look at the current habitat suitability of a stream reach, due to data limitations some of the variables developed use data that are from 2001 (LANDFIRE) and the vegetation can and does change. This model has also been developed using the best available data and new datasets developed in the future may improve the performance of this model

The beaver habitat suitability model has been developed specifically to represent conditions that are found in the Big Hole Watershed. While similar conditions exist in other watersheds in Montana, the results presented here have not been tested in other watersheds in Montana and may not be, transferable, suitable, or accurate for other locations. Any use of this model outside of the Big Hole Watershed should be field check for accuracy before decisions are based on the results. If the model is used is in another watershed and the results do not reflect on the ground conditions, the HSI variables described here within should be field checked to determine if they reflect on the ground conditions and any changes necessary. Furthermore, the model should be calibrated for that watershed based on the presence/absence of beaver and checked for accuracy through the use of a validation dataset and evaluating the omission and commission error rates.

Model development methods

The development of the beaver habitat suitability index (HSI) model has relied heavily upon peer reviewed literature and reports dealing with the hydrogeomorphic and food resources necessary to support beaver populations. Some expert opinion has been solicited, and when applicable incorporated into the habitat suitability model. It is understood that the habitat requirements of beavers are complex, and the HSI model has tried to incorporate as many variables as possible in order to accurately depict habitat requirements. In creating a spatial HSI model, though, we are limited by the quality and type of datasets that are available across the entire study area.

The habitat suitability model was developed as a spatial model using ArcGIS scripting in Python 2.5. This format was selected so that any user with ArcGIS and a Spatial Analysis license could use, with some modification, the python scripts and replicate the model for another area of interest. All datasets used are publically available through Montana's Natural Resource Information System, the National Wetland Inventory, LANDFIRE, NHDPlus or other federal GIS clearinghouses. The files used are in both vector and raster formats. All initial spatial datasets were left in their original format for processing. All analyses on rasters were conducted at a 30-meter resolution. The final habitat suitability model is a shapefile of the stream segments with a Strahler Stream order of four or less in the Big Hole Watershed with attribute information that includes; the HSI values given to each variable, probability of the presence of beaver in a given stream segment, and a final habitat suitability value. Habitat suitability values are categorical and describe the current habitat as (1) low quality, (2) marginal quality, or (3) high quality habitat for supporting and sustaining relocated beaver populations. Low quality habitat (1) is defined as habitat not able to support a population of relocated beaver. Marginal quality habitat (2) is defined as habitat that may support, for a short period of time, a population of relocated beavers. High quality habitat (3) is defined as habitat that will support and sustain a population of relocated beaver. Other attribute information incorporated in the final product are MFISH data (MT FWP 2010) on the presence/absence of Arctic Grayling and West Slope Cutthroat Trout that can be used to prioritize stream segments with suitable habitat.

Seven standard datasets that are readily available through the Web or Montana Natural Resource Information System were used to develop ten different habitat suitability variables describing different hydrogeomorphic features or food resources important to support beaver populations. The datasets used include:

1. 1:100,000 National Hydrography Dataset
2. LANDFIRE
    a. Tree Heights
    b. Canopy Cover
3. Montana ReGAP
4. National Wetland and Riparian Inventory (provisional)

5. 30 m Digital Elevation Model
6. 30 m Percent Slope Model
7. 1:100,000 Value Attribute Added NHDPlus

The variables modeled include:

1. Stream Gradient
2. Stream Permanence
3. Herbaceous Emergent Wetlands
4. Herbaceous Aquatic Bed Wetlands
5. Woody Vegetated Riparian Areas
6. Average Valley Width
7. Percent Canopy Cover of Trees
8. Percent Canopy Cover of Shrubs
9. Average Height of Shrub Canopy
10. Species Composition of Woody Vegetation

Statistical Analysis

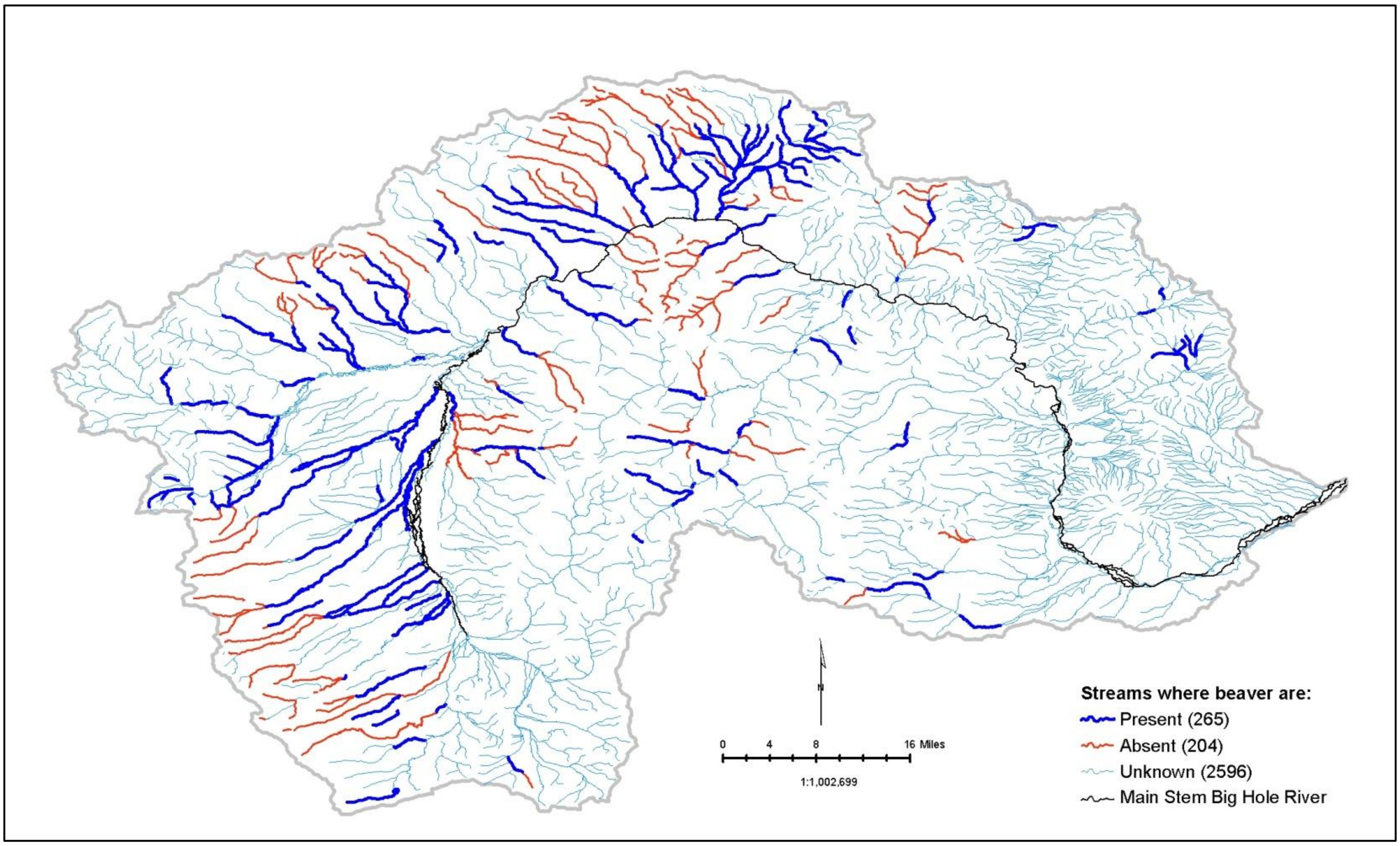
Habitat suitability models are compiled in a variety of ways. The most common use stepwise linear or logistic regression models to determine the effect of a set of variables on the presence of beavers within a study area (Slough and Sadleir 1977; Beier and Barrett 1987). Other suitability indices work under the assumption that for a list of variables explaining the presence/absence of beavers, the variable with the lowest value is the most limiting, and thus is the value reported for the habitat suitability index (Allen 1983; Suzuki and McComb 1998).

I used logistic regression analysis on a binomial probability of the presence or absence of beaver to fit a set of candidate models to evaluate the relationship between the presence of beavers in a given stream reach and different combinations of independent variables. Presence or absence of beavers in a given stream reach were determined from expert and local knowledge on the distribution of beavers within the last 5 years (2005 – 2010) for stream segments in the Big Hole Watershed, independent data from amphibian surveys conducted by the Montana Natural Heritage Program, and independent data from 2005 National Wetlands Inventory mapped wetlands with a hydrologic modifier indicating beaver (Map 1). Ten candidate models were developed to evaluate the relationships between hydrologic, geomorphic, and habitat variables and the presence of beavers (Table 4). A global model, incorporating all variables, was not included to reduce potential confounding results. A Hosmer and Lemeshow Goodness of Fit test was used to determine if there was significant difference ($p \leq 0.05$) in the observed and expected values (Hosmer and Lemeshow, 1989). A significant difference indicates lack of fit. To avoid multicolinearity in the candidate models, Pearson's correlations were calculated and all variables that had an $r^2 \geq 0.50$ were not included in the same candidate model. Moderately correlated variables ($r^2 \leq 0.515$) that were biologically relevant for explaining the presence and absence of beaver were retained in the same candidate models.

Akaike's Information Criteria (AIC) (Akaike 1973) adjusted for small sample bias (AICc) (Hurvich and Tsai 1989) was used to evaluate the relative fit of the ten candidate models relating hydrologic, geomorphic and habitat variables to the presence or absence of beavers. Akaike's weights (W_i), which rank the most plausible model based on AICc with low values indicating better fitting models, were used to rank each candidate model. To account for model selection uncertainty, a confidence set of candidate models was selected based on a threshold value of 12% of the candidate model with the greatest Akaike weight. 12% is derived from Royall's (1997) 1/8 rule of thumb for assessing strength of evidence. Any candidate model with an Akaike weight greater than this threshold was retained in the confidence set of models.

Interpretation of the variables and their effect on the presence of beaver may be influenced by the multiple models selected in the confidence set of models because the value of parameter estimates for the same variable can vary between models. To account for this, I calculated model averaged parameter estimates for all of the variables present in the composite model (Burnham and Anderson 2002). A composite model is a model including all variables that are present in the confidence set of models. The model averaged parameter estimates were then used to evaluate the probability that beaver would be present in a given stream segment. This was done by calculating the log-odds, which is strictly a linear regression equation summing the model averaged parameter estimates multiplied by the mean value of each variable. The probability of beaver being present in any given stream segment in the Big Hole Watershed is then calculated by the following equation: $\frac{1}{(1+e^{\log - odds})}$. Cross validation of the composite model was undertaken using a validation dataset derived from randomly selecting 10% of the calibration dataset to determine the omission and commission errors between observed and predicted values for the presence of beaver. Cutoff probability values to determine the presence/absence of the validation data set were calculated using Jenks Optimization on the probability of beaver presence: $\frac{1}{(1+e^{(-1\text{logit}[X])})}$. Where *X* is the value of a given stream segment determined using the composite model with the model averaged parameter estimates.

The model averaged parameter estimates and constant were then used to calculate the probability of beaver being present, based on the HSI variables, for all stream segments in the Big Hole Watershed. This probability was then grouped into the three categories describing low quality, marginal quality, and high quality habitat suitability for populations of relocated beaver. Grouping was accomplished using a choropleth classification approach known as Jenks Optimization (Dent 1999) which minimizes the within group variance while maximizing the variance between groups. The habitat suitability was then joined in ArcGIS to the medium resolution NHD streams shapefile to produce a final map identifying stream segments with suitable habitat that will support and sustain a population of relocated beaver (Maps 12 and 13).



Map 1: Streams segments identified as having beaver activity within the last 5 years (2005 – 2010)

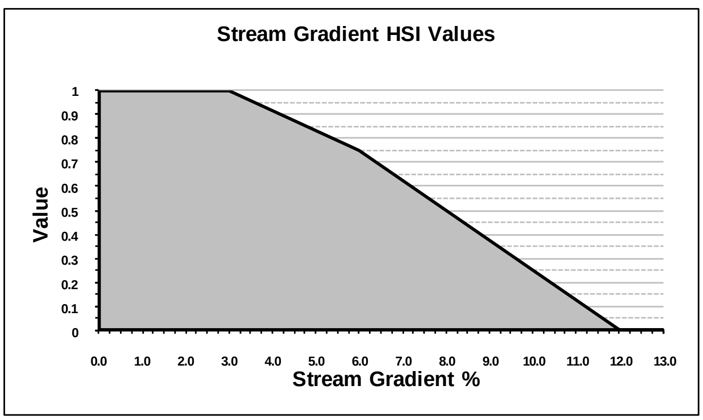
Habitat suitability index variables

The variables used in this model were taken from previous scientific studies done on habitat suitability for beavers or other landscape predictors of beaver occupancy. An initial test model was conducted on a small watershed in the Elkhorn Mountains to determine how well each variable was depicting the hydrologic, geomorphic or biological features on the landscape. Field testing was done in the summer of 2009 and any changes to the model were made and field verified to determine their effects. No testing for the relationship between beaver and HSI variables was conducted on the initial test model. The explanation of each variable is the tested variable and includes any modifications that were made to better describe actual on the ground conditions. Several variables were either changed or removed from the model as part of this review. The changes to, and removal of, variables is not discussed within this document.

Habitat Suitability Index variables that are describe below are either continuous (n=8) or categorical (n=2) with values ranging between 0 and 1. A HSI value of 0 indicates unsuitable conditions for supporting beaver populations. Where as a value of 1 indicates optimal conditions that will support and sustain beaver populations.

