MULTIVARIATE GEOSPATIAL DETECTION AND QUANTIFICATION OF
ECOLOGICAL THRESHOLDS CORRESPONDING TO DISPERSION OF
CASTOR CANADENSIS KUHL. (NORTH AMERICAN BEAVER) IN
CENTRAL MASSACHUSETTS

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ABSTRACT

Beaver (*Castor canadensis* Kul.) populations have increased greatly since the 1950s in Massachusetts, thereby amplifying beaver-human conflict. As such, it is important to understand the dispersal of beavers in relation to habitat characteristics. This is the main goal of this thesis. An annual census dataset of beaver habitat use since 1968 permitted two ecological models – a multiple logistic regression and a discriminant analysis – to be empirically developed and tested using multivariate statistical techniques within a geographical information system (GIS) to spatially evaluate ecological thresholds and interrelationships of beavers and their aquatic habitats within the Quabbin Reservation in Central Massachusetts. The beaver population has held relatively steady at the study area’s carrying capacity since approximately 1988. Input parameters for both methods include a variety of geomorphic and vegetative habitat variables that modulate the physical processes and biological responses of beavers, which subsequently influence the species’ geographic distribution and dispersal behavior. The multiple logistic regression (MLR) model produced probability maps depicting the likelihood of beaver occurrence over a continuous landscape, successfully predicting 72.2% of the habitats colonized by beavers in 2012 within the study area. Alternatively, the discriminant analysis (DA) model assigned individual habitats throughout the study area into three habitat quality groups (non-preferred, occasional, and preferred), successfully classifying 90% of the plots surveyed into their respective habitat quality groups.
Results of both ecological models suggest that gradual stream slopes, areas that are far away from the reservoir shoreline, and the presence of woody shrub species are the most influential environmental variables in identifying preferred beaver habitat. Moreover, the MLR model found that sustainable beaver colonization, over the course of several decades, usually occurs in areas with favorable geomorphic attributes (e.g. gradual stream slopes, large areas of upstream watershed), and exhibit a distinct vegetative signature of disproportionately higher coniferous tree cover. The MLR and discriminant function models are most applicable for any riparian habitats which share similar geomorphology and hydrology characteristics and harbor beaver populations at or near carrying capacity. These two models can ultimately be made readily available to land planners and managers, through the medium of a GIS, as tools to help guide and modify beaver management strategies to be proactive and adaptive to the ever-evolving land-use dynamics of beavers.
Chapter 1

BEAVER HABITAT MODELING AND SPECIES MANAGEMENT IN THE CONTEXT OF LANDSCAPE ECOLOGY

The analysis of species-environment relationships has always been a central issue in ecology. One prominent example is the often-studied concept of ecological thresholds, which Turner and Gardner (1997) have defined as any small changes in the spatial patterning of resources that produce abrupt, sometimes dramatic ecological responses. The multidisciplinary field of landscape ecology, which emphasizes the interaction between spatial pattern and ecological process, offers a new perspective with which to analyze these relationships in a broad-scale context (Turner et al., 2001). Such assessments of ecosystem structure and function are based on spatially distributed ecological data, which are necessarily recorded at a variety of spatial and temporal scales. Furthermore, ecological systems are spatiotemporally heterogeneous, making it very difficult to extrapolate from data collected at specific points to larger scales using conventional field techniques (Johnston and Naiman, 1990). For these reasons, a Geographic Information System (GIS)-based framework is optimal when attempting to analyze the ecosystem dynamics of a species population over a large geographic extent (Johnston et al., 1993).

The use of GIS technology in the field of ecology has rapidly become integrated with ecosystems research because it offers new concepts, theories, and methods that reveal the importance of spatial patterning on the dynamics of interacting ecosystems (Turner et al., 2001). Under this framework, locational data of an animal’s
presence can be easily coupled with modern geospatial datasets. A GIS thus provides a mechanism for performing empirical evaluations and quantifications of ecosystem processes at the landscape scale. This integration provides us with a substantial amount of information that can be used to investigate relationships between environmental data and animal behavior in far-reaching ways that are not possible with conventional field techniques. For example, Johnston and Naiman (1990) analyzed a series of aerial photographs within a GIS to quantify spatiotemporal changes in hydrology and vegetation-cover caused by beavers over a half-century throughout an entire landscape.

As an ecosystem engineer, the North American beaver has a large impact on other species in their local habitat, mainly through patch-creation in otherwise closed communities (Jones et al., 1994); therefore, field of landscape ecology – and subsequent utilization of a GIS – clearly plays a crucial role in the analysis and management of the population. The advancement and use of GIS tools and techniques has brought with it an increase of predictive habitat distribution models, which statistically relate the geographical distribution of a species to its present environment. The aim of this thesis is to examine the land-use/land-cover (LULC) trends and habitat selection dynamics of the North American beaver (Castor canadensis Kuhl.). In doing so, the author intends to illustrate how geospatial analyses within a GIS framework can serve as an indispensable tool for: (1) efficiently analyzing the physical characteristics of a landscape over a large geographic extent (∼ 50 km2) to understand beaver-habitat interactions; (2) extrapolating field data to the landscape as a whole; and (3) establishing and quantifying spatial ecological thresholds and interrelationships between beaver colonization and environmental variables, which
will ultimately be utilized for the systematic identification of quality beaver habitats at both the local and landscape scales. All references to “local” scale within this paper refer to a geographic extent at the individual habitat level (m2), while all references to the broader “landscape” scale refer to extents at the ecosystem level (km2).

1.1 Focus and Purpose of Study

Following a period of devastating overexploitation and extirpation from many parts of their historic range, beavers are once again abundant in North America. Consequently, human-beaver interactions and conflicts are inevitable as the increasing populations of beavers and humans collide. The increase in the population and distribution of a species which is able to significantly modify ecosystems and can damage human property clearly generates considerable scientific and management interest. Future management decisions designed to both support and sustain beaver populations while at the same time minimizing impacts to human construction and economics require an understanding of the dynamics of beaver colonization tendencies and behavior to effectively identify regions which are potential areas of human-beaver conflict.

Current trends in conservation are to move away from single-species management and towards ecosystem management to enhance and protect overall biodiversity (Wright and Jones, 2002). However, because of the beaver’s integral role within its ecosystem as both a keystone species and an ecosystem engineer, it may be important to focus on managing beaver populations from a single species perspective to sustain a healthy ecosystem and maintain populations of other species (Collen and Gibson, 2001).
While the descriptions and impacts of beavers as ecosystem engineers has been well documented (Johnston and Naiman, 1990; Jones et al., 1994; Muller-Schwarze and Sun, 2003), a systematic ability to predict which habitats are most likely to be colonized by beaver at both the local and landscape scales remains limited. What are the specific habitat variables that are most indicative for the colonization of a pond or stream by beavers? For instance, does the local composition of vegetation cover influence a beaver’s decision to colonize a given habitat? Can taking field measurements of a local habitat aid in determining the quality of that habitat? Can the time and location of a recolonization event by beavers be accurately predicted at the landscape scale? In the present study, these questions will be resolved by analyzing a detailed beaver census dataset using multiple logistic regression and discriminant analysis.

In ecology, it is rarely a single variable that influences the habitat preferences of a species. To create a more accurate assessment of beaver colonization trends, two multivariate models have been developed that analyze numerous influential environmental variables. First, modern geospatial data will be analyzed within a geographic information system to develop a multiple logistic regression (MLR) model that predicts beaver colonization events throughout a landscape. In particular, the model will suggest the geographic locations most likely to be colonized by beavers within the study area and then use colony presence data from the previous year to predict unoccupied habitats that are susceptible to being colonized by beaver. Second, a discriminant analysis will be utilized to assess local beaver habitat quality at a given site. Specifically, the discriminant analysis will be applied to data collected from a vegetation survey measured directly in the field to produce a discriminant function. If
successful, both the MLR model and discriminant analysis may be used as a tool, in singularity or in tandem, to help guide land managers to anticipate and avoid human-beaver conflicts and support the stewardship of healthy, viable wildlife resources.

1.2 Rationale of Study

As a keystone species, the North American beaver has a considerable impact on the course of succession, species composition and the structure of plant communities, causing it to be the focus of many ecological studies (e.g., Collen and Gibson, 2001; Johnston and Naiman, 1990; Wright et al., 2002). The presence of beavers doesn’t just impact and modify wetland ecosystems; it also can cause social impacts to landscapes occupied by humans. Within the Commonwealth of Massachusetts, human population levels are currently increasing while beaver populations are either also increasing or are persisting at high levels. In November of 1996, Massachusetts’ voters approved a ballot initiative that established the Massachusetts Wildlife Protection Act, which most notably prohibited the use of leg-hold kill traps on furbearing animals (Jonker et al., 2009). The immediate effect of this initiative was to restrict the ability of MassWildlife to manage populations of beaver, thus intensifying the already common occurrences of human-beaver contact. Such interactions are inevitable as increasing populations of beavers and humans occupy similar habitat.

The recolonization of historic wetland areas led to an increase in human-beaver interactions and subsequent conflicts, as beaver activity, namely dam building, can cause localized flood damage to roads and domestic property and has the potential to pollute drinking water. Water resource issues caused by localized flooding from
beaver dam construction include water quality impacts (e.g., increased turbidity, color, temperature and bacterial counts), disease transmission by gastrointestinal illness-causing protozoan parasites (e.g., Giardia lamblia and Cryptosporidium) and threats to the functioning of dams, dikes and other water supply infrastructure (Lyons, 1995). Beavers also plug culvert pipes and create dams that impound water against roadbeds, which may flood, wash out, or decrease the stability of roads (Jackson and Decker, 2004). Lastly, residential, commercial and agricultural development in low lying areas adjacent to streams and ponds are vulnerable to inundation caused by beavers. These problematic impacts are not necessarily related to beaver population levels, but are more a function of the location and duration of individual beaver colonies and the stability of their dams.

Due to such potentially severe disturbances, management actions are often necessary to control nuisance beavers or their socioeconomic impacts. As a result of the disturbance to human activities and profound ecological impacts related to beaver activity, the relationship between beavers and their riparian habitat has been under much investigation. To accomplish this, quantitative techniques can be used to relate beaver occurrence, persistence, and density to various physical and vegetative characteristics. Traditionally, these beaver-habitat studies have exclusively implemented field surveying methods to develop these ecological relationships (e.g., Beier and Barret, 1987; Howard and Larson, 1985; Suzuki and McComb, 1998). However, due to technical advances in geospatial software and data availability, modern studies have developed GIS-based habitat classification modeling techniques to explore beaver-habitat responses to a broader scale than could be established under traditional field surveying methods (e.g., Maringer and Slotta-Bachmayr, 2006; Allen,
1982; Robel et al., 1993). While such descriptions on the physical processes and biological responses between beavers and their ecosystem have been well documented (Johnston and Naiman, 1990; Jones et al., 1994; Muller-Schwarze and Sun, 2003), a systematic ability to predict which habitats are most likely to be colonized by beavers at both the local and landscape scales remains limited. The two empirically-derived multivariate ecological models (a multiple logistic regression function and a discriminant analysis) presented in this study have been developed based on expert knowledge from previous findings within the literature to improve habitat suitability evaluation of beavers.