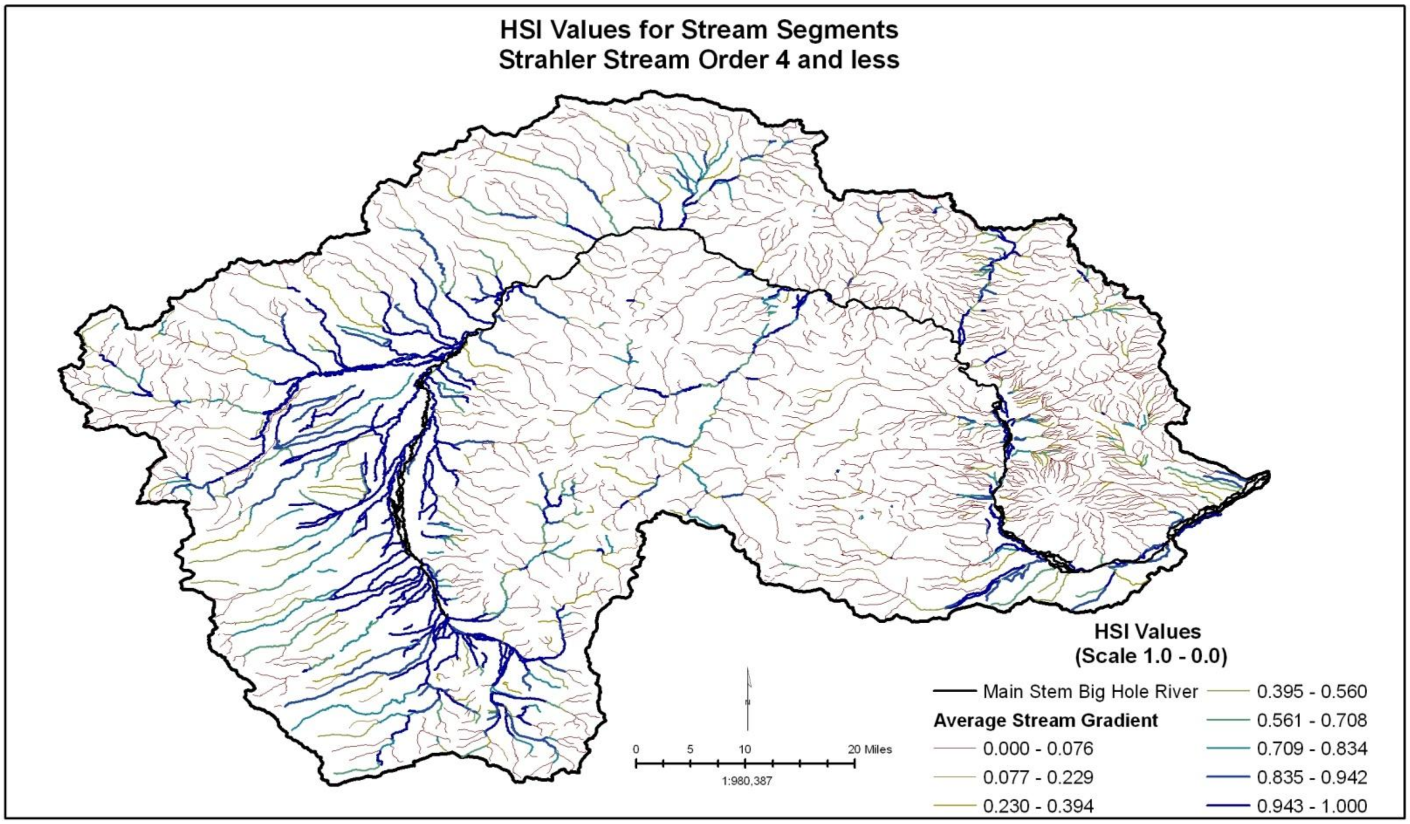
Variable 1: Stream gradient (SG)

The gradient of a stream (SG) has proven in numerous studies to be a dominate predictor of suitable habitat for beavers (Retzer et al. 1956; Slough and Sadleir 1977; Allen 1983; Howard and Larson 1985; Suzuki and McComb 1998). Depending on the geographic location of studies conducted, researchers have used varying stream gradient cutoff values for identifying suitable and unsuitable stream reaches. For example in Oregon, Suzuki and McComb (1998) classify suitable stream reaches as any with a stream gradient less than 3%, while Retzer et. al (1956), as reported in Allen 1983, used a stream gradient less than 6% for suitable stream reaches in the Colorado Rocky Mountains. Similarly, the stream gradients considered as unsuitable vary from 10% to 15% (Allen 1983). To give more latitude in identifying suitable stream reaches, stream gradients were split in to four different categories. Streams with gradients less than or equal to 3% are considered as optimal stream reaches and given a value of 1. The suitability of stream gradient was assumed to decline linearly from 3.01% to 6%, then decline linearly with a steeper slope from 6.01-12% (Graph 1). Those streams with gradient greater than 12% are considered as unsuitable habitat (value = 0). Comments from experts have suggested that beavers can occupy stream reaches with gradients greater than 12% and the establishment of beaver dams in these locations have important hydrologic benefits. This cutoff value was chosen because the Habitat Suitability Index was developed to identify optimal, permanent habitat that can support populations of relocated beavers. Beavers may occupy stream reaches with gradients greater than 12%, but these tend to be less permanent more ephemeral colonies because the kinetic energy of steeper streams have greater ability to "blow out" dams making these areas less desirable (Gurnell 1998).



Graph 1: Stream gradient HSI values

Stream Gradient	HSI Values
<= 3.0	1.0
3.0 < x <= 6.0	-0.0833 * x + 1.25
6.0 < x <= 12.0	-0.125 * x + 1.5
12.0	0



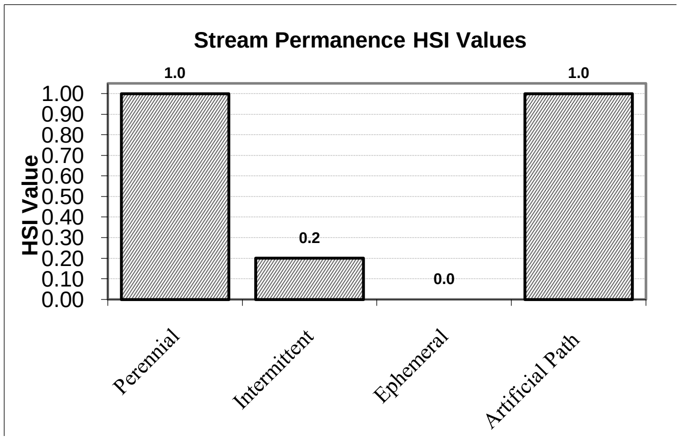
Map 2: Stream segments displaying HSI values for average stream gradient

Variable 2: Stream flow permanence (SFP)

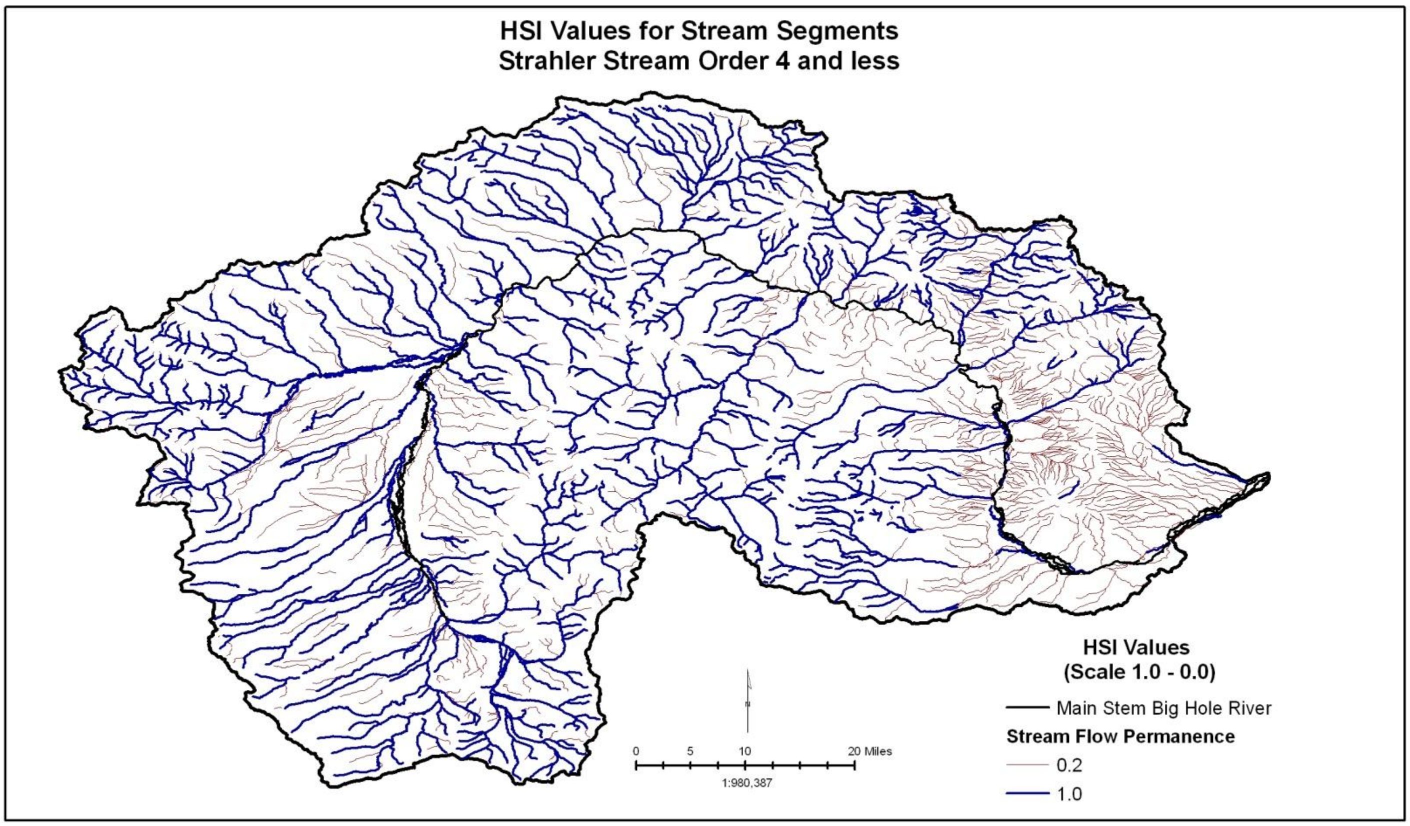
Permanence of stream flow (SFP) is regarded as a fundamental requirement of suitable habitat for beavers. While researchers have often stated that the permanence of stream flow is one critical factor, most reviewed literature and suitability indices use a combination of variables to describe this factor (Howard and Larson 1985; Suzuki and McComb 1998). When modeling landforms spatially many of the variables used to describe permanence of stream flow are unavailable, i.e. stream width. Only Allen (1983) provides an example where permanence of stream flow is an independent variable. Using the 1:100,000 National Hydrography Flowline Dataset Medium Resolution Classification (Perennial, Intermittent, Ephemeral, and Unknown), I translated these to the values Allen (1983) provides for water fluctuation and developed a single variable for stream permanence. See Table 1. The medium resolution NHD layer does not incorporate ephemeral streams so no zero values were calculated. Artificial paths in the NHD flowline dataset are used to represent flow through paths of the polygonal features found in the NHD Area dataset. In the NHD flowline dataset these include lakes, ponds and larger rivers. The artificial paths representing rivers were maintained in our dataset for the Big Hole Watershed. These represent the main stem of the Big Hole River which is considered as a large perennial river. In most instances artificial paths will not be reported in the final product because they represent streams that are greater than our maximum Strahler stream order of 4. Artificial paths representing lakes and ponds have been removed in a pre-processing step and are not represented in the model.

Table 1: NHD correlated to Allen 1983 for stream permanence HSI

NHD Classification	Correlated to Allen 1983	Stream Permanence HSI Value
Perennial	Small fluctuations	1.0
Intermittent	Moderate fluctuations	0.2
Ephemeral	Extreme fluctuations, or water absent during part of year	0
Artificial Path	Small fluctuations	1.0



Graph 2: Stream flow permanence HSI values



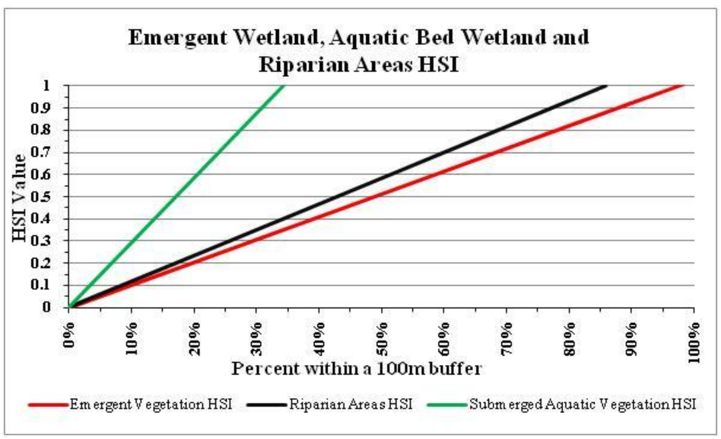
Map 3: Stream segments displaying HSI values for stream flow permanence

Variables 3 – 5: Herbaceous emergent wetlands (HEW), herbaceous aquatic bed wetlands (HAB), and woody vegetated riparian areas (WRA)

The herbaceous emergent wetlands (HEW), herbaceous aquatic bed wetlands (HAB) and woody vegetated riparian areas (WRA) variables are landscape descriptors describing the potential food resources available to beavers throughout the year. The herbaceous emergent and herbaceous aquatic bed wetland variables are used to describe food resources available during the growing season. When available the root stock and stems of herbaceous emergent and submerged aquatic vegetation are preferred food resources of beaver (Svendsen 1980). Svendsen (1980) showed a switch from predominately woody vegetation in the winter to an 80% reliance on herbaceous emergent and submerged aquatic vegetation from May to October. The woody vegetated riparian areas variable is a general descriptor of the percent of woody vegetation that may be available to beaver within a 100 meter buffer surrounding a stream segment. The woody vegetated riparian areas variable is a descriptor of winter food resources, as (Allen 1983) stated that an adequate cache of woody vegetation is important for supporting beaver colonies through the winter months.

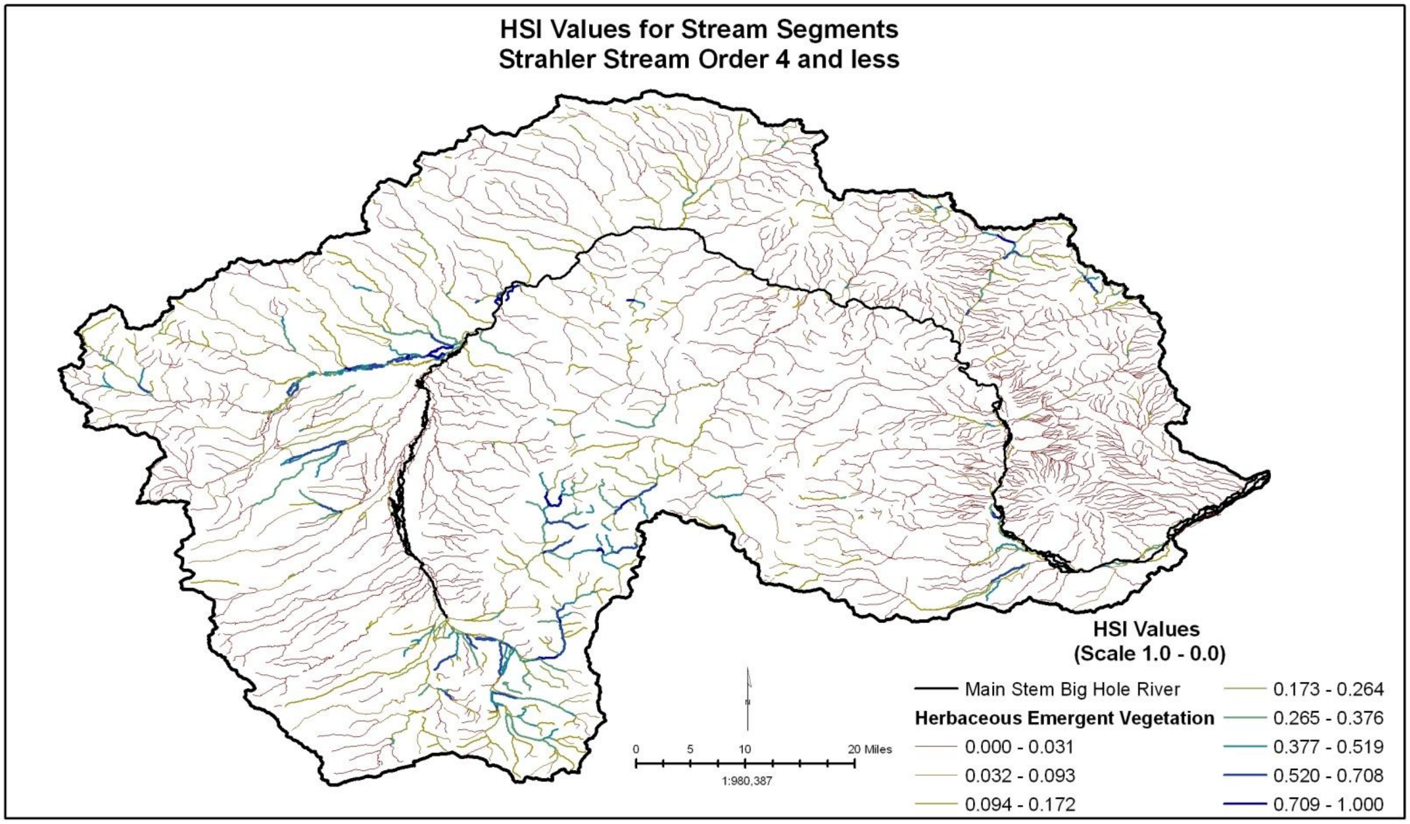
The National Wetland Inventory and associated riparian mapping was used to describe herbaceous wetlands and woody vegetated riparian areas in the Big Hole Watershed. Herbaceous aquatic bed wetlands are used as a surrogate for submerged aquatic vegetation and are NWI wetlands with the Cowardin Classification of "PAB". The Cowardin Classifications of "PEM" and "Rp#EM" were used to describe herbaceous emergent wetlands. The riparian classification of "Rp#EM" was included in herbaceous emergent wetlands because it is not a descriptor of woody vegetation but herbaceous emergent vegetation in the riparian zone. Riparian classifications included "PSS", "PFO", and all systems identified as "Rp" excluding emergent "EM" and aquatic bed "AB" systems. "PSS" and "PFO" were included in the riparian variable because they are palustrine wetlands with woody vegetation and thus are better descriptors of winter food resources. All hydrologic modifications were included in these classifications (Cowardin et al. 1977).

The National Wetland Inventory and associated riparian mapping has not previously been use as a variable in habitat suitability models for beavers. As a result there was little guidance on the values to ascribe to habitat suitability. For all of these variables I calculated the percent that herbaceous emergent wetlands, herbaceous aquatic bed wetlands, or woody vegetated riparian areas occupy within a 100 meter buffer of a given stream segment. This percentage was then normalized using the global maximum value to scale the HSI values from 0 (unsuitable) – 1 (optimal). The percent of herbaceous emergent wetlands within a stream buffer ranged from 0 – 97.7%. The HEW HSI values increase linearly from 0 to 97.7% with any value greater than or equal to 97.7% given a value of 1.0. The linear increase in woody vegetated riparian area HSI values is comparable to that of the herbaceous emergent wetlands with any value greater than or equal to 85.9% given a value of 1.0. Herbaceous aquatic bed wetlands showed a much different trend with the maximum percent of herbaceous aquatic bed wetlands within a stream buffer having a maximum of only 34.3%. Herbaceous aquatic bed wetland HSI values increase linearly from 0 to 34.3% with any value greater than or equal to 34.3% given a value of 1.0 (Graph 3).

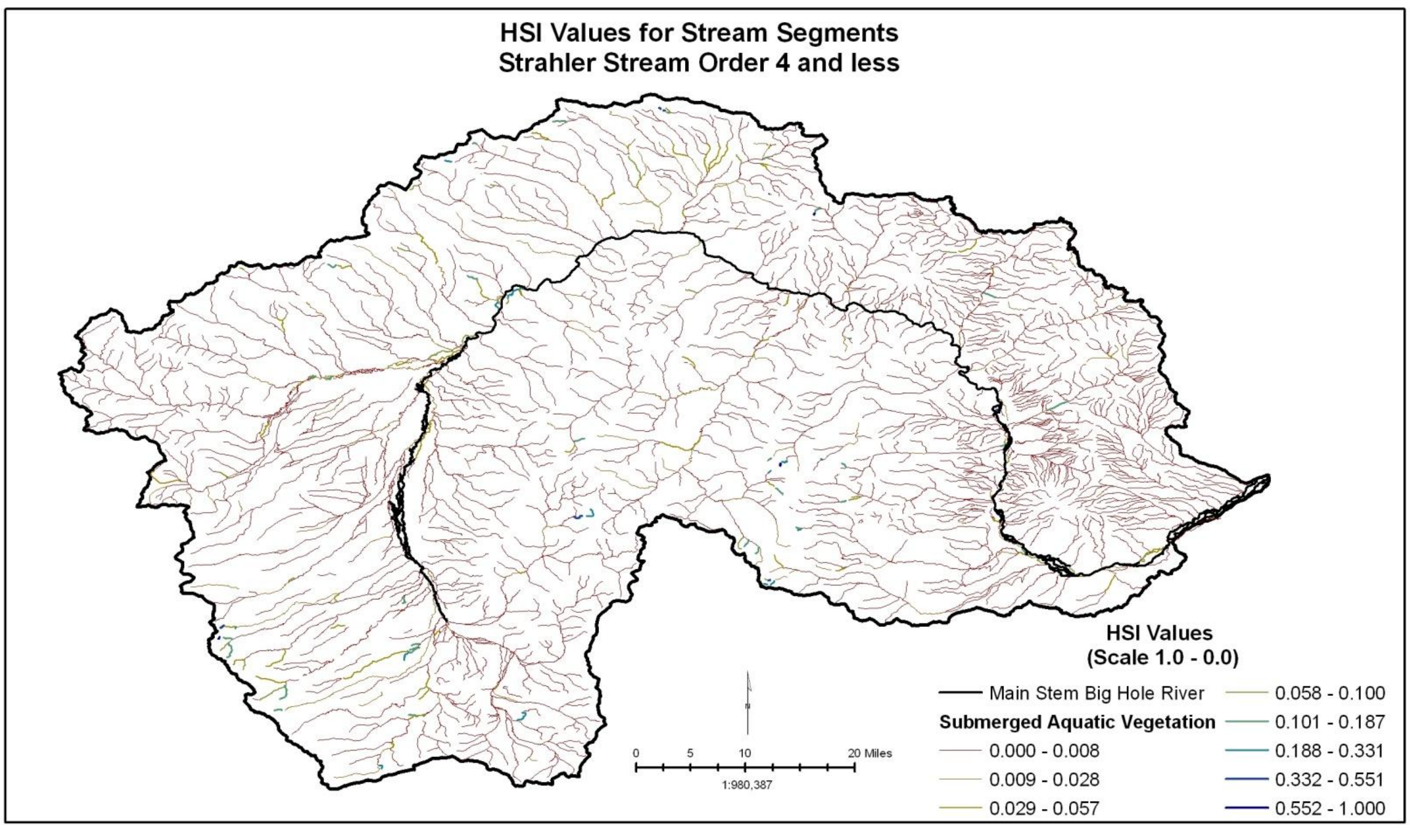


Graph 3: Herbaceous emergent wetlands, herbaceous aquatic bed wetlands, and woody vegetated riparian areas HSI values

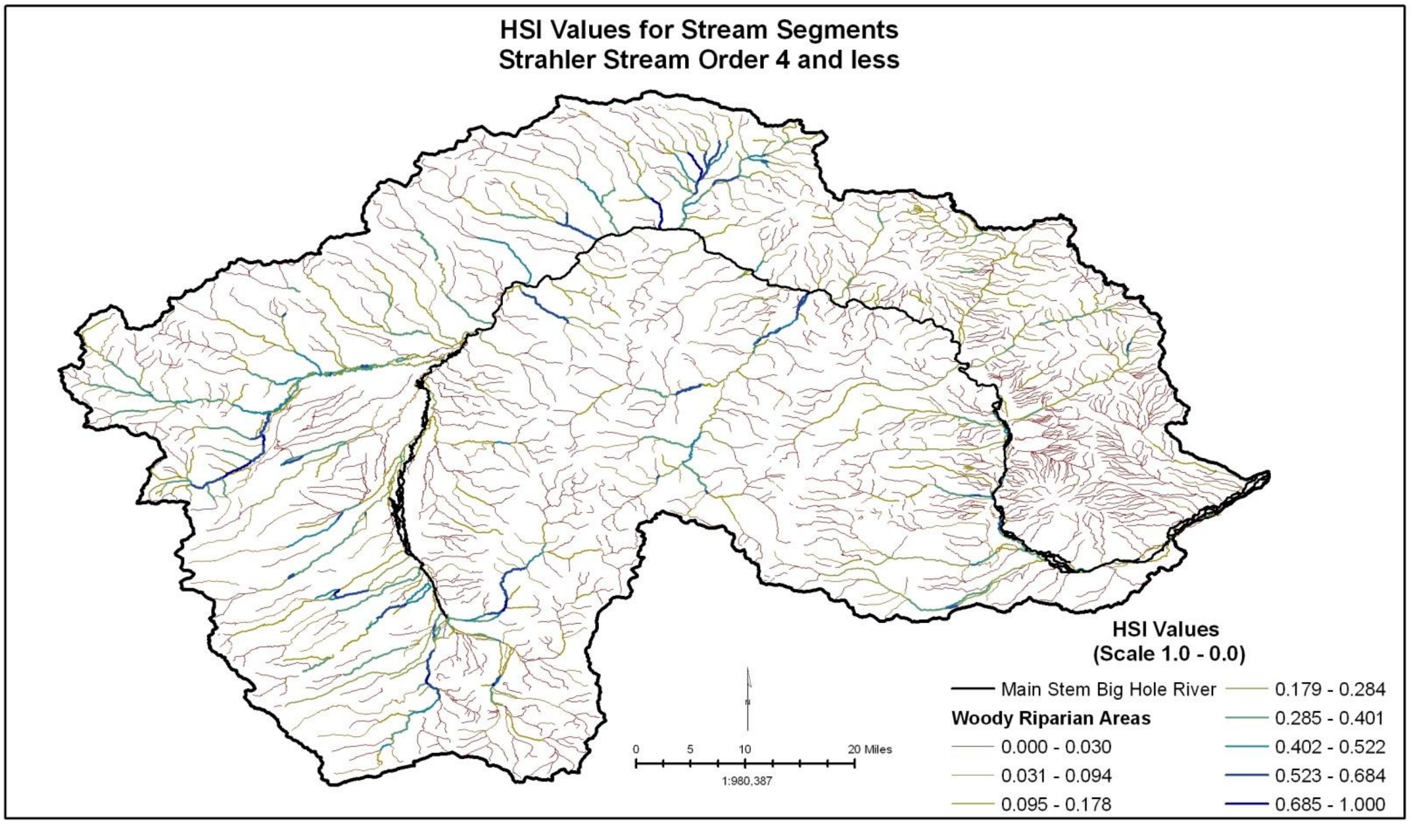
NWI HSI Variables	**HSI Value**
Herbaceous Emergent Wetlands	$1.0233*x – 3E^{-15}$
Herbaceous Aquatic Bed Wetlands	$2.9141*x – 2E^{-15}$
Woody Vegetated Riparian Areas	$1.1632*x + 3E^{-15}$