A multiple logistic regression analysis has been chosen as this study’s primary method with which to evaluate beaver habitat suitability because it has been utilized extensively in similar studies of habitat use to produce continuous probability maps depicting the likelihood of occurrence of certain species (Store and Kangas, 2001). Additionally, MLR models have been successfully utilized to statistically analyze the relationship between existing occurrences of a given species and its associated habitat properties. Likewise, a discriminant analysis has been selected as this thesis’ second method for analyzing beaver habitat suitability because it has been regularly used to produce reliable results for habitat classification in studies that have developed aquatic habitat models (Ahmadi-Nedushan et al., 2006). Each method measures habitat suitability differently and should complement one another nicely during the evaluation of preferred beaver habitat.

Future management designed to sustain beavers and minimize impacts to human livelihood will require an understanding of the dynamics of beaver populations at today’s increased population levels to locate where their associated disturbances are
most likely to occur across the Massachusetts landscape. Gaining an understanding of beaver-habitat dynamics is helpful in designing and implementing management strategies targeted in locations that are highly susceptible to such disturbances. Ecological information gained from this study can more effectively guide future policies and programs for managing the beaver species and can further help anticipate human-beaver conflicts. Such insights will help the many stakeholders of wildlife gain perspective on the importance of beavers as ecological engineers, as well as help identify the areas that are most susceptible to the associated disturbances. Utilization of the MLR model and discriminant analysis functions as tools can help land managers guide and modify beaver management strategies to be proactive and adaptive to the ever-evolving landuse dynamics of beavers.
Chapter 2
UNDERSTANDING THE NORTH AMERICAN BEAVER

2.1 The North American Beaver

The North American beaver is a semi-aquatic plant eating mammal (Family: Castoridae; Order: Rodentia) (Collen and Gibson, 2001). Beavers are highly social and territorial animals which normally live as a family unit, commonly called a "colony" (Baker and Hill, 2003; Bradt, 1938; Jenkins and Busher, 1979). Colonies typically consist of two parental adults, young born in the previous year, known as "yearlings", and young of the current year, known as “kits” (Wilsson, 1971, Jenkins and Busher, 1979). Beavers are able to inhabit a broad spectrum of ecosystems ranging from mountainous forests in the subarctic to low-lying wetlands in the subtropics, and are consequently found throughout much of the riparian habitats throughout the North America continent (Rosell et al., 2005).

Beavers require perennial access to water with sufficient depth to enable the construction of a lodge, burrow, or dam and, over most of their range, the construction of a winter food cache. Lodges and burrows, which are most often built on the river bank or on an island in the impoundment, enhance beaver survival by providing shelter, avoiding predators, and enhancing thermoregulation (Jenkins and Busher, 1979; Muller-Schwarze and Sun, 2003; Zurowski, 1992). A winter food cache, usually located adjacent to the main lodge, consists of an assortment of woody branches and aquatic vegetation collected by beaver every autumn to supply food for the winter. Additionally, beavers most famously cut down trees to construct dams,
which improves their habitat by raising water levels upstream. Such tree felling and
dam construction activities drastically alter a habitat’s plant community, hydrology,
and land cover, which substantially impacts the local ecology. Their roles as both
keystone species and ecological engineers have made beavers the focus of much
scientific research.

**Beavers as Agents for Land Use and Land Cover Change**

Few species have as large an impact on their local ecosystem and landscape
than beavers (Naiman et al., 1986). The beaver is also considered an ecosystem
engineer because its building activities create new ecosystems and microhabitats, as
well as increase heterogeneity and species diversity at the landscape scale (Gurney and
Lawton, 1996; Wright et al., 2002). Simply put, the construction activity of beavers
creates one of the most significant ecosystem modifications observed in the animal
kingdom.

By physically modifying their habitat through the construction of dams and the
felling of trees, beavers significantly change the land cover, and consequently the
hydrologic characteristics and biotic properties of the landscape. The presence of
beavers has been directly linked to an increase in total wetland area within a landscape
(Johnston and Naiman, 1990). Additionally, beaver impoundments widen riparian
habitat and recharge groundwater by elevating the water table (Bergstrom, 1985). By
creating more areas of standing water, beaver ponds increase a river system’s storage
capacity for water, as well as reducing annual stream discharge due to increased
evaporation. Beaver dams also stabilize streamflow, often leading to a decrease in
peak discharge and stream velocity during a runoff event, thereby reducing a stream’s
flood and erosion potential (Parker, 1986). Associated with this reduction in stream
velocity is a reduction in the suspended sediment carrying capacity of a stream and consequently an increase in deposition (Naiman et al., 1986).

Beaver dam construction ultimately transforms upstream areas from lotic to lentic conditions, often changing a stream’s temperature and chemical properties (Collen and Gibson, 2001). The creation of impoundments, which increases the area of shallow slow water as well as the harvesting of shade-producing riparian vegetation, stabilizes a stream’s temperature regime (Gard, 1961). By functioning as sediment and organic matter traps, beaver ponds can have a significant effect on water and sediment chemistry, which considerably influences the productivity of fresh water by altering nutrient levels. Although the magnitude and nature of induced changes in water chemistry varies across different habitats, beaver ponds commonly store approximately 1,000 times more nitrogen (N) in fluvial sediment, per linear meter of stream channel, than areas absent of beaver modification (Naiman and Melillo, 1984). Beaver activity is also often associated with elevated values of pH, acid-neutralizing capacity (ANC), dissolved organic carbon (DOC), iron (Fe2+), and manganese (Mn2+) and decreasing values of sulphate (SO2−), ionic forms of aluminum (Aln+) and dissolved oxygen concentrations (Smith et al., 1991).

Beaver foraging has a considerable impact on the course of ecological succession. Within one cycle of a beaver impoundment, beavers alter the successional stage of the riparian zone in two ways. First, damming raises the watertable. By stressing and often drowning flood intolerant plant species, this subsequent inundation rapidly decimates much of the adjacent plant community, which is then succeeded by a plant community more dominant in aquatic and riparian populations. Second,
following abandonment of sites by beavers, the dams eventually collapse and terrestrial succession begins on the drained mud flats (Nummi, 1989).

Beaver foraging also changes the composition and structure of plant communities. Tree felling by beavers for feeding and construction purposes rarely entails the consumption of the whole tree, thus altering the availability of organic material and creating habitat for other species. For example, at a pond in Minnesota, Johnston and Naiman (1990) found that beavers decreased the above ground biomass by over 40% over 6 years, with less than one-third being consumed. The continuous selective harvesting of early and mid-successional species by beavers can reverse the progress of succession and dramatically alter the species composition of the plant community. Moreover, beaver foraging increases light penetration and decreases competition for soil, usually increasing the net primary productivity of existing non-preferred woody species (Barnes and Dibble, 1988). For instance, Wright and Jones (2002) found that the presence of beavers increases gross primary production of the plant community and increases local plant heterogeneity by 33% within their riparian habitat. Consequently, beavers are likely to have a larger potential effect on the standing biomass than any other browser within their foraging range (Johnston and Naiman, 1990).

**Beavers as Both a Commodity and Pest to Humans**

A once common and flourishing species in North America, beavers suffered from overexploitation by humans, as great value was placed on their pelt for hats and clothing and castoreum (obtained from their castor glands) as a base for perfume (Muller-Schwarz and Sun, 2003; Rosell et al., 2005). Consequently, beavers were effectively hunted to near extinction by 1900 at middle and southern latitudes within
the North American continent. In fact, it is believed that the state of Massachusetts, where the study area is located, was completely devoid of any beaver population until as recently as the mid-1930s (Conlee, personal communication). A sharp drop in the demand for fur coupled with management programs designed to protect beavers in the early 1900s caused hunting and trapping practices to sharply decline, ultimately allowing beavers to re-colonize much of their Massachusetts range (Busher and Lyons, 1999). Today, beaver populations in the northeastern United States are healthy and appear to have made a full recovery.

Of course, anthropogenic activity has also grown in the Northeast. Beavers are highly adaptable and do well in proximity to human settlement, which is especially apparent in Massachusetts, where both human and beaver population levels have continued to increase and spread (Jonker et al., 2009). This phenomenon has led to an increase in human-beaver interaction and subsequent conflict, as beaver activity, namely dam building, can cause the flooding of roads and domestic property. Although beaver dams normally reduce the severity of flooding events, they may also contribute to them if dam failure occurs (Butler, 1991). This escalating interaction between humans and beaver drove many residents to once again trap and kill beavers, which were becoming increasingly viewed as a pest. In November 1996, Massachusetts’ voters approved a ballot initiative (55% in favor), commonly known as the Massachusetts Wildlife Protection Act, prohibiting the hunting and leg-hold kill trapping of furbearing animals throughout most of the state (Jonker et al., 2009). One immediate effect of the initiative was to modify the way MassWildlife managed beavers in the past. By the year 2000, beaver populations had tripled, and beaver damage and associated complaints had increased substantially. Although
MassWildlife stopped collecting population data and nuisance complaints in 2002, trends indicate that beaver populations and associated nuisance in Massachusetts have either continued to increase or have stabilized at historically high levels (MassWildlife, 2002).