Map 4: Stream segments displaying HSI values for herbaceous emergent wetlands



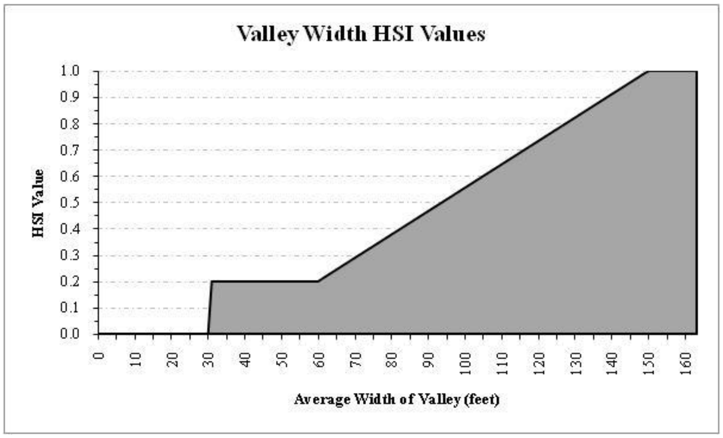
Map 5: Stream segments displaying HSI values for submerged aquatic wetlands



Map 6: Stream segments displaying HSI values for woody vegetated riparian areas

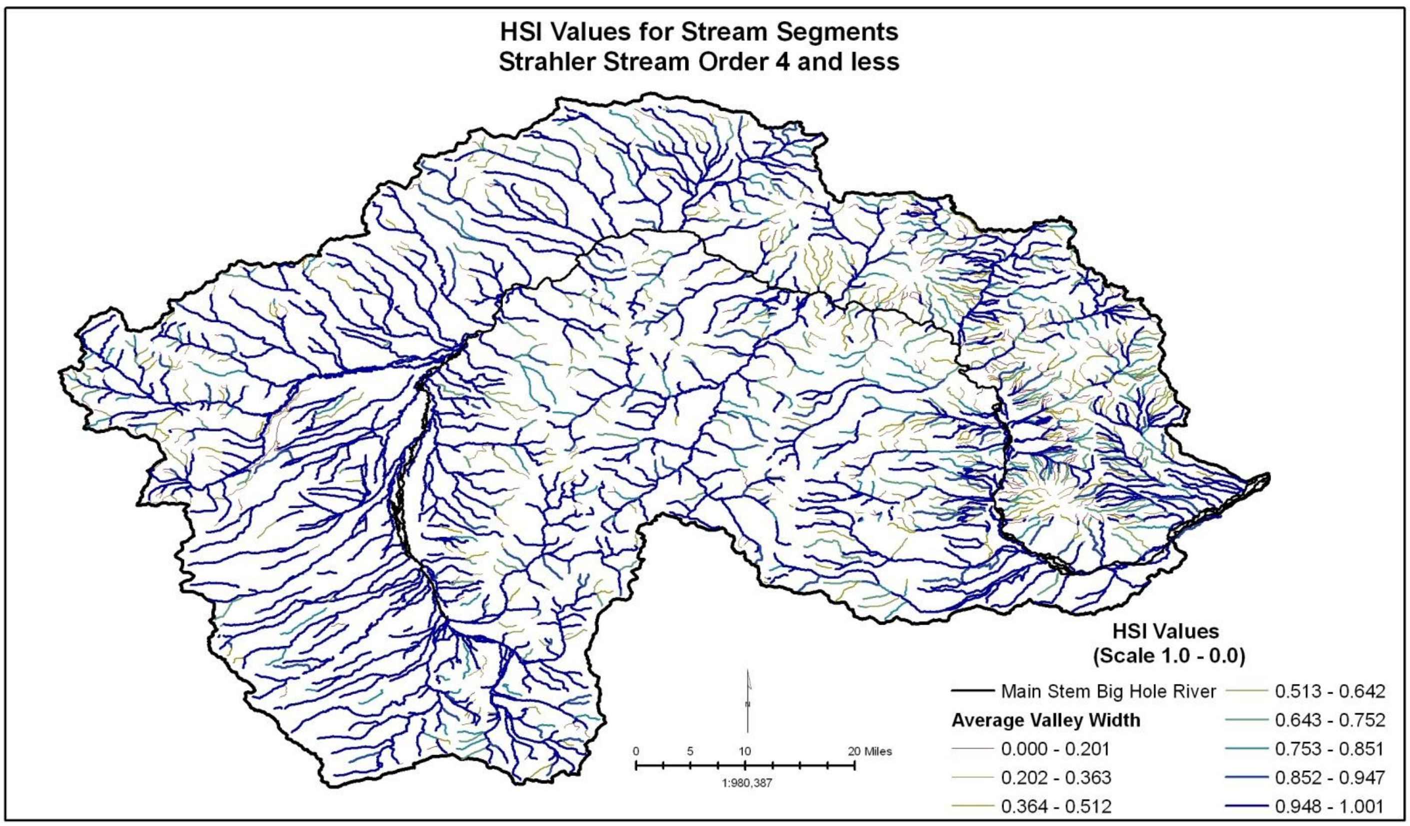
Variable 6: Average valley width (VW)

Accurate delineation and characterization of valley bottom widths are crucial to assess the biological and geomorphic features of a floodplain (Williams et al. 2000). Biological features represent the habitat requirements influencing the probability of beavers occupying a given stream segment. The geomorphic features of the valley bottom help to describe the flow found within a drainage and the potential for the growth and development of winter food resources as a result of the ponding and increased wetter perimeter from beaver dams. Valley width is an important factor in determining winter food resources by limiting their lateral extent and development capabilities. For beavers, preferred winter foods tend to be species that are associated with riparian areas that are topographically flat and experience seasonal flooding. Narrow and steep valleys inhibit the growth of these preferred food resources and thus are less likely to provide adequate winter food resources to support beaver populations. Conversely wide valleys allow for the development of more extensive riparian areas and greater concentrations of preferred winter food resources (Vore 1993). While, Beier and Barrett (1987) did not find any relationship between riparian width, a surrogate for total potential food supply, and beaver occupancy, Suzuki and McComb (1998) did find a significant relationship between the valley width and beaver occupancy. They found occupancy rates close to 100% in streams with valley widths greater than 50 m (150 ft), and beavers occupying streams with valley widths greater than 10m (30 ft). This fits well with Retzer et. al (1956), as reported in Vore (1993), who found that beavers occupied streams in valley widths greater than 150 ft in proportion to their availability, and did not occupy streams with valley widths less than 60 ft in proportion to their availability. Because Vore (1993) evaluated stream habitats for beaver in Southwestern Montana, I used his recommendation where an average valley width greater than 150 ft is given a value of 1.0, with the HSI value declining linearly until the average valley width is 60 ft, at which point any valley width between 30 – 60 feet is given a value of 0.2 (Graph 4). Below 30 feet in width the valley of a given stream segment is considered as unsuitable habitat (value = 0).



Average Valley Width	HSI value
0 – 30 ft.	0.0
30 – 60 ft.	0.2
60 – 150 ft.	0.0089*x-0.3331
> 150 ft.	1.0

Graph 4: Valley width HSI values



Map 7: Stream segments displaying HSI values for average valley width

Winter food

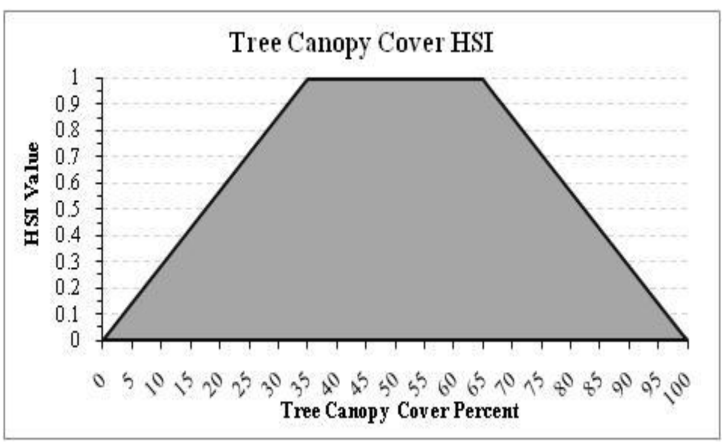
Winter food is often thought to be the limiting factor for beaver occupying stream reaches (Allen 1983). All of the beaver habitat models reviewed for this project initially included some measure of winter food resources. In developing their models only Slough and Sadleir (1977) found that a food variable was the most important in explaining the occupancy of stream reaches by beavers. Both Howard and Larsen (1985) and Suzuki and McComb (1998) found that food variables, while important, could not accurately predict occupied and unoccupied habitats alone, and in fact contributed to explaining occupancy much less than water and geomorphic variables. Beier and Barrett (1987) also found that food variables were not good predictors of site occupancy by beavers. The relatively low predictability of food variables are explained by Beier and Barrett (1987) in that current observed vegetative conditions used to build predictive models may be the result of alteration by beaver and thus may not be good predictors of potentially suitable sites prior to colonization by beaver. Even though all researchers have found minimal effects of food variables on predicting suitable beaver habitat, their importance to beavers has not been questioned and as a result I have included four additional food variables.

I have based winter food variables on Allen (1983), who described winter food as five different variables combined into several derived formulas. He states that food is a function of the density, size class, and species composition of woody vegetation. Due to the availability of data sources, all variables that Allen (1983) uses could not be modeled and thus are not included in the beaver HSI. Using the best available data sources, I was able to model the following four winter food variables:

1. Percent canopy cover of trees
2. Percent canopy cover of shrubs
3. Average shrub height
4. Species composition of woody vegetation

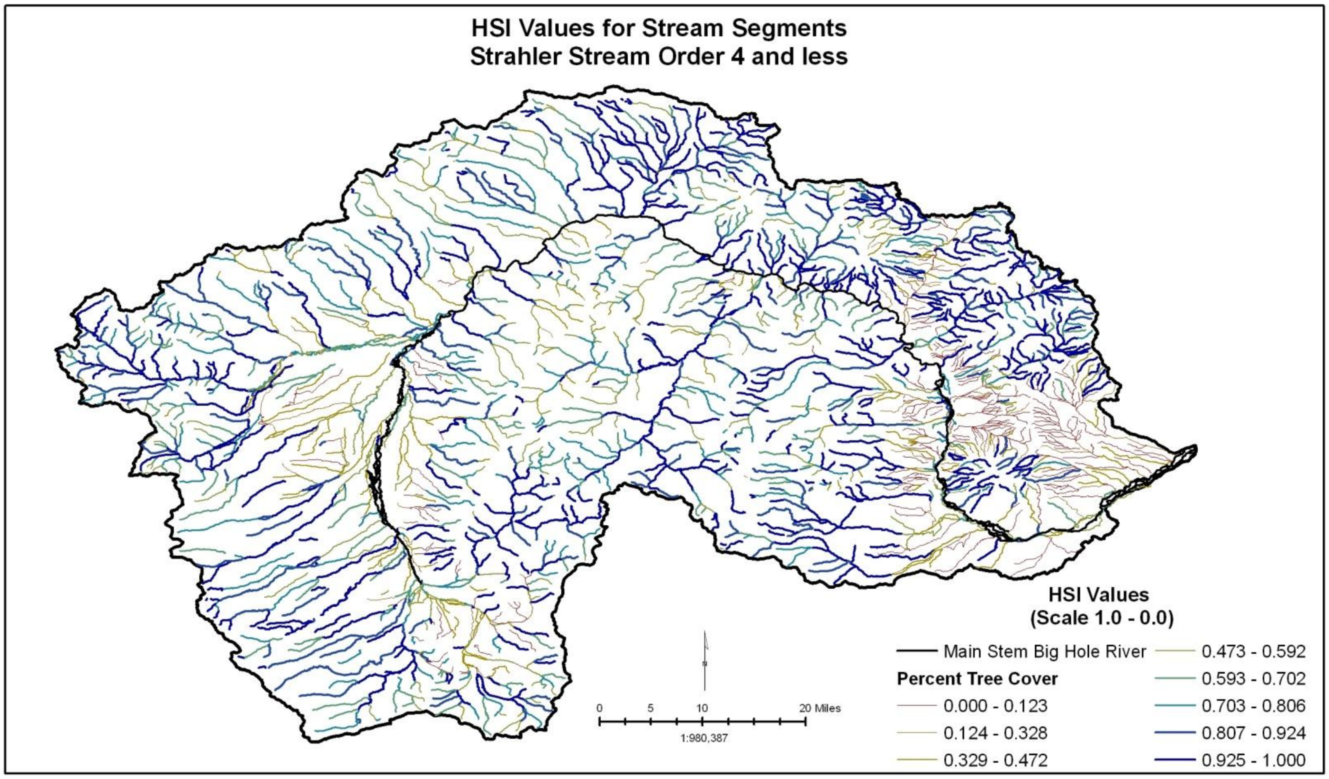
Each of these variables is calculated for a 100 meter buffer on either side of the stream bank. A conservative buffer of 100 meters is assumed as 90% of beaver foraging occurs within 200 ft of water (Hall 1970; Jenkins 1980) as reported in Allen 1983.

Variable 7: Percent canopy cover of trees (PCT)
Trees were defined as any point identified in the LANDFIRE Treeheight raster dataset that are greater than 7.5 meters in height (USGS 2006) and not identified as a majority shrub layer using the Ecological Classification Systems in the ReGAP layer (NatureServe 2009), Table 2. Allen (1983) identifies trees as anything greater than 5m in height. The LANDFIRE Treeheight dataset does not split tree heights at 5 meters, but 2.5 meters and 7.5 meters. Based on expert opinion of our study area, trees were classified as being greater than or equal to 7.5 meters in height, as this is more applicable and better describes the food preferences of beaver (Weaver, *pers comm.*). The percent of tree canopy cover is calculated as the percentage of a 100-meter buffer on either side of the stream bank that is shaded by the tree canopy. The HSI values for percent tree canopy cover are assumed to increase linearly from 0 – 35%, with the most suitable habitat ranging with canopy cover values from 35% - 65% (Graph 5). At percent of canopy cover greater than 65%, it is assumed that the habitat suitability decreases linearly to a value of 0 at 100%. Mid range canopy covers are considered as the most suitable habitat because holes in the canopy allow for growth of shrubs and other vegetation that are considered as preferred food resources. Increasing tree or shrub canopy closures are assumed as less suitable habitat due to decreased accessibility of food and growth of preferred food resources.



Graph 5: Percent canopy cover of trees HSI Values

Percent canopy cover of trees	**HSI Value**
0 - 35	0.0286*x
35-65	1.0
65-100	-0.0286*x + 2.8571



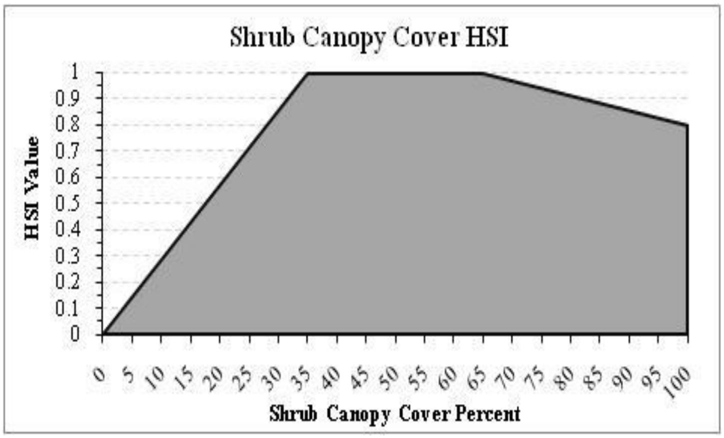
Map 8: Stream segments displaying HSI values for percent canopy cover of trees

Table 2: Ecological Systems identified in ReGAP that have a majority shrub component

ReGAP ID	Ecological System (NatureServe 2009)
4303	Inter-Mountain Basins Mountain Mahogany Woodland and Shrubland
5203	Inter-Mountain Basins Mat Saltbush Shrubland
5207	Rocky Mountain Alpine Dwarf-Shrubland
5209	Wyoming Basins Dwarf Sagebrush Shrubland and Steppe
5257	Inter-Mountain Basins Big Sagebrush Shrubland
5258	Inter-Mountain Basins Mixed Salt Desert Scrub
5262	Northwestern Great Plains Shrubland
5263	Rocky Mountain Lower Montane-Foothill Shrubland
5312	Northern Rocky Mountain Montane-Foothill Deciduous Shrubland
5326	Northern Rocky Mountain Subalpine Deciduous Shrubland
5454	Inter-Mountain Basins Big Sagebrush Steppe
5455	Inter-Mountain Basins Montane Sagebrush Steppe
7118	Rocky Mountain Subalpine-Montane Mesic Meadow
8402	Introduced Upland Vegetation - Shrub
8503	Recently burned Shrubland
8602	Harvested forest-shrub regeneration
9155	Northern Rocky Mountain Lower Montane Riparian Woodland and Shrubland
9156	Rocky Mountain Lower Montane Riparian Woodland and Shrubland
9187	Rocky Mountain Subalpine-Montane Riparian Shrubland
9203	Great Plains Prairie Pothole
9217	Rocky Mountain Alpine-Montane Wet Meadow
9234	Rocky Mountain Subalpine-Montane Fen

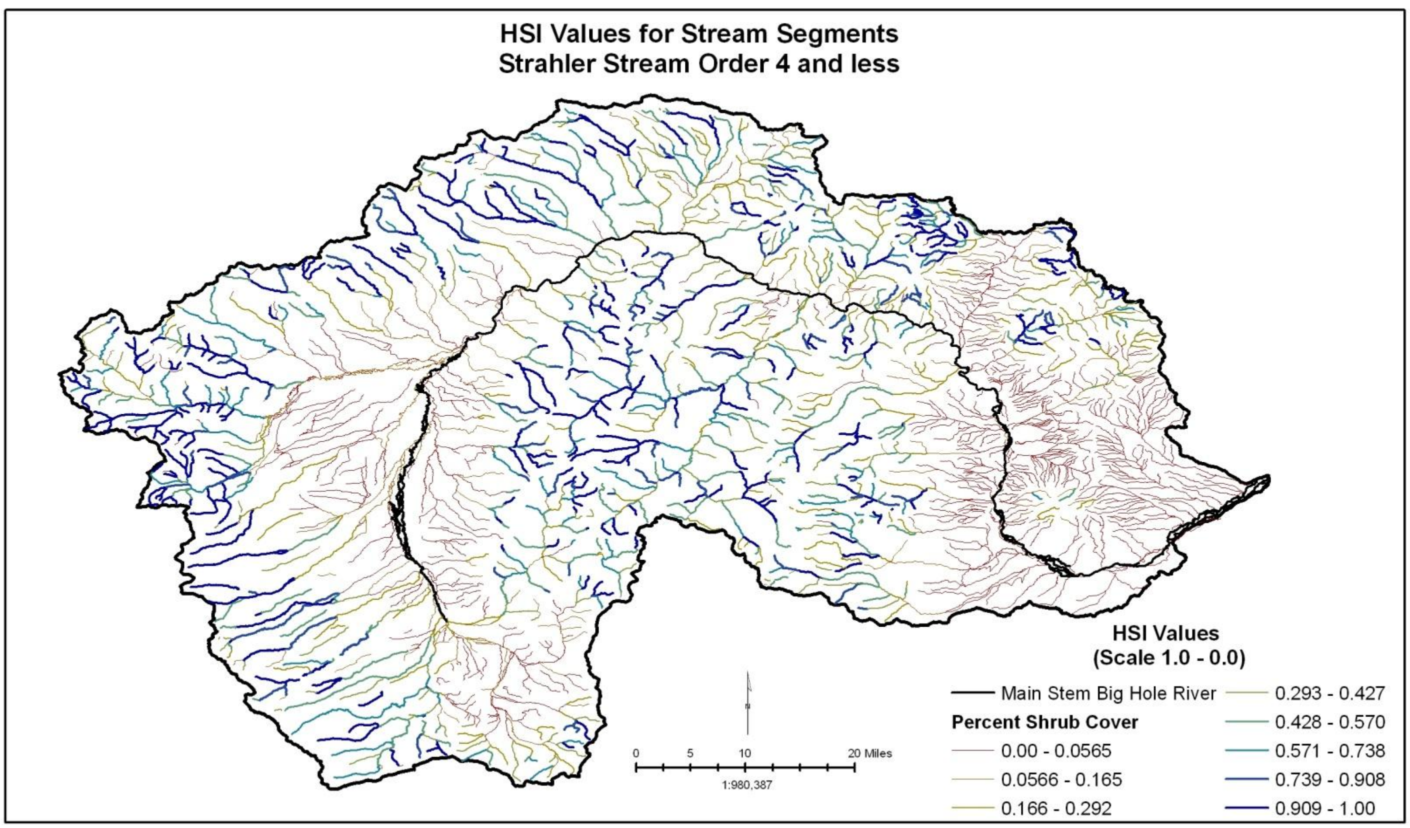
Variable 8: Percent canopy cover of shrubs (PCS)

The percent canopy cover of shrubs is defined as the percent canopy cover of any ReGAP vegetation class within a 100-meter buffer of a stream segment that LANDFIRE Treeheight identifies as having a height of less than 7.5 meters or any Ecological System identified in Table 2 that has a majority shrub component (USGS 2006; NatureServe 2009). The percent canopy cover of shrubs is calculated in the same way as the percent canopy cover of trees with the exception that 100% shrub cover is not assumed to be unsuitable habitat. Instead the HSI value for the percent shrub canopy cover decreases linearly from 1.0 at 65% to 0.8 at 100% shrub canopy closure (Graph 6). This is supported by the negative relationship of an increasing percent shrub cover in explaining occupancy by beavers in Suzuki and McComb's (1998) study.



Percent Shrub Canopy Cover	HSI Value
0 – 35%	0.0286 * x
35% – 65%	1.0
65% – 100%	-0.0057 * x + 1.3714

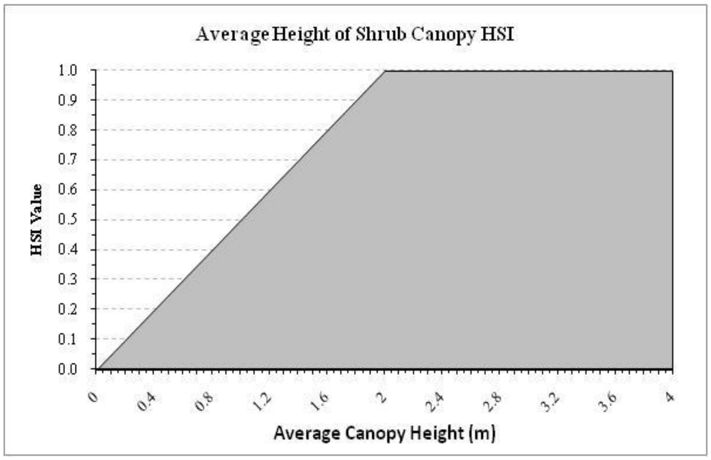
Graph 6: Percent shrub canopy cover HSI values



Map 9: Stream segments displaying HSI values for percent canopy cover of shrubs

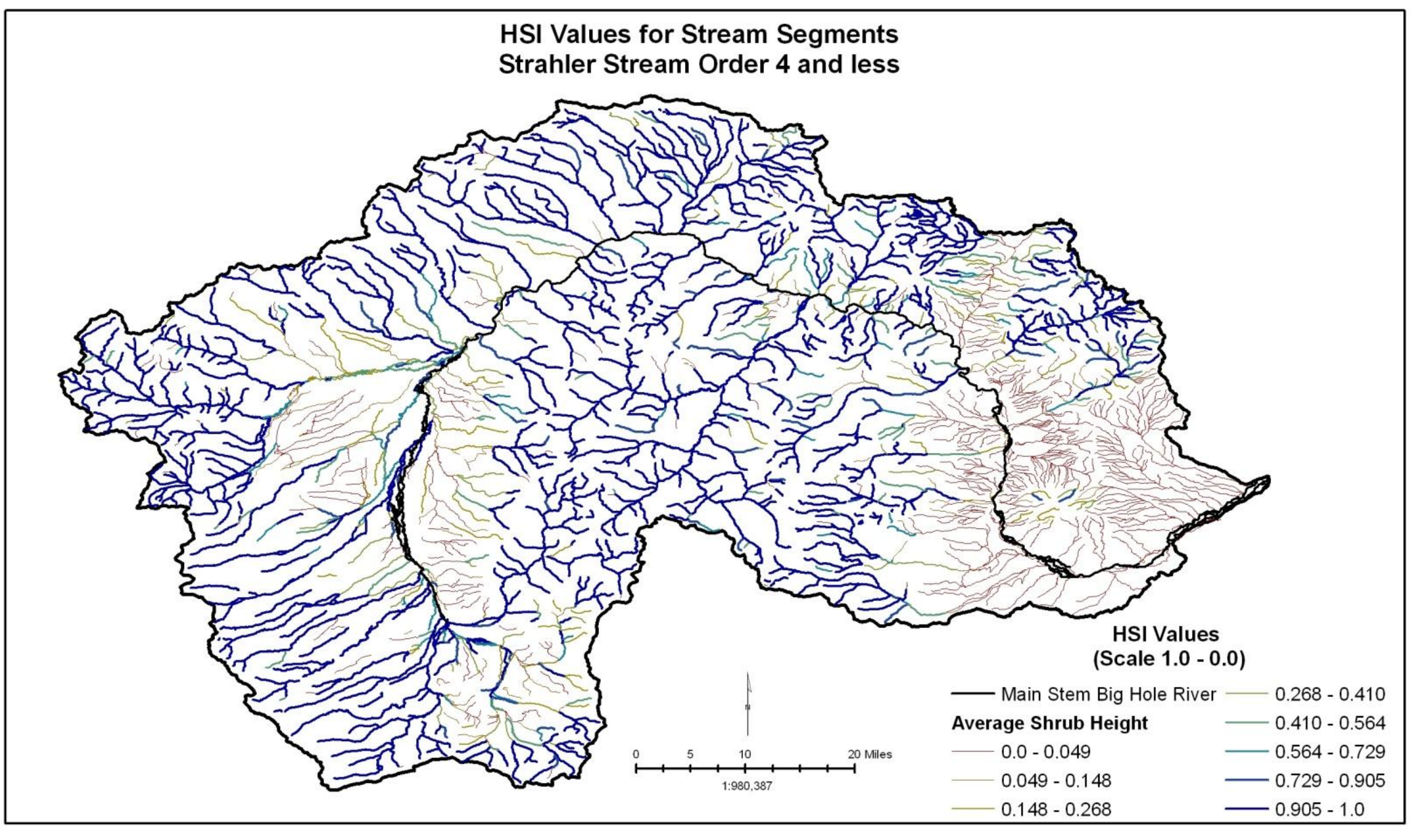
Variable 9: Average height of shrub canopy (ASH)

The average height of shrub canopy is calculated using the same shrub dataset developed for percent canopy cover of shrubs. Shrubs are defined as any ReGAP vegetation class that LANDFIRE Tree height identifies as having a height of less than 7.5 meters or any Ecological System identified in ReGAP that has a majority shrub component (USGS 2006; NatureServe 2009). The average shrub height is included in that larger/taller preferred food resources are considered to provide a greater energy/effort benefit than smaller vegetation. The HSI values for average shrub height are taken directly from Allen (1983), whereby he states that for a maximum suitability value, shrubs should be at least an average of 2 meters in height (Graph 7).