2.2 Environmental Variables Pertaining to Beaver Habitat Assessment

Vegetation Preference

An adequate and accessible food supply must be present at any location where a beaver colony will be established (Allen, 1982). Beavers are generalized herbivores, feeding on bark, leaves, and shoots of woody plants, terrestrial herbs, ferns, and aquatic vegetation (Jenkins, 1975). More specifically, beavers are commonly described as choosy generalists, favoring certain woody species and size classes over others, both as a source for food and as construction materials for dam building (Jenkins and Busher, 1979). As a general rule, deciduous trees are favored over coniferous, which are considered a poor quality source of food (Williams, 1965). Still, Brenner (1962) observed that beavers can subsist in some areas by feeding on coniferous trees. In North America, Denney (1952) found that beavers most commonly select Populus spp. (aspen), Salix spp. (willow), P. balsamifera (cottonwood) and Alnus spp. (alder).
Table 2.1: Woody Plant Species Utilized by Beavers as Food

<table>
<thead>
<tr>
<th>Preferred</th>
<th>Occasional or Seasonal</th>
<th>Not Preferred</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alder</td>
<td>Apple</td>
<td>Eastern hemlock</td>
</tr>
<tr>
<td><em>Alnus spp.</em></td>
<td><em>Malus spp.</em></td>
<td><em>Tsuga canadensis</em> (L.)</td>
</tr>
<tr>
<td>Aspen</td>
<td>Ash</td>
<td>Carr.</td>
</tr>
<tr>
<td><em>Populus spp.</em></td>
<td><em>Fraxinus spp.</em></td>
<td>Eastern white pine</td>
</tr>
<tr>
<td>Birch</td>
<td>American beech</td>
<td><em>Pinus strobus</em> L.</td>
</tr>
<tr>
<td><em>Betula spp.</em></td>
<td>Ehrh.</td>
<td><em>Other conifers</em></td>
</tr>
<tr>
<td>Dogwood</td>
<td>Blueberry</td>
<td>Red maple</td>
</tr>
<tr>
<td><em>Cornus spp.</em></td>
<td><em>Vaccinium spp.</em></td>
<td><em>Acer rubrum</em> L.</td>
</tr>
<tr>
<td>Willow</td>
<td>Cherry</td>
<td>Elder</td>
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<tr>
<td><em>Salix spp.</em></td>
<td><em>Prunus spp.</em></td>
<td><em>Sambucus</em> spp. L.</td>
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<tr>
<td></td>
<td>Hazelnut</td>
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<td></td>
<td><em>Corylus spp.</em></td>
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<td>Maples (other than red)</td>
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<td></td>
<td><em>Acer spp.</em></td>
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<td>Oak</td>
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<td><em>Quercus spp.</em></td>
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<td></td>
<td>Witch hazel</td>
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<td></td>
<td><em>Hamamelis virginiana</em></td>
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<td>Viburnum</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Viburnum</em> spp.</td>
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</tr>
</tbody>
</table>

Source: DeStefano *et al.*, 2006

Of course, the availability of woody species, and with it, beaver vegetation preferences, varies geographically throughout North America. The EPA classifies the Central Massachusetts level III eco-region as “Northeastern Highlands”, whose vegetation is characterized by the typical mixed coniferous-deciduous forests of the east (EPA, 2011). Several studies have investigated the behavior of vegetation selection by beavers within the commonwealth of Massachusetts. Busher (1995)
found that witch hazel (Hamamelis virginianas) was consistently cached more often than other species. Jenkins (1975) discovered that beavers most often harvest birch over maples, pines, and oaks, while DeStefano et al. (2006) found dogwood (Cornus spp. L.) to be a preferred species by beavers. A detailed list of all woody vegetation utilized by beavers is presented in Table 2.1, which has been grouped by food preference. In general, preferred species are favored and subsequently felled by beavers over neighboring vegetation.

Preferences in Diameter at Breast Height (DBH) of Vegetation

As a general rule, beavers prefer cutting woody stems that are small in circumference. Hacker and Coblentz (1993), for example, found that beavers are significantly more likely to colonize habitats containing woody species with average DBH values less than 25cm. Similarly, Destefano et al. (2006) discovered that the average DBH for trees near natal colonies was 12% less than trees near dispersal sites. Such findings in the literature can be explained by the fact that cutting and transporting a woody stem with a smaller DBH costs less energy from a beaver’s perspective than harvesting a larger, more cumbersome woody stem. Accordingly, Jenkins (1981) reported a decrease in mean stem DBH with increasing distance from the water’s edge. As a result of this phenomenon, Allen (1982) has suggested that a DBH range between 2.5 and 15.2 cm of woody stems is most preferred by beaver.

Optimal Percent Canopy Cover of Beaver Habitat

A habitat’s average percent canopy cover can also be utilized as a good predictor of quality beaver habitat. As tree or shrub crown closures approach high levels, mobility decreases and the likelihood of harvested trees getting caught hanging
up in adjacent trees increases, creating a less suitable habitat. At the same time, extremely sparse canopy cover allows for greater amounts of light penetration into the forest floor, thereby increasing local evaporation levels. Such conditions induce a hotter and dryer environment, resulting in less riparian vegetation and food availability, thus decreasing overall habitat quality. Accordingly, beavers favor an ideal canopy cover range that is not too high or too low. Allen (1982) suggested that a habitat’s ideal canopy cover ranges between 40% and 60%, which is an indication of optimum food availability.

**Trends in Beaver Foraging Distance Away From the Water’s Edge**

Beavers are highly specialized aquatic rodents, as the majority of beaver activity, including foraging, is limited to the immediate vicinity of aquatic environments (Maringer and Slotta-Bachmayr, 2006). Foraging distance, as it pertains to this study, is defined as the maximum distance from the water’s edge where the majority of vegetation caching activity takes place by beaver. Although beavers have been observed foraging at distances up to 200 meters from water (Bradt, 1938), the majority of foraging occurs significantly closer to the water’s edge. Furthermore, vegetation that is closest to the water’s edge is generally consumed first (Jenkins, 1981). This relationship between foraging behavior and vegetation distance from the shore exists because harvesting vegetation further away from the water’s edge is more taxing on a beaver’s time and energy than harvesting close by vegetation.

**Optimal Stream Gradient for Beaver Colonization**

During the colonization of stream habitat, beavers must construct dams for their survival. Not surprisingly, there is considerable evidence and agreement that the
gradient of a stream is a major determining factor of beaver habitat suitability (Allen, 1982; Maringer and Slotta-Bachmayr, 2006; Suzuki and McComb, 1998). The more gradual the slope of a stream, the more suitable it becomes for beaver colonization. A stream slope of less than 3% creates the ideal beaver habitat (Beier and Barret, 1987; Stocker, 1985). Furthermore, no beaver colonies have ever been observed in streams with a gradient of 15% or more (Allen, 1982). The strong relationship between stream slope and beaver colonization exists because steeper streams generate higher flow velocities, making dam construction and maintenance by beaver substantially more difficult and taxing. Beavers will, therefore, choose to colonize streams with more gradual slopes to minimize the labor intensive cost of dam construction.

**Optimal Stream Flow and Discharge for Beaver Colonization**

Beavers are aquatic dependent creatures, requiring a permanent water supply to prevent lodge and burrow entrances from ever becoming dry and provide cover for feeding and reproductive activities (Slough and Sadlier, 1977). Furthermore, minimal seasonal fluctuations of stream discharge allow beaver dams to regulate and maintain advantageous flow levels. Beavers can usually control water depth and stability on small stream and ponds, however, beaver’s still prefer seasonably stable water supplies, as intense fluctuations in stream discharge can damage, and even destroy lodges and dams. According to Stocker (1985) and Heidecke (1989), stream depths less than 50 cm prevent beaver colonization. A stream, therefore, qualifies as an optimal beaver habitat by possessing a seasonally stable, year-round flow with reasonable depth.
2.3 Understanding Beaver Dispersal for Habitat Assessment

To most effectively advance ecological understanding and manage populations, it is imperative to identify the ecological mechanisms that dictate why beavers emigrate and how they select a new habitat to colonize. Beaver dispersal behavior is highly variable, yet is a critical component in determining the distribution, resource allocation, and demographic characteristics of a population (DeStefano et al., 2006). As young beavers disperse and become established in new territories, the quality of the habitat can be a key determinant in their survival. Furthermore, dispersal provides the primary means by which beavers occupy new areas, and accurate knowledge of their dispersal is essential for species management.

Dispersal Behavior

Beavers are highly territorial creatures that frequently migrate throughout a stream network during the course of their adult lives. Bradt (1938) describes beaver colony territories as distinct and non-overlapping. A colonized area is typically made up of beaver-constructed lodges and dams that create a series of ponds which vary in age, size, and depth. Beavers within each colony may establish and utilize all lodges within their territory (Rutherford, 1964). A typical beaver colony is comprised of a monogamous pair of adults, a few sub-adults (offspring from the previous year's litter), and a few young born that year, called kits (Svendsen, 1980). Once they reach to age of 2 or 3, sub-adult beavers must leave their natal home and establish their own territory elsewhere to become independent. The dispersal of sub-adult beavers tends to occur during the early spring, coinciding with increased runoff from snowmelt.

The average distance that a beaver moves during a relocation event is largely unpredictable and depends on many factors, including the quality of the
surrounding habitat, the traversability of the landscape, and the local beaver population density (Muller-Schwarze and Sun, 2003; Saveljev et al., 2002). Consequently, beaver dispersal distances are case specific, broadly ranging between 0.1 km to 236 km (Van Deelen and Pletscher, 1996; Hibbard, 1958). A Massachusetts-based study conducted by DeStefano et al. (2006) found the average dispersal distance of sub-adult beavers to be 4.5 km, which is most applicable to this study.

**Vegetation as a Driving Factor of Dispersal**

A much more pressing question regarding beaver dispersal is whether local vegetation cover influences a beaver’s habitat selection decision during a relocation event. It is well established that beavers favor certain woody species over others, both as a source for food and for construction materials for dam building. One would consequently expect areas with vegetation cover dominated by preferred species to yield superior beaver habitat over areas containing non-preferred species. For example, Collen and Gibson (2001) reported that the availability of woody plants is one of the most important factors in influencing the range, distribution, density, and movement of a beaver population. Surprisingly, however, this phenomenon has been questioned by several studies that found no such correlation between beaver colonization behavior and habitats occupied by preferred vegetation cover (Beir and Barret, 1987; Barnes and Mallik, 1997; Saveljev et al., 2002). Instead, they hypothesized that other habitat variables, most commonly the gradient of a stream, take precedent over vegetation cover for beaver habitat selection decision making.

Though the importance of vegetation in beaver dispersal may accurately apply to quality habitats harboring a newly reintroduced and expanding beaver population,
evidence suggests that it likely does not apply to regions that have limited resources and space due to habitat saturation by a large and dense beaver population. When beavers were sequentially released into a previously unoccupied area in the Netherlands, for instance, they successively settled in good and then poor habitat, and eventually became floaters as their population density rose (Nolet and Rosell, 1994). In the densely populated habitats of Massachusetts, DeStefano et al. (2006) similarly found that beaver-preferred woody vegetation tended to be more common at natal colonies than at dispersal sites. This same study also found dispersal sites to be smaller, shallower, and located in areas with higher over-story canopy closure than natal colonies. McNew and Woolf (2005) concluded that sub-adult beavers likely were forced away from their natal family unit because of resource limitations caused by high population densities. This pattern provides evidence that dispersing beavers living in densely populated areas are forced to colonize habitats of poorer quality than their previous natal colony.