Graph 7: Average Height of Shrub Canopy HSI Values

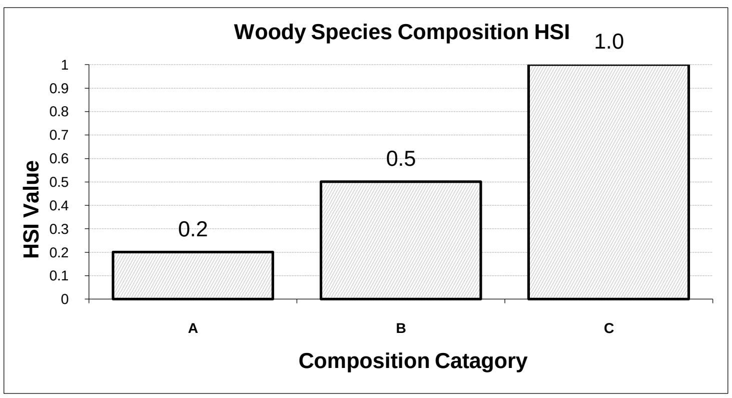
Average height of shrub canopy	HSI Value
0-2.0 m	0.5 * x
≥ 2.0 m	1.0



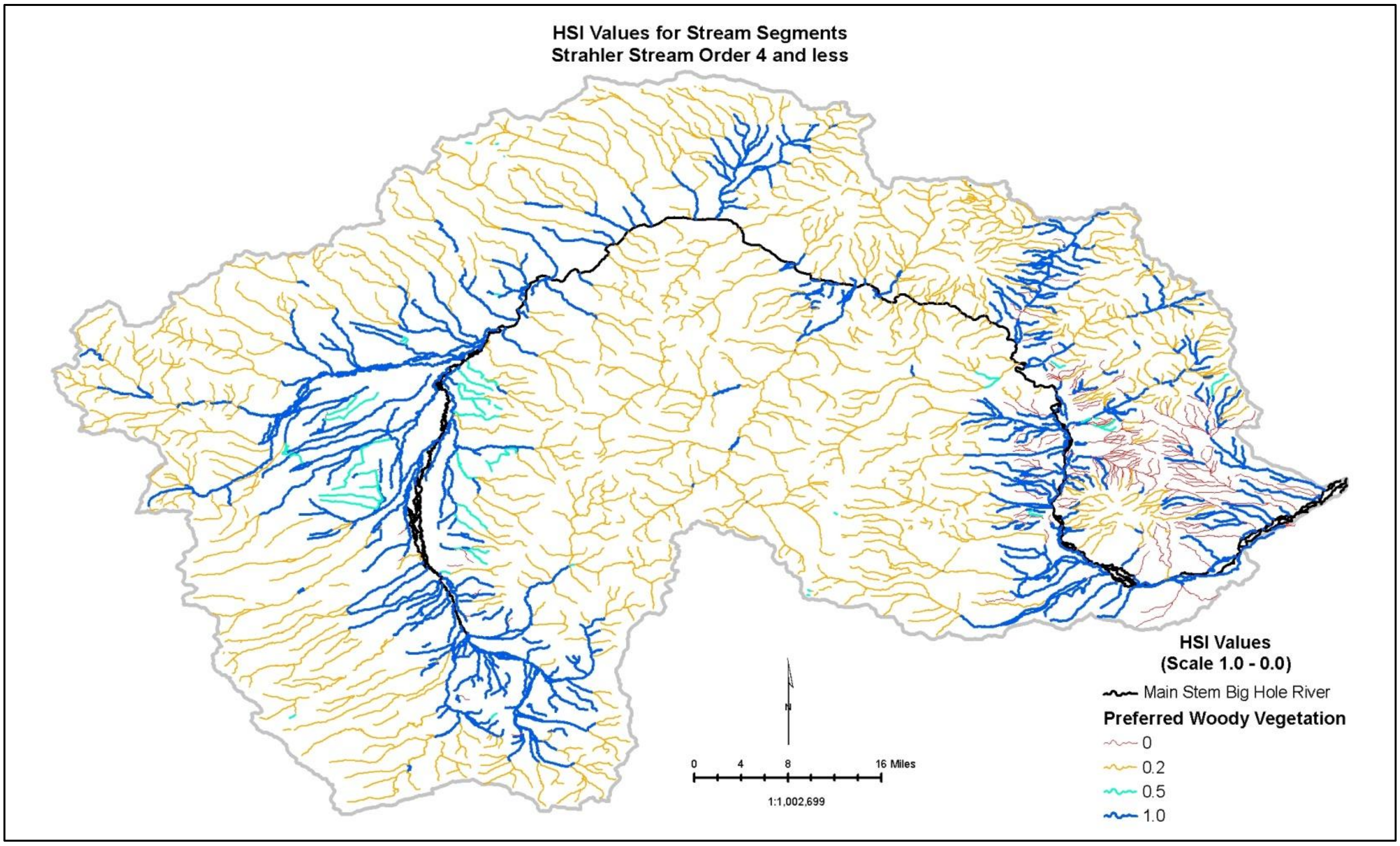
Map 10: Stream segments displaying HSI values for average height of shrub canopy

Variable 10: Species composition of woody vegetation (WVC)

The last winter food variable modeled was the species composition of woody vegetation within a 100m buffer on either side of a stream segment. This is a direct adaption of Allen's (1983) species composition of woody vegetation variable (V5). Whereby, the species composition of the woody vegetation present influences the values of the density and size class of available resources (percent canopy cover of trees and shrubs, and shrub canopy height). Stands of preferred woody species (i.e. Aspen, willow) increase the suitability of habitat for beaver, while less preferred species (i.e. fir and pine) reduce the suitability of the habitat. The species composition of woody vegetation is broken down into composition categories based on the dominate species present. To determine the dominate species present I used the ReGAP data and their associated definitions in NatureServe's Ecological Systems (NatureServe 2009), Table 3. If the dominate vegetation present ($\geq$ 50%) was one or more of the following species; aspen, cottonwood, willow or alder, a HSI value of 1.0 was given (C) for that ecological system. If the woody vegetation was dominated by other deciduous species a value of 0.5 was given (B) for that ecological system. Woody vegetation dominated by conifers, and other previously unclassified ecological systems, were given a value of 0.2 (A) for that ecological system. Ecological systems given a value of zero were given when woody species were not dominate (Graph 8). The species composition of woody vegetation HSI value for each stream segment is calculated based on which composition category is found in the highest percentage within 100 meters. When calculating the WVC HSI value, Ecological Systems with a value of zero (for example grasslands) were excluded as these generally do not represent a winter food resource.



Graph 8: Species Composition of Woody Vegetation HSI values



Map 11: Stream segments displaying HSI values for species composition of woody vegetation

Model Results

The NHDPlus dataset indicated that 3065 stream segments in the Big Hole watershed have a Strahler Stream Order of four or less. Of this, beaver were known to be present in 265 stream segments, absent in 204 stream segments, and unknown in 2596 stream segments. Pearson correlations (Table 5) indicated that several of the variables describing winter food resources were correlated ($r^2 \geq 0.50$) and thus combinations of them were not used in the same candidate model. Percent canopy cover of trees, percent canopy cover of shrubs, and species composition of woody vegetation variable were all positively correlated to the average height of shrub canopy ($r^2 = 0.590$, 0.756 and 0.623, respectively). The average height of shrub canopy was dropped from all candidate models to remove the correlations associated with it. It was decided to completely remove the average height of shrub canopy as the data associated with it has the greatest error and lowest resolution. Woody vegetated riparian areas and species composition of woody vegetation were also positively correlated ($r^2 = 0.670$) and are not used in the same candidate models. Percent canopy cover of trees and the woody vegetated riparian areas were moderately correlated ($r^2 = 0.515$), these two variables do occur in the same candidate models because of their biological relevance. Hosmer and Lemeshow Goodness of Fit tests indicated that five of the ten candidate models; H4, H5, H7, H8 and H10, were significantly different ($p \leq 0.05$) and showed a lack of fit (Table 4). These models were removed from further consideration when calculating the confidence set of models and model average parameter estimates. Results of the Hosmer and Lemeshow Goodness of Fit test on the remaining candidate models show that the calibration data meets all assumptions and that the observed and expected values are not significantly different ($n = 423$, $p \geq 0.05$). Evaluation of C-hat for the confidence set of models used to develop the composite model, H9 and H6, indicated that the calibration data are not over dispersed (n=423, value/df<1).

Based on the logistic regression using Akaike's Information Criteria and Royall's (1977) rule of thumb for assessing the strength of evidence, two candidate models were selected for in the confidence set of models (Table 6). The models selected were H9: Geomorphic and Food (Allen 1983) and H6: Geomorphic and All Food (Table 4). Based on Akaike weights the best approximating candidate model, H9 ($W_i = 0.7220$), contained 6 HSI variables while the second best candidate model, H6 ($W_i = 0.2780$), contained 7 HSI variables (Tables 4 and 6). The best approximating candidate model, H9, was 2.6 times better at predicting the presence of beaver than the next candidate model, H6. The Akaike weights for all other candidate models did not meet the 12% threshold (threshold $W_i \geq 0.0867$) and are not considered as plausible explanations of beaver presence.

Using the model average parameter estimates from the confidence set of models, the composite model is:

$$\text{logit}[X] = -6.067 + 1.807 * SG + 0.110 * SFP + 2.009 * VW + 0.076 * HEW + -0.601 * HAB + 3.241 * PCT + 3.084 * WVC + 0.136 * PCS$$

The model averaged parameter estimates of the composite model indicate that the HSI values for the percent canopy cover of trees has the greatest positive effect on the probability of the presence of beavers (3.241, OR = 25.65, Table 9). Using scaled odds ratios, for every 3.6% increase in canopy cover from 0-35%, corresponding to a 0.1 increase for the HSI value for PCT, a stream is 2.57 times more likely to have beaver present. From 36-65% canopy cover (HSI = 1) a stream is 25.57 times more likely to have beaver present than a stream with a canopy cover of either 0% or 100%. Conversely for every 4.05% increase in canopy cover from 66-100%, corresponding to a 0.1 decrease in the HSI value for PCT, a stream is 2.57 times less likely to have beaver present. HSI values for Stream Gradient, valley width, stream flow permanence, herbaceous emergent vegetation, percent canopy cover of shrubs and preferred woody vegetation species also show a positive effect on the probability of the presence of beaver. The model averaged parameter estimates for herbaceous aquatic vegetation (-0.601, OR=0.548, Table 9) indicate that as the HAB HSI values increase there is a decreasing likelihood of beaver being present in a given stream segment. The model averaged parameter estimates for herbaceous emergent wetlands, stream flow permanence, herbaceous aquatic vegetation and percent canopy cover of shrubs all have 95% confidence intervals that span zero and thus I have less confidence in the direction of effect that each of these HSI variables have on the presence of beaver (Table 9).

The model average parameter estimates from the composite model were used to evaluate the log-odds and the probability of beavers being present in any stream segment given a set value of coefficients (Table 8.) Given the HSI variables in the composite model there is a 64.6% probability (log-odds = 0.600) that for any stream segment in the Big Hole Watershed beavers will be present. Evaluating the applicability of our composite model using cross validation on the validation dataset (n = 46), indicated that the model may be under performing (Table 7). Using a cutoff probability of 0.533, calculated using Jenks Optimization on the probabilities of the calibration dataset, to indicate presence or absence of beaver in a given stream segment, the omission error rate, which is misclassifying known presences as absences, was 18.52%. The commission error rate, failing to predict the presence of beaver, was 15.38%.

Jenks Optimization, using the probabilities for the calibration and validation datasets (n=469), indicated that probability cutoff values (p_i) for categorizing the streams into habitat suitability classes were: Low quality, $p_i < 0.266035$; Marginal Quality, $0.266035 \leq p_i < 0.648910$; and, High quality, $p_i \geq 0.648910$. Evaluating the cross validation error rates of the habitat suitability classes versus known presence and absence of the validation dataset indicated 91.7% (22 of 24) of the time streams classified as high quality habitat had beavers present. Conversely, 90% (9 of 10) of the streams classified as having low quality habitat beaver were absent. 26.1% (12 of 46) of the time streams were classified as marginal quality habitat, 66.7% of the time these streams were absent of beaver and 33.3% of the time these streams had beaver present (Table 10). In total, of the 3065 stream segments classified, 1183 (38.6%, 1312.5 stream miles) were low quality habitat, 822 (26.8%, 1168.6 stream miles) were marginal quality habitat, and 1060 (34.6%, 1145.23 stream miles) were high quality habitat (Map 12). For the 2800 stream segments that are currently unoccupied or their occupation status is unknown in the Big Hole Watershed, 1166 (41.6%, 1282.8 stream miles) were low quality habitat, 765 (27.3%, 1039.6 stream miles) were marginal quality habitat, and 869 (31.0%, 835.7 stream miles) were high quality habitat (Map 13).