2.4 Evaluation of Literature

The roles that environmental variables play in assessing beaver-habitat dynamics have been often studied. Specifically, many studies (e.g., Collen and Gibson, 2001; Suzuki and McComb, 1998) have used quantitative techniques to relate beaver occurrence, persistence, and density to various physical and vegetative characteristics. This has often been achieved by measuring some combination of stream and vegetation characteristics, which are then statistically related to trends in habitat utilization by beavers within the given study area. However, some of traditional beaver-habitat studies have exclusively implemented field surveying
methods to develop these ecological relationships (e.g., Howard and Larson, 1985; Robel et al., 1993; Suzuki and McComb, 1998), which inherently limits the analysis in both scope and detail by confining the analyzed environmental data to merely the surveyed areas. Only by considering a continuous region of interest, which can most practicably be achieved under a GIS framework, can one more thoroughly analyze beaver-habitat dynamics at the landscape scale.

Due to technical advances in desktop computing, the availability of remotely sensed data, such as satellite images, and the development of powerful GIS computer software packages for storing, manipulating and displaying spatial data, it is now feasible to implement quantitative approaches such as ecological modeling and spatial statistics with relative ease. (Turner et al., 2001). As a result, the GIS framework today serves as a powerful tool for modeling spatially distributed ecosystems and processes by efficiently evaluating environmental variables as model parameter data. Accordingly, various GIS-based habitat classification modeling techniques have been developed to explore beaver-habitat responses to a broader scale than could be established in a traditional field experiment (e.g., Allen, 1982; Maringer and Slotta-Bachmayr, 2006; Robel et al., 1993). The specific aim of these studies is to identify actually or potentially suitable beaver habitat, or to identify those factors that are important in habitat selection. The methodology in such applications is to locate the area or areas where a set of given criteria required for beaver colonization are met using a Boolean logic classification system. Here, an area is either accepted or rejected based on a given threshold value. The final outcome of these applications is a map depicting areas simultaneously fulfilling all the conditions set by the researcher.
However, problems have been noted with classifications using Boolean logic (Store and Cangas, 2001). In situations where the threshold value is not precise, as is often the case in the field of ecology, loss of information or error propagation may occur. Furthermore, although conventional habitat suitability models do provide general suitability indexes, such methods do not identify which habitats are the most suitable for a species beyond the feasible areas that meet the predefined threshold values. To avoid such problems associated with Boolean overlay, both analyses presented in this study instead utilize additive techniques whereby the environmental variables associated with beaver presence and absence are first standardized into principal components and then multiplied by an associated weight factor, which ultimately determines each component’s contribution to assessing beaver habitat. Lastly, the final criterion score is calculated by summing the results.

Another common drawback of some habitat suitability studies (e.g., Allen, 1982; Beier and Barret, 1987) is the use of an incomplete or corrupt population dataset, often caused by a limited temporal window or by anthropogenic pressures on the study area’s population (Slough and Sadler, 1977). The former problem can occur when beaver population data is obtained during just one season of surveying, while the latter problem occurs when the beaver population being studied is subjected to hunting and trapping pressures by humans. The beaver population dataset used in this study, on the other hand, is free of both problems, as the Massachusetts Department of Conservation and Recreation (DCR) has data from the initiation of the population in 1952, has conducted an annual beaver census within the Prescott Peninsula since 1968, and has protected this pristine New England forest since the 1930s. Consequently, this combination of abundant habitat and limited human access within
the study area makes this census one of the most unbiased and comprehensive beaver population datasets available in North America, if not the world. Furthermore, because the population being studied has fully reached the carrying capacity of the Prescott Peninsula, an assumption can be made that active beaver colonies seen today likely occupy quality habitats that possess the necessary ecological conditions for sustainable beaver colonization (Busher and Lyons, 1999).

Wildlife managers have long been concerned with disturbances and destruction of riparian areas by beavers, emphasizing a critical need to define landscape-beaver colonization trends as they apply to conservation and nuisance avoidance objectives (Jackson and Decker, 2004). What are needed today are techniques for measuring ecological processes over large geographic areas so that geospatial information can be related to ecosystem function. While the descriptions and impacts of the beaver as both a keystone species and an ecosystem engineers have been well documented (Collen and Gibson, 2001; Johnston and Naiman, 1990; Jones et al., 1994), a systematic ability to predict which habitats are most likely to be colonized by beavers at both the local and landscape scales remains limited.

To help fill this void, as well as build upon insights gained from previous work, this study has empirically developed two ecological models: a multiple logistic regression model and a discriminant function model. Input parameters for both models were obtained by utilizing a GIS in conjunction with modern geospatial data to summarize representative (or average) environmental conditions of various types of beaver habitats throughout the study area. An emphasis has been given to those primary environmental attributes which modulate the physical processes and biological responses of beavers. When used in tandem, these models can provide a
comprehensive understanding of land-use/landcover dynamics brought by beavers. These two models can ultimately be made readily available to land planners and managers, through the medium of a GIS, as tools to help guide and modify beaver management strategies to be proactive and adaptive to the ever-evolving landuse dynamics of beavers.

Selection of Multivariate Statistical Techniques

Multivariate statistical approaches are more appropriate for the analysis of aquatic habitat as they inherently consider the interrelation and correlation structure of the environmental variables (Ahmadi-Nedushan, et al., 2006). Specifically, multivariate analysis methods take into account the interaction of physical variables and determine species response based on the cumulative effect of a number of environmental characteristics. Because the geographic distribution of beavers is certainly dependent on numerous environmental variables, both models presented in this study were developed using multivariate statistical techniques. Without this multivariate approach, a habitat suitability model would incorrectly assume that all environmental variables are equally important to the growth and survival of the Prescott beaver population. This assumption can be relaxed because both the MLR and DA models utilized in this study implement weighted additive equations to consider the relative importance of each habitat variable for evaluating the distribution and dispersion of beavers.

Multiple logistic regression is a popular statistical method for the ecological modeling of species-environment relationships and is often used to produce probability maps depicting the likelihood of occurrence of certain species (Store and Kangas, 2001). Furthermore, multiple logistic regression has been used extensively in
studies of habitat use by various aquatic species to identify different variables that affect species distribution and are therefore important in discriminating the presence of those species (Ahmadi-Nedushan, et al., 2006). Finally, multiple logistic regression techniques can be easily implemented with a GIS, but must only be used when the response variable (e.g. species abundance) is continuous (Ahmadi-Nedushan, et al., 2006). Because the comprehensive beaver census dataset utilized in this study is continuous throughout the entire Prescott Peninsula, a multiple logistic regression analysis has been chosen as this study’s primary method for quantifying beaver habitat suitability over the continuous aquatic ecosystems of the Prescott Peninsula.

Alternatively, when concerned with modeling the distribution of individual habitats throughout a larger ecosystem, Guisan and Zimmermann (2000) suggest that a discriminant analysis should be used. Discriminant analysis techniques, which are a more traditional statistical approach for ecological modeling, have been extensively used to successfully distinguish sites of species presence and absence (Ahmadi-Nedushan, et al., 2006). Therefore, a multivariate discriminant analysis has been chosen as this study’s second method for evaluating and classifying the quality of a given beaver habitat. Specifically, beaver presence and absence data were projected onto predictor-environmental variable space to develop a pair of discriminant functions capable of partitioning environmental thresholds into three habitat-quality types: preferred, occasionally preferred, and non-preferred.

Although the MLR and DA ecological models developed in this study evaluate habitat suitability differently, both share common strengths and potential weaknesses. For instance, both techniques have the ability to analyze the relationship between habitat suitability and explanatory environmental variables, such as the degree to
which each variable contributes to the identification of varying levels of habitat quality. By analyzing such ecological relationships, the ability to interpret the results in a biologically meaningful way is retained in both analyses, allowing important differences between habitats of poor and high quality to be identified and quantified. However, both methods also make two assumptions that could be considered model weaknesses if not accounted for (Ahmadi-Nedushan, et al., 2006). The first assumption is that the distribution of predictor variables is multivariate normal, while the second is that the predictor variables considered by each method share a common covariance. However, the utilization of a principal components analysis to transform all environmental variable data into uncorrelated standardized eigenvalues ensures that the assumptions of multivariate normality and common covariance amongst the variables are met.

**Ecological Thresholds and Habitat Suitability Models**

Ecological thresholds are an important concept to consider when modeling species-ecosystem relationships. Turner and Gardner (1997) define ecological thresholds as any small change in the spatial patterning of resources that produce abrupt, sometimes dramatic ecological responses. Ecological threshold concepts are commonly incorporated in the development of habitat suitability models to help predict where these critical thresholds occur, and thus, how the structure of landscape resources might affect ecological processes (With and Crist, 1995). Specifically, thresholds enable habitat suitability models to quantify the upper and lower tolerance limits of an environmental variable (or combinations of environmental variables) which govern the survival and overall distribution of a species (With and Crist, 1995). For example, one objective of this study is to determine the cumulative ecological
threshold of various vegetative and geomorphic conditions at which beaver populations can sustainably occupy a given habitat. Therefore, the evaluation and quantification of the ecological thresholds that regulate the survival and overall distribution of beavers has been investigated in great detail within this study.
Chapter 3

STUDY AREA

The focus of this research is on the Prescott Peninsula (42° 25' N, 72° 20' W) in New Salem, Massachusetts (Figure 3.1). The Prescott Peninsula is located within the Quabbin Reservation in central Massachusetts, which was established in 1939 along with the Quabbin Reservoir by the damming of the Swift river and Beaver Brook (State of Massachusetts, 2012). Today, the reservation is coveted as a valuable area for water resources and provides over 3 million people with drinking water on a daily basis, as it now contains the primary watershed and reservoir for the greater Boston metropolitan area (Busher and Lyons, 1999). The elevation of the Prescott Peninsula ranges from a low of 160 m at the surface of the reservoir to a high of 269 m at the peninsula's peaks. The peninsula averages 16 km in length and 4km in width, totaling approximately 50 km2 of land, 92% of which is covered by forest (Figure 3.2 and 3.3). Its climate has fairly stable year-round precipitation and consists of warm, wet summers and cold, long winters with substantial snowfall. The vegetation is dominated by species typical of the Northeastern mixed coniferous-deciduous forest (see Table 2.1).
Figure 3.1: Prescott Peninsula, Quabbin Reservation
Figure 3.2: Aerial Imagery of Prescott Peninsula (MassGIS)
Figure 3.3: Vegetation Distribution Throughout Prescott Peninsula (Mass. DCR)
3.1 Beaver Population History within the Quabbin Reservation

The once common beaver was hunted to extirpation in the northeastern United States by the mid-19th century. Although populations are once again thriving, beavers continue to be trapped and killed by humans throughout much of North America due to their increasing notoriety as a pest. Long-term comprehensive beaver population data are exceedingly rare. Additionally, much of the population survey data that have been incorporated in other studies have historically come from areas with high anthropogenic pressures on the local beaver population (Fustec et al., 2001; Maringer and Slotta-Bachmayr, 2006; Slough and Sadleir, 1976;). Beaver populations from these studies could have been subjected to potential hunting, trapping, and habitat pollution from industrial activity. Consequently, the quality of most beaver survey data has been, to some extent, corrupted.