Discussion

When evaluating the model average parameter estimates there is a large gap between the effect of winter food variables and growing season food variables on the likelihood of the presence or absence of beaver in a given stream segment. Increases in the HSI values for two winter food variables, percent canopy cover of trees and preferred woody vegetation species, have the largest effect on the likelihood of beaver being present in any given stream segment. This is similar to Allen (1983) that winter food is the limiting factor in beaver occupancy of stream reaches and in agreement with Slough and Sadleir (1977) that winter food is most important in explaining the presence or absence of beaver in a stream segment. But, like Howard and Larsen (1985) and Suzuki and McComb (1998) my winter food variables alone cannot accurately predict the presence or absence of beaver. When including hydrogeomorphic variables, such as valley width, stream gradient, and streamflow permanence, and food variables into one candidate model (H9) that model was 6 orders of magnitude more likely to accurately predict the occupancy of beavers than a candidate model with only food variables (H3, Table 4). While Svendsen (1980) documented the importance of herbaceous emergent and submerged aquatic vegetation during the growing season for beaver, evaluation of the model average parameter estimates indicate that growing season food variables are not good predictors of site occupancy by beavers. One variable that is giving confounding results is stream flow permanence when compared to other cited literature. Permanence of stream flow is regarded as a fundamental requirement of suitable habitat for beavers. Yet, my model indicates that between a perennial and intermittent stream there is no real difference in likelihood of a beaver being present. And, a perennial stream is only 1.116 times more likely to have beaver present than an ephemeral stream. One explanation may be the accuracy of the medium resolution national hydrography dataset that was used to determine stream flow permanence. The medium resolution NHD is based off of the 1:100,000 topographic maps that were created in the 1960s and 70s and it is unknown how accurately they were able to identify intermittent and perennial streams. As indicated in the results though, I have less confidence in this variable as the 95% CI span zero.

Classification of stream segments into three categories based on the presence/absence of a species is based on an assumption and can lead to misinterpretation when using the final product to determine the best stream segment for the relocation of beaver. This assumption is the existence of marginal quality habitats and their use by beaver. When all of the best available habitat is occupied, beaver will move into marginal quality habitats and set up territories that in general are more ephemeral. Likewise there may be marginal habitats that could be occupied but currently are not. The use of marginal quality habitat by beaver and the habitat they create is extremely important. In marginal streams with steeper stream gradients, beaver dams can reduce the hydrologic energy in the system and increase the storage of organic inputs that otherwise may be transported out of a watershed. Storing organic inputs within the watershed increases the resiliency of streams to perturbations such as drought and fire (Naiman et. al 1986). The habitat created also increases water storage capacity on the landscape and can increase the period of time that ephemeral streams flow. Maintaining these aquatic habitats in ephemeral systems is important for wildlife species that rely on aquatic habitats for at least one stage in their life history cycle. In marginal quality habitats, habitat created by beaver persists for much longer than the active period of occupation. These abandoned habitats substantially influence the nutrient cycling capacity within a watershed by maintaining an increased rate of biogeochemical processing as compared to upland areas (Naiman et. al 1994). Thus, while the beaver habitat suitability model was developed to identify high quality habitat, depending on the management objective for relocating beaver, there are cases where evaluating marginal quality habitats, especially those with pockets of high quality habitat, is appropriate.

Evaluating the model with the validation dataset for presence and absence showed omission and commission error rates of 18.52% and 15.38% respectively (Table 7). These error rates, while indicating that the model may be under performing, may be overstated when considering the three categories of habitat suitability. The commission error rate that predicted incorrectly 15.3% (n=4) of the stream segments as having beaver present may in fact have suitable habitat that could support a population of beaver yet are currently unoccupied. When breaking these misclassified stream segments into their habitat suitability classes, two of these stream segments were classified as marginal quality and two were classified as high quality (Table 10). The two unoccupied high quality stream segments that were predicted to have beaver present may be suitable relocation sites needing further on the ground verification. Furthermore, the known absence of beaver in a given stream segment is not based on the whether the habitat is suitable to support beaver, only that beaver do not currently occupy this stream reach.

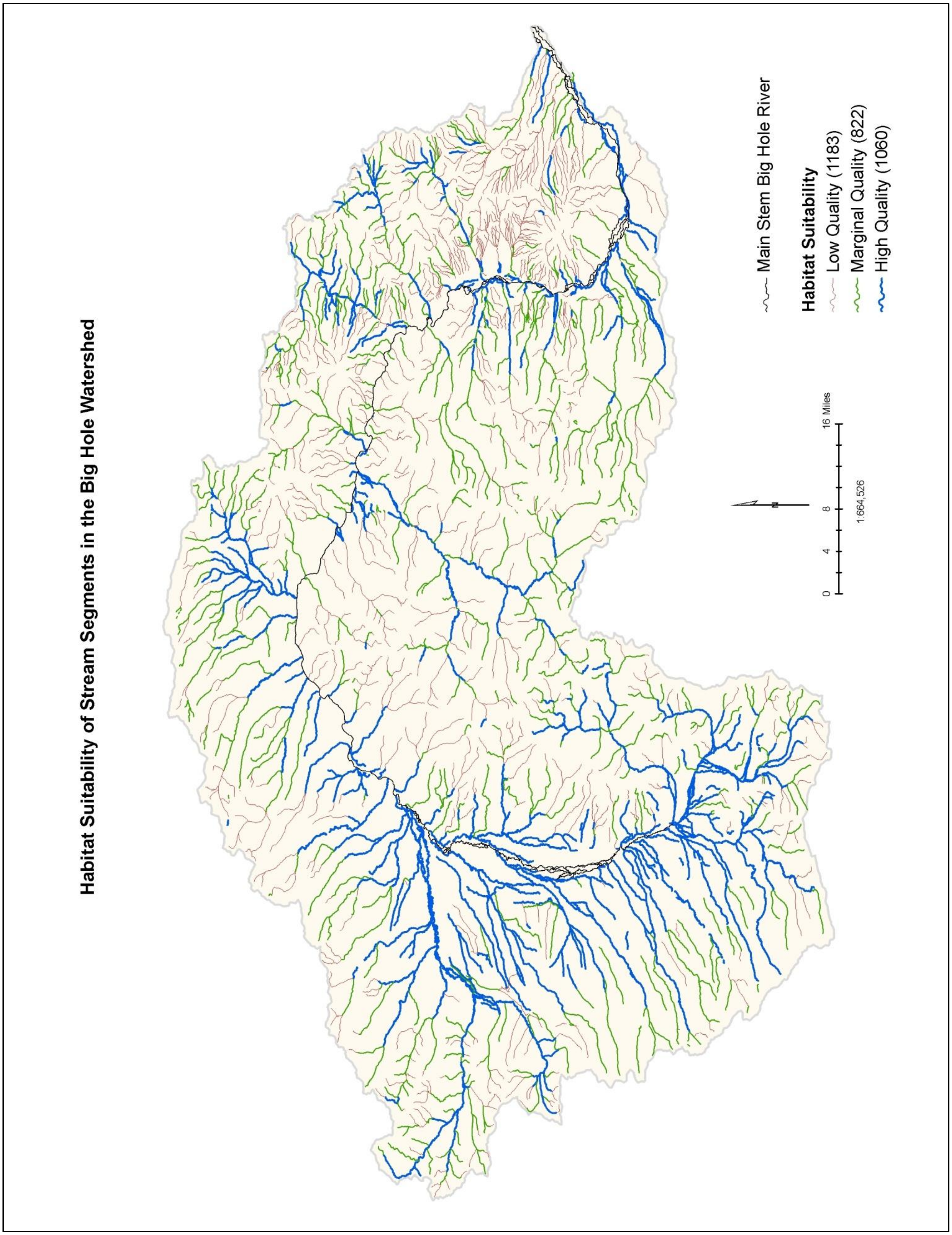
Likewise for the omission error rate, the predicted absences of beaver in streams known to have beaver (n=5), can be explained that when these stream segments are classified into habitat suitability the majority (n=4, 80%) were classified as marginal quality habitat suitability. The misclassification of know beaver presence as absence, and the inclusion of these as marginal habitat can be further explained by the heterogeneity of the habitat and geomorphic features of a stream segment. Conditions along a stream segment may not be uniform. Low, marginal and high quality habitat may be interspersed along the same stream segment. This is known in a few streams segments in the Big Hole Watershed where beavers are present; yet, the streams have been identified as being of marginal quality habitat. The majority of the habitat along these stream segments are marginal quality habitat, with pockets of high quality habitat that are currently occupied by beaver. The beaver habitat suitability model, in general, identifies stream segments based on the majority type of habitat suitability present. Thus, as mentioned in the Use and Limitations, this model this model should be used to evaluate potential relocation at a stream reach scale and on the ground determination should be conducted to verify site specific information.

The majority of land ownership in the Big Hole Watershed is an interspersion of state (5.5%), federal (68.1%) and private lands (26.3%). Private lands, which are the second largest percentage of lands in the Big Hole watershed, in general contain the downstream portions of streams and have the majority (61.48%) of the stream miles (704.1 miles) identified as high quality habitat for beaver.

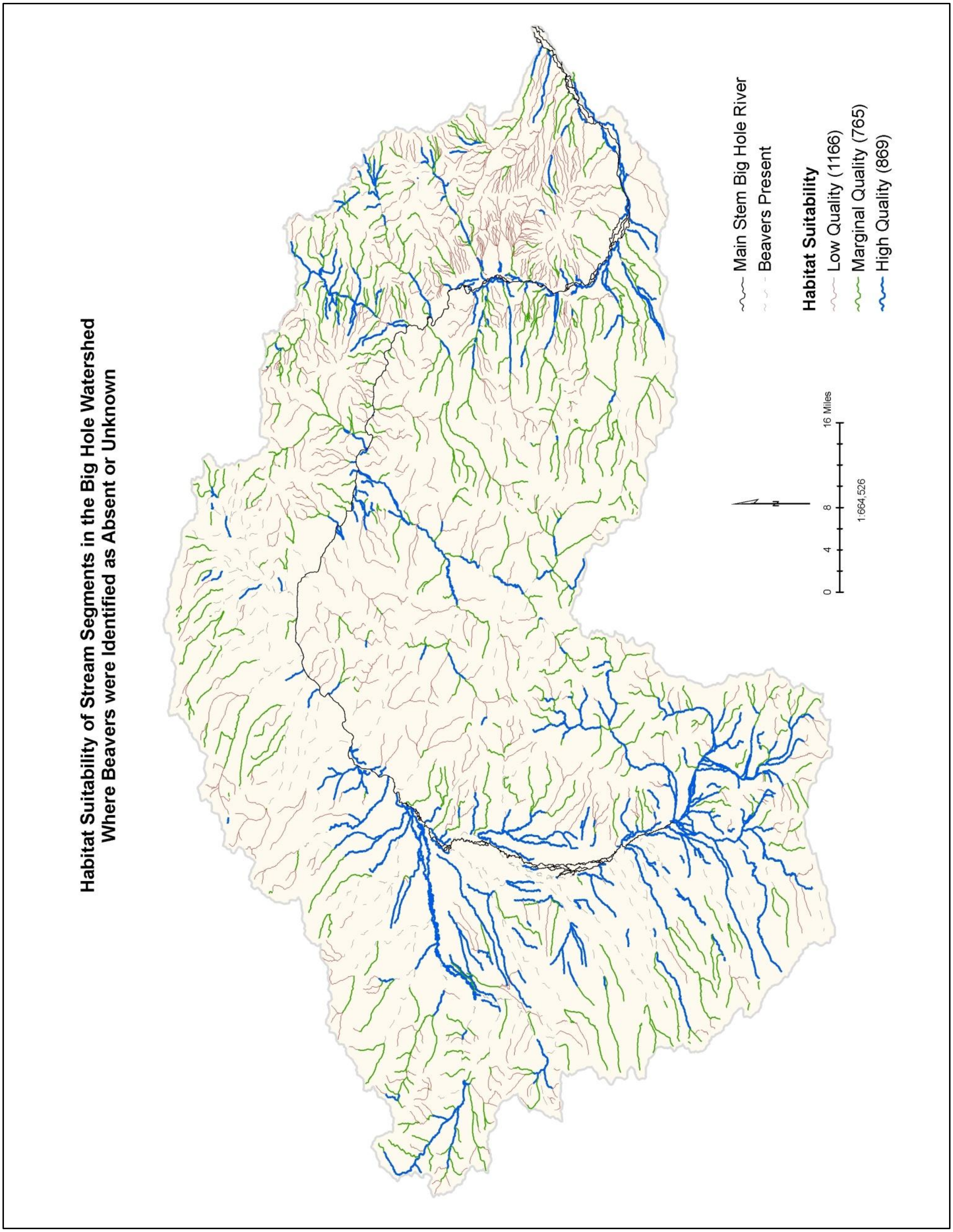
Federal lands contain 26.1% and state lands contain 7.0% of the stream miles, 298.9 and 80.2 miles respectively, that are considered as high quality habitat. This is similar to the findings reported in the “Big Hole water storage scoping project and water management review” (DTM Consulting Inc. 2005). Where they found that of the 2050 acres of habitat with potential for hosting beaver in the upper Big Hole watershed, 70.7% of this was on private land while 29.3% was under non-private ownership.

The beaver habitat suitability model and the water management alternative report highlight the importance of private lands for sustaining beaver populations and the benefits they provide in the Big Hole watershed. Any beaver relocation project should include the involvement from surrounding land owners and take into consideration the opportunities that exist on private lands. Part of this involvement is educating the public as to the role of beaver in a watershed and the importance of keeping them on the land. It should also include information as to the movement of beavers and their expansion within a drainage, especially to the high quality habitat found on private lands. And, it should take into consideration the needs of the private land owners and provide information on the different methods and options available for reducing conflicts with beaver. Thus, while there are suitable sites that provide opportunities to relocation beavers on non-private lands, sustaining populations of relocated beaver in the Big Hole watershed will require the support private lands owners who could potentially be affected by any project.