The Quabbin Reservation has been actively managed as a watershed by the Metropolitan District Commission (MDC), now the Massachusetts Water Resource Authority (MWRA), since its inception in 1939, mainly for high water quality protection (Lyons, 1995). Consequently, wetland, aquatic, and forest habitats within the Quabbin reservation have gone relatively untouched since its inception due to its rural location and strictly controlled human activity and development. This includes the absolute prohibition of all hunting and trapping on the reservation for more than 50 years (Lyons, 1995), thereby eliminating anthropogenic influences on its local beaver population. Thanks to the conservation efforts of the Massachusetts DCR, the Prescott Peninsula, Quabbin Reservation offers a unique opportunity to analyze an unexploited beaver population within an untouched New England forest.
3.2 The Annual Beaver Census Dataset and Associated Population Trends

This combination of abundant habitat and limited human access has enabled beaver to re-establish their population in the Quabbin area. However, it was not until the early 1950’s that beavers were first observed on the reservation since their extirpation decades earlier (Hodgdon, 1971). Anecdotal reports and analyses of aerial photographs provided some spotty data on population growth during the 1950s and 1960s. Since 1969, however, complete annual surveys have been conducted through the cooperative efforts of the MDC, the United States Fish and Wildlife Service, The Massachusetts Cooperative Wildlife Research Unit, Boston University, and the University of Massachusetts, Amherst (DCR, 2011). These surveys, which take place in late November or early December of each year, consist of having observers walk predetermined routes along streams, ponds, and through other potential beaver habitat on the Prescott Peninsula (Figure 3.4). A separate boat survey is used to locate active beaver sites along the reservation shoreline. In effect, all potential beaver habitats within the Prescott Peninsula are surveyed for active sites. Active sites are identified by the presence of a food cache (usually located near a lodge), recent tree and shrub cutting, and evidence of lodge and dam maintenance (fresh mud and/or freshly cut branches). The locational coordinates of each discovered active beaver colony gets recorded. It should be noted, however, that each purple dot used to symbolize the location of a historically occupied beaver colony in Figure 3.4 (and in all figures following Figure 3.4) represents one year of occupation within the local habitat and not an actual focal point of a family during a given year. Therefore, the total number of purple dots mapped within a local habitat signifies the number of years in which that habitat has been occupied by an active beaver colony.
Figure 3.4: Observer Survey Routes for Annual Prescott Beaver Census
Since 1936, the hunting and trapping of beaver has been strictly prohibited within the Quabbin Reservation. Additionally, much of the beaver’s natural predators (i.e. wolves, black bears, and coyotes) were also extirpated from Massachusetts long before the beaver population study began in 1952. This untouched environment ensures that the beaver population trends shown in Figure 3.5 can be explained solely by the ecological interaction between beaver and their habitat. It is important to note that the beaver census data incorporated in this study is not an estimate of population obtained by a model or algorithm, but is rather a comprehensive survey of every single stream in the entire study area, thus making it a true count of beaver population within the Prescott Peninsula for each year. This comprehensive beaver census dataset creates the foundation for the MLR model and discriminant analysis of this study.

**Figure 3.5:** Number of Active Beaver Colonies per Year, 1952-2011 (Mass. DCR)
The results from this annual census, which captures the historic beaver population of the Prescott Peninsula from 1952 to 2011 is shown in Figure 3.5. Changes in beaver population can be characterized into five phases, together exhibiting the classic sigmoid growth response that is often associated with populations colonizing new habitat (Busher and Lyons, 1999). The initial phase (1952-1968) was a time of modest population growth in which the number of colonies increased from 2 to 16 at a rate of 0.82 colonies per year. This was likely a time for the young beaver population to establish itself within the newly colonized ecosystem. A second phase is observed from 1968 to 1975 and is characterized by a time of unprecedented population explosion in which the number of colonies increased from 16 to 46 at a rate of 4.29 colonies per year. This period of great prosperity can likely be attributed to beavers migrating into new and unexploited riparian habitats with abundant resources. The third phase (1975-1983) was a time of relatively small change, with beavers maintaining their unprecedentedly high population levels. The fourth phase (1983-1987) marks a time of exceptional population loss in which the number of colonies declined from 44 to 12 with an average loss of 6.4 colonies per year. Busher and Lyons (1999) suggest that this rapid decline occurred as a consequence of the beavers running out of new quality habitats to colonize, while simultaneously exhausting their food and construction resources in many of the habitats that had historically been occupied. Essentially, the beavers exceeded the carrying capacity of the Prescott Peninsula and were forced to either leave the peninsula or perish. The period from 1988 to the most recent survey year in 2011 represents the fifth and final phase and was a time of relatively stable beaver
population. This is a result of the population reaching the peninsula’s carrying capacity, forcing beavers to only colonize quality habitats that can be occupied on a semi-sustainable basis.
Chapter 4
MATERIALS AND METHODS

4.1 Overview of Methodology

Two multivariate methods – a GIS-based multiple logistic regression (MLR) model and a field surveying-based discriminant analysis (DA) – were developed to assess land-use/land-cover trends and suitable habitats for beavers within the Prescott Peninsula, Quabbin Reservation (Figure 4.1). Both analyses involved the acquisition of historic beaver colonization data within the Prescott Peninsula obtained from the Massachusetts DCR. This colonization data, which includes the known locations of all colonies from 1968 to 2011, provide the basis for evaluating beaver habitat preference. Both analyses presented in this paper ultimately implement a GIS to summarize representative (or average) topographic, hydrologic and vegetative conditions used as parameters for each model.

The GIS-based method (referred to as the “MLR model” in this paper) is a cartographic model most applicable for land managers possessing GIS resources and processing capabilities who would like to identify locations that are highly likely to contain active beaver colonies throughout a continuous landscape. The MLR model has been developed through the evaluation of geospatial data within presence/marginal/absence (PMA) areas based on the frequency of historic beaver colonization instances. A multiple logistic regression is ultimately performed to produce a map that displays the probability that an active beaver colony is present within a given habitat throughout the study area.
The discriminant analysis (DA) method employs a local scale categorical model designed to assign a given beaver habitat into one of three quality classes (preferred, occasional, or non-preferred) for predefined, discrete locations throughout the study area. The DA method is site specific, requiring several vegetative properties within a plot of land to be measured directly in the field. Furthermore, the only GIS data necessary to perform the DA method is a digital elevation model (DEM), which is one of the more common and easily attainable geospatial datasets. In fact, a continuous DEM dataset spanning the entire commonwealth of Massachusetts can be downloaded, free of charge, from the MassGIS.gov website. A discriminant analysis is performed on the data acquired from vegetation surveying and a DEM to produce two discriminant functions. These two functions are ultimately used to determine the habitat quality class of the area being surveyed.
A principal components analysis (PCA), which is a restricted type of ordinary least squares (OLS) regression, was performed on all environmental variables before being implemented into each analysis to account for and eliminate collinearity in the variables making up the two multivariate equations. Collinearity occurs when some of the dependent variables are highly intercorrelated, which is often the case for environmental variables. The utilization of PCA reduces the confounding effects of
collinearity (lack of independence among explanatory variables) that frequently occur with regression analyses to simplify the description of a set of potentially interrelated variables (Clark and May, 2004). PCA implements a mathematical procedure that uses orthogonal transformation to convert a set of observations of possibly correlated variables into a set of linearly uncorrelated (independent) variables called principal components. Together, these components account for all variation within the original variables and can also help indicate the direction and degree to which each variable contributes to assessing habitat quality. This process ultimately assigns a distinct mathematical weight to each of the original habitat variables, transforming them into completely uncorrelated variables.

4.2 Determination of Ecological Parameters for Habitat Modeling

Stream Buffer

Beavers are highly specialized aquatic rodents found within the immediate vicinity of aquatic habitats. In fact, Hall (1960) reported that 90% of all cutting of woody material by beavers was within 30 meters of the water’s edge. Therefore, it is important to only evaluate locations within and directly adjacent to aquatic habitats when modeling beaver distribution. No consensus exists on an appropriate value for foraging distance amongst the literature – each beaver habitat suitability study uses a different value ranging from 20 m (Maringer and Slotta-Bachmayr, 2006) to 100 m (Barnes and Mallik, 1997) from the water’s edge.

A 50 m buffer along the edge of the water has been chosen for this study. This value is the best compromise between only considering locations that are frequently
utilized by beaver while ensuring that as much influential habitat is analyzed as possible. As a result, all calculations and habitat suitability considerations presented in this study are limited to a 50 meter buffer surrounding all hydrologic features within the Prescott Peninsula.

**Area of Watershed Upstream**

The two hydrologic variables that dictate beaver habitat suitability are a stream’s discharge and seasonal fluctuation. Obtaining a high-resolution stream discharge dataset throughout such a large study area, however, proved to be very difficult, requiring either intensive field work or access to a rare stream gauge dataset, which does not exist within the small tributaries of the Prescott Peninsula. Fortunately, these tributaries have fairly stable seasonal fluctuations in stream discharge and are rarely limiting. Therefore, the only limiting hydrologic variable for beaver colonization within the study area is the presence of a sufficient supply of water. Conveniently, the total area of watershed upstream from a given location can be successfully implemented as a satisfactory proxy for stream discharge. For example, studies conducted by Barnes and Mallik (1997), as well as Howard and Larson (1985), found upstream watershed area to be a significant habitat variable for predicting the location of beaver colonies. A simple and common GIS analysis using the HYDROLOGY toolkit was performed on a five meter resolution digital elevation model (DEM) to calculate the upstream watershed area throughout the study area. The resulting upstream watershed area raster dataset has been utilized in this study to measure and locate suitable and reliable hydrologic conditions for beaver habitat.
Minimum Habitat Area

Minimum habitat area is defined as the minimum amount of contiguous habitat that is required before an area will be occupied by a species (Allen, 1982). There is no precise agreement on an exact value for the minimum habitat area of beaver, which ranges between 0.32 and 0.56 hectares throughout the literature (Allen, 1982; Maringer and Slotta-Bachmayr, 2006). Considering the 50 meter restrictive buffer on each side of a stream, the lower limit of 3.2 hectares of contiguous suitable habitat (approximately 320 meters of stream length) must be present before an area is considered suitable for colonization by beaver.

Vegetation and Habitat Preference

An adequate and accessible food supply must be present at any location where a beaver colony will be established (Allen, 1982). Furthermore, woody vegetation is more limiting than herbaceous vegetation in providing an adequate winter food source, which is essential for beaver survival. Therefore, this study will consider the presence of preferred woody species to be the most deterministic class of vegetation when evaluating beaver habitat quality. Based on our field observations, along with data presented in the literature, all woody plant species have been grouped into one of three classes displayed in Table 2.1 – preferred, occasional/seasonal, or not preferred.

Since 1988, when the once overcrowded beaver population stabilized to the area’s carrying capacity (Figure 3.5), streams within the Prescott Peninsula have been saturated with beaver activity. A high population density decreases the availability of ideal habitat, which forces migrating beavers to colonize less favorable habitats during dispersal. One would similarly expect the existence of a high density beaver population within the Prescott Peninsula to limit the availability of quality, vacant
habitats for dispersing sub-adult beavers in pursuit of a new habitat to colonize. Consequently, when a habitat becomes saturated as a result of its beaver population reaching carrying capacity, as is the case in this study, the presence of preferred vegetation must be an important variable to consider when predicting suitable beaver habitat. Therefore, it is hypothesized that frequently colonized areas are more likely to have preferred vegetation than habitats that are sparsely colonized by beaver.

**Beaver Census Years Considered**

A fundamental assumption of both analyses presented in this study is that habitats (along with their associated environmental characteristics) which have been most frequently occupied by beavers are considered to be of higher quality than sparsely occupied habitats. In essence, frequently colonized areas are likely to share common ecological traits which separate them from beaver habitats of poor quality. As displayed in Figure 3.5, the Prescott Peninsula’s beaver population first dropped to the land’s carrying capacity in 1988, entering the fifth and final phase of the modified sigmoid response curve that is still presently seen today. This phase of population stability indicates that beaver dispersal is relatively restricted to semi-sustainable, quality habitats, thus confirming the fundamental assumption made by both analyses. Therefore, only beaver census datasets from 1988 to 2012 are utilized in this study.

### 4.3 Geospatial Data Acquisition and Pre-Processing

The management, production, and analysis of all geospatial data was performed using Environmental Systems Research Institute (ESRI) Desktop ArcGIS 10.1 GIS program package. Any “tools” referred to herein are component features of the
ArcToolbox package. All of the geographic data mapped in this study is visualized using the Massachusetts Mainland State Plane (FIPS 2001) projection with the NAD83 (North American Datum 1983) datum. The selected Massachusetts Mainland State Plane (FIPS 2001) projection is one of the most common projections used in thematic (statistical) mapping of the Central Massachusetts region because it preserves area relationships and ensures high locational accuracy. Since habitat data inherently varies by area, using a projection that preserves area relationships is essential.

Table 4.1: Geospatial Data Considered in both analyses

<table>
<thead>
<tr>
<th>Variable</th>
<th>Datum</th>
<th>Source</th>
<th>Analysis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elevation (m)</td>
<td>DEM</td>
<td>Mass. DCR</td>
<td>MLR</td>
</tr>
<tr>
<td>Stream Slope (°)</td>
<td>DEM,</td>
<td>Mass. DCR</td>
<td>Both</td>
</tr>
<tr>
<td>Upstream Watershed Area (m²)</td>
<td>Watershed Boundary</td>
<td>Mass. DCR</td>
<td>Both</td>
</tr>
<tr>
<td>Soil Drainage Type</td>
<td>Soil Type</td>
<td>Mass. DCR</td>
<td>Both</td>
</tr>
<tr>
<td>Distance from Reservoir (m)</td>
<td>Quabbin Reservoir</td>
<td>MassGIS.gov</td>
<td>MLR</td>
</tr>
<tr>
<td>NDVI</td>
<td>ASTER</td>
<td>USGS</td>
<td>MLR</td>
</tr>
<tr>
<td>Riparian Grass Cover (%)</td>
<td>ADS40</td>
<td>MassGIS.gov</td>
<td>MLR</td>
</tr>
<tr>
<td>Coniferous Cover (%)</td>
<td>ADS40</td>
<td>MassGIS.gov</td>
<td>MLR</td>
</tr>
<tr>
<td>Deciduous/Shrub Cover (%)</td>
<td>ADS40</td>
<td>MassGIS.gov</td>
<td>MLR</td>
</tr>
<tr>
<td><em>Cornus</em> spp. Cover (%)</td>
<td>ADS40</td>
<td>MassGIS.gov</td>
<td>MLR</td>
</tr>
<tr>
<td>Grass Cover (%)</td>
<td>ADS40</td>
<td>MassGIS.gov</td>
<td>MLR</td>
</tr>
<tr>
<td>Habitat Type (stream/pond)</td>
<td>Field Observation</td>
<td>N/A</td>
<td>DA</td>
</tr>
<tr>
<td>Canopy Cover (%)</td>
<td>Field Measurement</td>
<td>N/A</td>
<td>DA</td>
</tr>
<tr>
<td>Tree Density (#/m²)</td>
<td>Field Measurement</td>
<td>N/A</td>
<td>DA</td>
</tr>
<tr>
<td>DBH (cm)</td>
<td>Field Measurement</td>
<td>N/A</td>
<td>DA</td>
</tr>
<tr>
<td>Preferred Trees (%)</td>
<td>Field Measurement</td>
<td>N/A</td>
<td>DA</td>
</tr>
<tr>
<td>Occasionally P. Trees (%)</td>
<td>Field Measurement</td>
<td>N/A</td>
<td>DA</td>
</tr>
<tr>
<td>Preferred Understory (%)</td>
<td>Field Measurement</td>
<td>N/A</td>
<td>DA</td>
</tr>
<tr>
<td>Occasionally P. Understory (%)</td>
<td>Field Measurement</td>
<td>N/A</td>
<td>DA</td>
</tr>
</tbody>
</table>
Habitat requirements utilized to evaluate beaver-ecology relationships (outlined in Section 4.2) have been defined as those abiotic features of the environment that are necessary for the survival and persistence of beavers (Ahmadi-Nedushan et al., 2006). Specifically, the environmental components which affect the distribution and dispersion of beavers have been divided into two types of geospatial data: geomorphic and vegetative. Geomorphic variables influence water reliability and affect key biological processes of beavers, such as lodge and dam construction. Additionally, vegetative variables, such as the spatial distribution and composition of preferred woody species, affect food availability.

All collected and produced geospatial data were managed so that the data for every environmental variable were stored in separate map layers displayed in Table 4.1. Both methodologies in this study evaluate many of these environmental variables for their locational significant with respect to beaver habitat preference and associated colonization within the Prescott Peninsula. Overall, eleven deterministic habitat variables were used in the development of the MLR model, while ten deterministic variables were utilized in the discriminant analysis (Table 4.1). Seven of the environmental variables utilized by the discriminant analysis were collected in the field through the physical measurement of various vegetative properties within a survey plot. All other data used for the development of both models were obtained from the pre-processing of existing GIS layers and remotely sensed images. The metadata of both remotely sensed images incorporated in the MLR analysis are displayed in Table 4.2.
### Table 4.2: Remotely Sensed Imagery Utilized by MLR Method

<table>
<thead>
<tr>
<th>Sensor</th>
<th>Acquisition Data</th>
<th>Pixel Resolution (m²)</th>
<th>Spectral Range (µm)</th>
<th>Derived Variables</th>
</tr>
</thead>
<tbody>
<tr>
<td>ADS40</td>
<td>4/24/2009</td>
<td>0.3</td>
<td>0.430-0.885</td>
<td>% Vegetation Cover</td>
</tr>
<tr>
<td>ASTER</td>
<td>6/21/2011</td>
<td>15</td>
<td>0.520-0.860</td>
<td>NDVI</td>
</tr>
</tbody>
</table>

### Variables Derived from GIS Layers

Many of the GIS layers incorporated into the two analyses were calculated using spatial analysis functions on layers obtained from external sources using ArcGIS tools. Both the watershed boundary and 5 m by 5m pixel resolution DEM files were obtained from the Massachusetts DCR. Analysis of the DEM was limited to the area within the watershed boundary, which defines the drainage basin of the Prescott Peninsula. The topographic features of elevation and slope were derived from this DEM file using the TOPOGRAPHY tools found in the Spatial Analyst extension. The area of upstream watershed raster (also known as “flow accumulation”) was derived from the HYDROLOGY tools using the DEM and watershed boundary source layers as inputs. To provide consistency within the GIS, these three DEM-derived layers were all evaluated at the same 5 m pixel resolution.

The ‘distance from the Quabbin Reservoir’ raster file was generated using the EUCLIDEAN DISTANCE tool on the Quabbin reservoir shapefile, which was downloaded via file transfer protocol (FTP) from the MassGIS.gov webpage. All distances were measured in meters and were calculated from the Quabbin’s vector shoreline. The soil shapefile, created and obtained from the Massachusetts DCR, was converted into a 5m raster. All values from this soil raster file fall within a range...
between 1 (excessively drained) and 5 (very poorly drained), each representing a soil drainage class defined by the Natural Resources Conservation Service (NRCS).

**Variables Derived from ASTER Imagery**

All ponds and streams were hand-digitized at the 1:800 scale to create the hydrologic network shapefile that defines that spatial boundaries of both analyses. Aerial imagery captured by the ADS40 sensor was coupled with the NDVI image to assist in the detection and accurate digitization of these hydrologic features. The ASTER scene utilized in this analysis was chosen based on the availability of a recent coverage that corresponded with a cloud-free day during the summer months, when vegetation is at its most productive levels. A normalized difference vegetation index (NDVI) raster layer was derived from a satellite image captured by the ASTER sensor aboard NASA’s Terra satellite. The NDVI is commonly utilized in remote sensing applications for the estimation of Leaf Area Index (LAI), which may serve as a proxy for vegetation productivity (Jenson, 2005). The NDVI is calculated using Equation 1 by dividing the difference between the near infrared and red ASTER reflectance bands by the sum of those same two bands:

\[
NDVI = \frac{\rho_{\text{NIR}} - \rho_{\text{RED}}}{\rho_{\text{NIR}} + \rho_{\text{RED}}} \tag{1}
\]

where \(\rho_{\text{NIR}}\) is the near-infrared band 3 (0.760 to 0.860 μm) reflectance and \(\rho_{\text{RED}}\) is the red band 1 (0.520 to 0.600 μm) reflectance. This process transformed raw pixel values from the ASTER satellite image into a raster dataset that has real ecological
meaning, which was ultimately used as an ecological input into the MLR model to evaluate habitat suitability.