As was stated in the Use and Limitations section of this report it is important to understand that this spatial model was developed using the best available data and that we split a binary (presence/absence) model into three categories based on an assumption of habitat use by beavers. Because of this it is important to remember that this is a tool to help managers identify suitable stream segments for possible beaver relocation as a “first cut” and that field verification is always necessary to ensure the habitat will support and sustain a population of relocated beavers.



Map 12: Final Habitat Suitability of Stream Segments



Map 13: Habitat Suitability of Stream Segments where beavers were identified as absent or unknown

Table 3: HSI Values for woody species by NatureServe Ecological Systems.

HSI Value	0.2 (A)		0.5 (B)		1.0 (C)	
	ReGAP ID	**Ecological System**	**ReGAP ID**	**Ecological System**	**ReGAP ID**	**Ecological System**
	3129	Rocky Mountain Cliff, Canyon and Massive Bedrock	4233	Northern Rocky Mountain Subalpine Woodland and Parkland	4104	Rocky Mountain Aspen Forest and Woodland
	3173	Inter-Mountain Basins Cliff and Canyon	4302	Inter-Mountain Basins Aspen-Mixed Conifer Forest and Woodland	5207	Rocky Mountain Alpine Dwarf-Shrubland
	4103	Inter-Mountain Basins Cliff and Canyon	4303	Inter-Mountain Basins Mountain Mahogany Woodland and Shrubland	5326	Northern Rocky Mountain Subalpine Deciduous Shrubland
	4232	Northern Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest	4328	Western Great Plains Wooded Draw and Ravine	9155	Northern Rocky Mountain Lower Montane Riparian Woodland and Shrubland
	4236	Rocky Mountain Foothill Limber Pine-Juniper Woodland	5263	Rocky Mountain Lower Montane-Foothill Shrubland	9156	Rocky Mountain Lower Montane Riparian Woodland and Shrubland
	4237	Rocky Mountain Lodgepole Pine Forest	5312	Northern Rocky Mountain Montane-Foothill Deciduous Shrubland	9162	Northern Rocky Mountain Wooded Vernal Pool
	4240	Northern Rocky Mountain Ponderosa Pine Woodland and Savanna			9171	Rocky Mountain Subalpine-Montane Riparian Woodland
	4242	Rocky Mountain Subalpine Dry-Mesic Spruce-Fir Forest and Woodland			9187	Rocky Mountain Subalpine-Montane Riparian Shrubland
	4243	Rocky Mountain Subalpine Mesic-Wet Spruce-Fir Forest and Woodland			9218	Western Great Plains Open Freshwater Depression Wetland
	4266	Middle Rocky Mountain Montane Douglas-fir Forest and Woodland				
	4267	Rocky Mountain Poor-Site Lodgepole Pine Forest				
	5426	Northern Rocky Mountain Foothill Conifer Wooded Steppe				
	9103	Inter-Mountain Basins Greasewood Flat				
	9111	Northern Rocky Mountain Conifer Swamp				

Table 4: Candidate models evaluated to determine stream segments in the Big Hole Watershed suitable for beaver relocation.

Candidate Model Description	Model Formula
H1: Geomorphic Descriptors – The presence of beaver in a given stream segment is a function of the stream reaches mean gradient, permanence of flowing water and the average width of the valley.	SG + SFP + VW
H2: All Food Descriptors - The presence of beaver in a given stream segment is a function of the interaction of the availability of food resources to beaver in both the summer and the winter.	HEW + HAB + PCT + PCS + WVC
H3: Winter Food Descriptor #1- The presence of beaver in a given stream segment is a function of the availability of woody vegetation during the winter months.	PCT + PCS + WVC
H4: Winter Food Descriptor #2 – The presence of beaver in a given stream segment is a function of the area and canopy cover riparian woody vegetation available during the winter months.	PCT + PCS + WRA
H5: Food Combination #1 – The presence of beaver in a given stream segment is a function of the herbaceous vegetation available in the summer and preferred woody vegetation in the winter months.	HEW + HAB + WVC
H6: Geomorphic and All Food – The presence of beaver in a given stream segment is a function of the stream reaches mean gradient, permanence of flowing water, average width of the valley, and the interaction of the availability of food resources to beaver in both the summer and the winter.	SG + SFP + VW + HEW + HAB PCT + WVC
H7: Geomorphic and Winter Food #1 – The presence of beaver in a given stream segment is a function of the stream reaches mean gradient, permanence of flowing water, average width of the valley and of the availability of woody vegetation during the winter months.	SG + SFP + VW + WRA + PCT + PCS
H8: Geomorphic and Winter Food #2 – The presence of beaver in a given stream segment is a function of the stream reaches mean gradient, permanence of flowing water and the availability of preferred woody vegetation in the winter.	SG + SFP + WVC
H9: Geomorphic and Food (Allen 1983) – The presence of beaver in a given stream segment is a function of the stream reaches mean gradient, permanence of flowing water, average width of the valley, the canopy closure of trees and shrubs and the composition of woody vegetation within 100m of a stream segment.	SG + SFP + VW + PCT + PCS + WVC
H10: Geomorphic and Food (NWI) – The presence of beaver in a given stream segment is a function of the stream reaches mean gradient, permanence of flowing water, average width of the valley and the availability of food resources in both the summer and the winter months.	SG + SFP + VW + HEW + HAB + WRA

Table 5: Pearson Correlation values for HSI variables. Those with $r^2 \geq 0.50$ are highlighted in *italics*.

	HEW	WRA	SG	SAV	PCT	VW	PCS	ASH	WVC	SFP
HEW	**1**									
WRA	0.142	**1**								
SG	0.451	0.480	**1**							
SAV	0.052	0.065	0.066	**1**						
PCT	0.030	0.230	-0.112	0.110	**1**					
VW	0.267	0.313	0.439	0.056	-0.007	**1**				
PCS	-0.123	-0.006	-0.303	0.010	0.398	-0.094	**1**			
ASH	0.072	0.210	-0.113	0.084	*0.590*	0.053	*0.756*	**1**		
WVC	0.146	*0.670*	0.205	0.084	*0.515*	0.177	0.466	*0.623*	**1**	
SFP	0.249	0.386	0.237	0.077	0.350	0.384	0.309	0.464	0.498	**1**

Table 6: Model selection using Akaike's weights to rank candidate models.

Candidate Model	n	K	Log(£)	AICc	Δ_i	W_i	Percent Maximum W_i
H9 - Geomorphic and Food (Allen 1983)	423	7	-190.38	372.38	0.00	0.7220	1.000
H6 - Geomorphic and All Food	423	8	-204.91	374.29	1.91	0.2780	0.385
H3 - Winter Food Descriptor #1	423	4	-226.75	405.32	32.94	0.0000	0.000
H2 - All Food Descriptors	423	6	-238.55	406.34	33.96	0.0000	0.000
H1 - Geomorphic Descriptors	423	4	-232.41	430.48	58.10	0.0000	0.000

Table 7: Cross Validation using the modeled averaged parameter estimates on a validation dataset.

		Predicted		
		Absent	**Present**	**Total**
Known	**Absent**	15	4	**19**
	Present	5	22	**27**
	Total	**20**	**26**	**46**

Table 8: Probability of beaver presence in any stream segment using the model averaged parameter estimates.

SG	SFP	VW	HEW	HAB	PCT	WVC	PCS	Log-Odds	Probability
0.377	0.854	0.895	0.063	0.011	0.768	0.500	0.482	0.600	0.646

Table 9: Model averaged parameter estimates and odds ratios of the composite model.

Parameter	Estimate	S.E.	Upper (95%)	Lower (95%)	Odd Ratio	Upper Odds Ratio (95%)	Lower Odds Ratio (95%)
Constant	-6.067	0.954	-4.197	-7.937			
Steam Gradient	1.807	0.429	2.648	0.966	6.093	14.123	2.628
Stream Flow Permanence	0.11	0.442	0.976	-0.756	1.116	2.655	0.469
Valley Width	2.009	0.752	3.483	0.535	7.457	32.555	1.708
Herbaceous Emergent Vegetation	0.076	0.393	0.846	-0.694	1.079	2.331	0.499
Herbaceous Aquatic Vegetation	-0.601	1.163	1.678	-2.880	0.548	5.357	0.056
Percent Canopy cover Trees	3.241	0.695	4.603	1.879	25.565	99.803	6.546
Preferred Woody Species Composition	3.084	0.57	4.201	1.967	21.839	66.766	7.148
Percent Canopy Cover Shrubs	0.136	0.316	0.755	-0.483	1.145	2.128	0.617

Table 10: Cross validation of the validation dataset for habitat suitability classification.

		Habitat Suitability			
		Low	**Marginal**	**High**	**Total**
Known	**Absent**	9	8	2	**19**
	Present	1	4	22	**27**
	Total	**10**	**12**	**24**	**46**

Reference List

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267-281 in Second International Symposium on Information Theory. B.N. Petrov and F. Csake, editors. Akademiai Kiado, Budapest, Hungry.

Allen, A. W. 1983. Habitat suitability index models: beaver. U.S. Fish and Wildlife Service. FWS/OBS-82/10.30 Revised.

Beier, P. and R. H. Barrett. 1987. Beaver habitat use and impact in Truckee River basin, California. Journal of Wildlife Management 51:794-799.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and inference: an information-theoretic approach. Springer-Verlag, New York.

Cowardin, L.W., V. Carter, F.C. Golet, and E.T. Laroe. 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C. Jamestown, ND: Northern Prairie Wildlife Research Center Homepage. http//www.npwrc.usgs.gov/resource/1998/classwet/classwet.htm (Version 04DEC98).

Dent, B. D. 1999. Cartography: Thematic map design. WCB/McGraw-Hill, New York.

DTM Consulting Inc. 2005. Big Hole Water Storage Scoping Project and Water Management Review: Final Report Water Management Alternatives. Prepared for Big Hole Watershed Committee and Big Hole River Foundation. Pages: 85.

Gard, R. 1961. Effects of beaver on trout in Sagehen Creek, California. The Journal of Wildlife Management 25(3): 221-242

Gurnell, A. M. 1998. The hydrogeomorphic effects of beaver dam-building activity. Progress in Physical Geography 22:167-189.

Hall, J. G. 1970. Willow and aspen in the ecology of beaver in Sagehen Creek, California. Ecology 7:316-321.

Harig, A.L. and K.D. Fausch. 2002. Minimum habitat requirements for establishing translocated cutthroat trout populations. Ecological Applications 12:535-551.

Hosmer, D.W. and S. Lemeshow 1989. Applied logistic regression. Wiley, New York.

Howard, R. J. and J. S. Larson. 1985. A stream habitat classification system for beaver. Journal of Wildlife Management 49:19-25.

Hurvich, C. M. and C. Tsai. 1989. Regression and time series model selection in small samples. Biometrika 76:197-307.

Jenkins, S. H. 1980. A size-distance relation in food selection by beavers. Ecology 61:740-746.

MT FWP. 2010. Montana Fisheries Information System (MFISH). Available online http://fwp.mt.gov/fishing/mFish/.

Naiman, R.J., J.M. Melillo, and J.E. Hobbie. 1986. Ecosystem alteration of boreal forest streams by beaver (*castor canadensis*). Ecology 67(5):1254-1269.

Naiman, R.J., C.A. Johnston, and J.C. Kelley. 1988. Alteration of North American streams by beaver. BioScience 38(11):753-762.

Naiman, R.J., G. Pinay, C.A. Johnston, and J. Pastor. 1994. Beaver influences on the long-term biogeochemical characteristics of boreal forest drainage networks. Ecology 75(4): 905-921.

NatureServe. 2009. NatureServe Explorer: An online encyclopedia of life [web application]. Version 7.1. NatureServe, Arlington, Virginia. Available http://www.natureserve.org/explorer. .

Retzer, J. l., H. M. Swope, J. O. Remington, and W. H. Rutherford. 1956. Suitability of physical factors for beaver management in the Rocky Mountains of Colorado. Colo. Dept. Game, Fish and Parks, Tech. Bulletin 2:1-32. .

Royall, R. M. 1997. Statistical evidence: a likelihood paradigm. Chapman and Hall, New York.

Slough, B. G. and R. M. F. S. Sadleir. 1977. A land capability classification system for beaver (*Castor canadensis Kuhl*). Canadian Journal of Zoology 55:1324-1335.

Suzuki, N. and W. C. McComb. 1998. Habitat classification models for beaver (*Castor canadensis*) in the streams of Central Oregon coast range. Northwest Science 72:102-110.

Svendsen, G. E. 1980. Seasonal change in feeding patterns of beaver in Southeastern Ohio. The Journal of Wildlife Management 44:285-290.

USGS. 2006. The National Map LANDFIRE: LANDFIRE National Existing Vegetation Type layer. (2006, September - last update). U.S. Department of Interior, Geological Survey. [Online]. Available: http://gisdata.usgs.net/website/landfire/ [2007,February 8]. .

Vore, J. 1993. Guidelines for the reintroduction of Beaver into Southwest Montana Streams. Montana Department of Fish, Wildlife and Parks.

White, S.M. and F.J. Rahel. 2008. Complementation of habitats for Bonneville cutthroat trout in watershed influenced by beavers, livestock, and drought. Transactions of the American Fisheries Society 137:881-894.

Williams, W. A., M. E. Jensen, C. Winne, and R. L. Redmond. 2000. An automated technique for delineating and characterizing valley-bottom settings. Environmental Monitoring and Assessment 64:105-114.