**Variables Derived from Aerial Imagery (ADS40)**

All vegetation variables considered by the MLR model originated from a 25-class unsupervised classification, which was performed on aerial imagery captured by the ADS40 sensor using ERDAS Imagine software. This unsupervised classification process partitions the remotely sensed data in multispectral feature space to extract land-cover information, which ultimately results in a land-use/land-cover (LULC) map consisting of 25 spectral classes (Jenson, 2005). Each of these 25 spectral classes was then assigned into one of the 6 thematic land-cover categories (shown in Table 4.3) and imported into a GIS with distinctive pixel values for each of the categories. These 6 land-cover categories were ultimately determined based on a balance between classification limitations and vegetation preferences by beavers. For instance, because the aerial imagery was captured during the winter season when all deciduous trees have lost their leaves, distinguishing shrubs in the understory from the leaf-off deciduous trees proved to be extremely difficult. As a result, shrub and deciduous tree species were merged into a common land-cover class. Cornus spp. was assigned its own land-cover class because it was observed in the field as a favorite food source by beavers.
Table 4.3: Land-cover descriptions for unsupervised classification

<table>
<thead>
<tr>
<th>Land-Cover Categories</th>
<th>Description</th>
<th>Preferred</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water</td>
<td>Contains the Quabbin Reservoir, ponds and streams.</td>
<td>N/A</td>
</tr>
<tr>
<td>Coniferous Trees</td>
<td>Contains coniferous trees (most commonly Pine and Hemlock)</td>
<td>N</td>
</tr>
<tr>
<td>Deciduous Tree/Shrubs</td>
<td>Contains deciduous trees (Maple, Birch) and understory shrubs</td>
<td>Y</td>
</tr>
<tr>
<td>Riparian Grass</td>
<td>Contains Riparian grass spp.</td>
<td>N</td>
</tr>
<tr>
<td>Cornus spp.</td>
<td>Contains Dogwood</td>
<td>Y</td>
</tr>
<tr>
<td>Grass/Bare Ground</td>
<td>Contains grass and bare ground</td>
<td>N</td>
</tr>
</tbody>
</table>

A total of 92 ground trothing points, stratified into the 6 land-cover categories, were collected over a random spatial distribution throughout the Prescott Peninsula over the course of four field days. The locations of all 92 ground truth points were determined through careful observations in the field. A minimum area of five m² of continuous and homogenous land-cover was required to be present before a ground truth point was taken, which helped ensure that the six land-cover categories (represented by each ground control point) were correctly identified and classified during the unsupervised classification process. Once the location of a sample point was selected for a given land-cover category, a GPS device was used to obtain the geographic coordinates at the center of each in-situ measurement, which was later identified on satellite imagery for ground-truth points and spectral analysis. Each point’s land-cover type and corresponding area (in m²) was also recorded.

Due to time and resource limitations, it was not possible to obtain a statistically significant number of ground truth points. Therefore, a balance between what was
statistically sound and what was practicably attainable was found. Nineteen of the 92
total ground truth points taken were used to spectrally analyze the classified aerial
image in order to empirically guide in the process of merging the 25 unsupervised
classes into the final 6 land-cover classes (Table 4.3). The remaining 73 points were
later used as in situ data to populate an error matrix, providing the bases on which to
describe the image’s classification accuracy. Overall, the aerial image’s fine
resolution allowed for the detection of small-scale plant communities during the
classification process. Additionally, the six expansive land-cover categories used in
the unsupervised classification were broadly defined, which further helped to
successfully classify the heterogeneous landscape. As a result, the unsupervised
classification proved to be very accurate (Table 4.4).

**Table 4.4:** Error Matrix Table for Accuracy Assessment of Unsupervised
Classification

<table>
<thead>
<tr>
<th>Unsupervised Classified Data</th>
<th>Actual Land-Cover Type</th>
<th>Water</th>
<th>Aquatic Vegetation</th>
<th>Grass/BG</th>
<th>Cornus</th>
<th>Conifer</th>
<th>Decid/Shrub</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water</td>
<td>25</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Aquatic Vegetation</td>
<td>0</td>
<td>6</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Grass/BG</td>
<td>0</td>
<td>0</td>
<td>10</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Cornus</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>7</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Conifer</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>10</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Decid/Shrub</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td><strong>Class Accuracy</strong></td>
<td><strong>100%</strong></td>
<td><strong>100%</strong></td>
<td><strong>100%</strong></td>
<td><strong>77.78%</strong></td>
<td><strong>90.91%</strong></td>
<td><strong>83.33%</strong></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Total Sample Points:</th>
<th>73</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Total Accuracy</strong></td>
<td>93.15%</td>
</tr>
<tr>
<td><strong>Kappa-Value</strong></td>
<td>91.24%</td>
</tr>
</tbody>
</table>
The overall accuracy of the unsupervised classification (image shown in Figure 4.2) was 93.15%, as 68 of the 73 ground control test points were correctly classified (Table 4.4). A Kappa analysis, which measures the relationship between beyond chance agreement and expected disagreement, was also used to further evaluate the classified map’s error matrix (Equation 2). Following the unsupervised classification’s error matrix (Table 4.4), the Kappa Coefficient of agreement was calculated as:

\[
\frac{N \sum_{i=1}^{k} x_{ii} - \sum_{i=1}^{k} (x_{i}^{c} \times x_{i}^{o})}{N^2 - \sum_{i=1}^{k} (X_{i}^{c} \times X_{i}^{o})}
\]  

[2]

where \(k\) is the number of rows (e.g., land-cover classes) in the error matrix, \(x_{ii}\) is the number of correctly classified observations in row/column \(i\), \(x_{i}^{c}\) and \(x_{i}^{o}\) is the marginal totals for row \(i\) and column \(i\), respectively, and \(N\) is the total number of observations. Overall, this process yielded an accuracy of 91.24%, signifying a strong agreement between the unsupervised classification map and the ground reference information (Jenson, 2005). The vegetation cover-types derived from the final classified image were later separated into five individual raster layers, each mapping the geographic distribution of their respective cover-types, and were ultimately used as ecological inputs into the MLR model to evaluate habitat suitability.
Figure 4.2: Unsupervised Classification Map
4.4 GIS-Based Multiple Logistic Regression Analysis Methodology

The methodology of the multiple logistic regression method outlined in this section (Figure 4.3), implements a larger-scale GIS-based model capable of evaluating the quality of a given beaver habitat throughout a landscape. The heart of the model involves the analysis of digital geospatial datasets measuring habitat variables believed to be most influential in explaining the locations of ideal beaver habitat. These deterministic habitat variables were evaluated within 54 zones based on the historical frequency with which they have been colonized by beavers. A logistic regression equation capable of predicting the probability that a given habitat is occupied by a beaver colony is ultimately created, which is then extrapolated throughout the entire study area. In addition to assessing beaver habitat, this model is also able to identify locations currently unoccupied by beavers that are likely to be colonized in the near future.
Selection and Evaluation of Presence/Marginal/Absence Areas

The first step in the logistic regression model is to determine which habitats within the Prescott Peninsula have historically been the most and least preferred by beavers. This step is critical as it allows the model to calibrate which combination of environmental variables creates good, bad and marginal beaver habitat. To assess the historic frequency of beaver colonization throughout the Prescott Peninsula, the POINT DENSITY tool (set at a 100 meter search radius) was used to calculate the density of all beaver colonies along the stream network since 1988. The resulting beaver colony density along a Northeastern subset of the Peninsula was used to
identify the three categorical beaver habitat areas found throughout the study area: Presence, Marginal, and Absence (PMA). Figure 4.4 displays several of the PMA regions within a subset of the Prescott Peninsula used to train the MLR model. The top 5% most densely occupied areas were considered regions of beaver presence, while areas containing the 5% to 30% most densely occupied areas were considered to be regions of marginal habitat. All areas that have never harbored a colony were considered regions of beaver absence. Only continuous regions that were greater than 3.2 hectares (the minimum habitat area of beavers) were considered. A total of 54 regions (22 presence, 11 marginal, and 21 absence) were ultimately selected through this process. Next, a python script was developed to systematically extract and calculate the geometric average of the raster cell values from all 11 environmental variables contained within each PMA region. Environmental data within these 54 regions provided the foundation for the statistical analysis and subsequent model development.
Figure 4.4: Historic Beaver Colony Density (1988-2011)
Statistical Analyses

A principal components analysis (PCA) was first performed to account for and eliminate collinearity in the 11 environmental variables utilized in the multiple logistic regression equation (see Section 4.1 for further detail). Next, values of 0.999, 0.700 and 0.001 were assigned as the dependent variable (probability of beaver presence) for each presence, marginal and absence region, respectively. These dependent variables delimit to the model that there is a 99.9% chance of beavers occupying locations within the defined “presence” regions, while there is only a 0.1% chance that a beaver colony exists within “absence” regions. 0.700 was chosen as the cut-off value for marginal regions because they represent the top 70% to 95% most densely occupied areas. Finally, a regression analysis was performed on the resulting 11 components to derive coefficient (bp) and intercept (b0) values for the multiple logistic regression function as follows:

\[
\text{odds} = P_z = \frac{1}{1 + e^{-(b_0 + b_1 x_1 + \cdots + b_p x_p)}} \quad [3a]
\]

\[
\text{odds} = \left[ \frac{1 - P_z}{P_z} \right] = e^{-(b_0 + b_1 x_1 + \cdots + b_p x_p)} \quad [3b]
\]

\[
\ln[\text{odds}] = \ln \left[ \frac{1 - P_z}{P_z} \right] = b_0 + b_1 x_1 + \cdots + b_p x_p \quad [3c]
\]

where \( P_z \) represents the odds, or probability of beaver presence in a given raster cell with a logistic regression value of \( Z \), \( b_0 \) represents the intercept value derived from the
regression analysis, \( b_p \) represents the coefficient value derived from the regression analysis, and \( X_p \) represents the principal component value.

The final multiple logistic regression equation (Equation 3c) used to map the probability of beaver presence was obtained by performing some algebraic manipulation on equations 3a and 3b. Computing the odds is a commonly used technique of interpreting probabilities (Clark and May, 2004). The natural logarithm of the odds is linear in the independent variables \( X_1, X_2, \ldots, X_p \). Therefore, the coefficients (\( b_p \)) in this equation can be interpreted as regression coefficients (Clark and May, 2004). This multiple logistic regression equation was ultimately used to convert the average environmental variable values contained within the 54 defined habitat quality regions into true probabilities of beaver presence (\( Z \)), as predicted by the model.

The theoretical S-curve that is produced from a logistic regression analysis is shown in Figure 4.5. Note that \( P_z \) must always be positive and render a value between 0 and 1 because it is a probability. As \( X_z \) (which represents the cumulative influence of all 11 environmental variables at a given location) increases, so too does the probability (\( P_z \)) that a beaver colony will occupy that habitat.
Logistic Regression within GIS

The final step to complete the model was to extrapolate the derived multiple logistic regression equation throughout the entire Prescott Peninsula using a GIS. To accomplish this task, all 11 environmental variables were first converted into their own distinct raster file. The SNAP RASTER geoprocessing option was implemented within ArcMap to ensure that the grid cells of every raster layer were perfectly aligned and overlaid on top of one another, as illustrated in Figure 4.6. Additionally, all raster datasets were preserved at a common resolution of 5 m. The NDVI image was resampled from its original resolution of 15 m into this same 5 m resolution shared by the other raster datasets. Given the geographic extent of the study area, local habitat
characteristics are effectively resolved at this resolution, which made it ideal for this model.

![Graphical Representation of Raster Overlay](image)

**Figure 4.6:** Graphical Representation of Raster Overlay

All 5 vegetation cover values derived from the unsupervised classification map were utilized in the multiple logistic regression analysis. The remaining areas classified as ‘water’ were ignored from the logistic regression analysis to isolate vegetation-cover. All pixel values designating vegetation cover in the classified aerial image was assigned a distinct integer value between 1 and 5, each representing a land-cover type at a given location (see Table 4.4 for list of vegetation categories). However, the mere presence of a vegetation-cover type was not helpful in assessing
beaver habitat preference; instead, raster values had to be implemented into the model as a percent of vegetation cover over a given area. To remedy this data requirement, the FOCAL STATISTICS tool was run on the classified image, which systematically analyzes every cell in the dataset and counts the total number of mutual pixel values found within a 10,000 m² radius surrounding that cell (100m by 100m). The percent vegetation cover was then easily calculated using the RASTER CALCULATOR tool by dividing the number of cells sharing the same cover-type by the total number of cells analyzed, which was 400. For example, if 100 cells representing coniferous trees were counted, then it can be determined that they occupy 25% of the surrounding 10,000 m² area. This process essentially calculates the percent of each vegetation-cover type as a moving average throughout the study area, ultimately converting the original classified image into five separate rasters.

After all 11 environmental variables were converted into their respective raster files with appropriate cell resolution (5m by 5m) and alignment, a raster-based multiple logistic regression analysis was performed within the GIS in the same manner as described in the previous “Statistical Analyses” section. After converting each raster layer into its respective principal component, the RASTER CALCULATOR tool was once again employed to apply the 11 principal component raster layers into the multiple logistic regression equation derived in the previous section. The result of this process is a single map output raster layer representing the model-predicted likelihood, as a percentage, that a given cell is occupied by a beaver colony based on the 11 local environmental variables. This final map is presented in Chapter 5.
Model Verification

Eighteen point locations from the 2012 annual beaver survey of the Prescott Peninsula were mapped in the GIS and used to determine how well the multiple logistic regression model performed. Data of active beaver colonies in 2012 were not incorporated into the development of this model and were, therefore, regarded as an unbiased dataset with which to effectively test the model’s accuracy. To begin calculating this accuracy, a 100 meter radius buffer was created around all active 2012 colonies, which was then overlaid in the GIS with the final MLR-derived map. An average probability value was calculated from the final map within each of the 18 buffer zones. All 2012 colony locations with a probability value greater than 0.70 were deemed as correctly predicted by the model, while values less than 0.70 were considered incorrectly classified. A radius of 100 meters was chosen as the buffer distance for two reasons; first, it ensured data consistency because it was the same distance used to create the five moving average percent vegetation-cover rasters, and second, it ensured that all habitat areas on both sides of a stream would be assessed.

Prediction of Recolonized Habitats for 2012 Census

The final goal of the MLR model was not only to map the probability that an active beaver colony is present throughout the Prescott Peninsula, but also to identify areas that are likely to be newly colonized in 2012 that were not occupied by beavers in 2011. As discussed in Section 2.3, beavers are a highly territorial species that will defend against the colonization of any habitat contained within their established territory. Therefore, an area must meet three criteria to be considered a candidate habitat that is likely to be newly colonized in 2012: first, it must be considered a
quality habitat by the MLR model; second, it must not be located within the territory of an active 2011 colony; and third, it must have a continuous area greater than or equal to the minimum habitat area required to harbor beaver colonization. To satisfy the first criteria, all locations that were identified by the model as quality beaver habitats (cells containing probability values greater than 0.70) were selected. The next step was to eliminate all selected areas that had been occupied by a beaver colony during the previous year so that quality habitats vacant of beaver habitation could be isolated and identified. To accomplish this, a 250 m buffer was created upstream and downstream of all 2011 active colonies. This distance of 250 m corresponds to the average territorial distance across a stream network in which beavers will defend their habitat from the colonization of a relocating beaver (Busher, 2012). The overall purpose of this territorial buffer was to identify habitats that had been established as beaver territories in the previous census year. All cells contained within these preexisting beaver territories were removed from consideration as candidate habitat likely to become newly colonized by beavers in 2012. From the remaining selection, only those continuous areas larger than 3.2 hectares (the minimum habitat area for beavers) were kept. This process has identified eight large, quality habitats within the Prescott Peninsula that were not occupied by beaver in the previous year. It is hypothesized that these identified areas, presented in Chapter 5, are the most likely habitats to become newly colonized by beavers in 2012.

4.5 Discriminant Analysis

While the logistic regression model of Section 4.4 is best implemented over a large area and requires a fair amount of geospatial software and analyses, the
discriminant analysis method, shown in Figure 4.7, is better suited for assessing beaver habitat suitability at a more local scale and only requires elementary GIS capabilities. To analyze local habitat variables, namely vegetation cover, this method requires a targeted vegetation inventory to be taken directly in the field. These locally measured vegetative properties are coupled with data obtained from the DEM to ultimately produce two discriminant functions capable of assigning a given habitat into one of three quality classes: preferred, occasional, or non-preferred.

Figure 4.7: Flow Chart of Discriminant Analysis Methodology
Field Surveying Techniques

A targeted vegetation inventory was conducted on beaver-impacted and non-impacted streams and ponds within the Prescott Peninsula to create a discriminant function capable of determining the quality of a beaver habitat. Vegetation characteristics were analyzed within 20 semicircular sample plots distributed throughout the entire study area on two trips during the autumn of 2012 (Figure 4.8 and 4.9). Sample plot boundaries are defined by a 15 meter radius semicircle lying directly perpendicular to its respective hydrologic feature (Figure 4.9). The location of each survey plot was strategically chosen to ensure that a representative sample of all beaver habitats was obtained within the Peninsula.
Figure 4.8: Vegetation Survey Plot Locations
Field work was conducted at each of the 20 carefully selected survey plots to measure that habitat’s vegetative properties. A spherical densitometer with an angle of view of 60° was used for the acquisition of canopy cover, which measures the proportion of sky hemisphere obscured by vegetation. Within each plot, the instrument was held at 5 survey points (illustrated in Figure 4.9): the first in the center of the plot and the other four at a 7 meter distance from the center point in the directions of North, South, East and West. In each sample point, four measurements were taken with the spherical densitometer oriented in the direction of a different cardinal point. The final canopy closure value of each survey plot was calculated as the average of the five survey points, each including four cardinal point measures. The diameter at breast height (dbh) was measured for each tree within each plot, along with the species name off all trees and shrubs. All plant species were later classified as “Preferred”, “Occasional/Seasonal”, and “Non-preferred” by beaver (see Table 2.1). The proportion of understory occupying the forest floor within each survey plot was visually estimated from a 2m2 representative section of the local understory. Values for stream slope and upstream watershed area for each of the 20 survey plots were derived from the DEM within a GIS using the same methodology as described in Section 4.3.
Assigning Habitats into Habitat Type

Two types of beaver habitat exist within the Prescott Peninsula – ponds and streams. Ponds are large, natural depressions, such as vernal pools, that create a micro-wetland habitat that exists independent from beaver activity (Pullen, 1971). Pond habitats, which have more gradual slopes and less canopy cover than streams, are most preferred by beavers and can be continuously occupied by one family over many consecutive years. Stream habitats are composed of smaller ponds that are connected to the stream network and are created by the process of beaver dam construction. Beaver colonization and abandonment of stream habitats seem to be much more frequent and unpredictable, making these habitats less preferred by beaver (Pullen, 1971). It is hypothesized that beaver dispersal amongst stream habitats are most likely to be driven by local vegetation. Because ponds and streams possess such distinct, non-comparable ecological characteristics that influence beaver colonization behavior, it is important to analyze and compare each habitat solely within the context of similar habitat types. To account for these ecological differences, the distribution
of the sample plots was first stratified into the two primary beaver habitat types – ten streams and ten ponds.

**Criteria for Assigning Habitats into Quality Groups**

In addition to the two habitat types, survey plots were also stratified based on habitat quality. The comprehensive beaver census dataset provided by the Massachusetts DCR served as a unique and powerful tool to assess habitat quality. Maps like Figure 4.8, which display the locations of historically active beaver colonies between 1988 and 2011, were created in ArcGIS to help assess the quality of a given habitat. To account for the wide range in historic beaver habitat utilization throughout the study area, the distribution of sample plots was further stratified into three classes of beaver habitat quality – Non-Preferred, Occasional, and Preferred.

To begin the formulation of these discriminant functions, each survey plot was assigned into one of three distinct habitat quality groups – (I) Non-preferred, (II) Occasional or (III) Preferred – which have been designated based on historic beaver colonization behavior. Historic beaver colonization behavior has been defined as the number of beaver colonization events which have occurred within 800 meters (the maximum foraging distance of beaver) from the center of each survey plot along the stream network between the years of 1988 and 2011. Any historically active colonies within 800 meters of a survey plot have likely utilized that habitat and, therefore, were counted. Table 4.5 defines the ranges used to assign each survey plot into one of the three habitat quality classes.
Table 4.5: Designation of Habitat Quality Classes Based on Historic Presence of Beaver

<table>
<thead>
<tr>
<th>Class</th>
<th># of Colonies</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-preferred</td>
<td>0 to 5</td>
</tr>
<tr>
<td>Occasional</td>
<td>6 to 15</td>
</tr>
<tr>
<td>Preferred</td>
<td>16+</td>
</tr>
</tbody>
</table>

Statistical Techniques

Once the habitat variables were measured and the habitat quality groups were determined for all 20 survey plots, a discriminant analysis was performed. A discriminant analysis is analogous to logistic regression analysis, in which the dependent variable (also referred to as the grouping variable) assumes a value indicating membership to one of two or more populations on the basis of a set of measurements which, in this study, are the uncorrelated principal components derived from the environmental variables (Clark and May, 2004). Therefore, the first step in accomplishing this goal was to perform a Principal Components Analysis (PCA) to account for and eliminate collinearity within the 10 habitat variables considered in this analysis (see section 4.1 for further detail). Habitat type, which is a binary variable (Streams = 0, Ponds = 1), was excluded from the PCA. The ‘habitat type’ variable was then incorporated with the nine independent principal components as inputs into the discriminant analysis to construct two equations which define the relationship between the ten habitat variables and the quality of that habitat.

Ultimately, two discriminant functions were developed as linear combinations of the uncorrelated variables that maximized separation between the three habitat quality groups. Figure 4.10 illustrates the theoretical classification procedure
employed by this discriminant analysis. The dividing lines used to classify each survey plot into one of the three habitat categories is a graph of the discriminant functions F1 and F2. A survey plot falling in the region between both dividing lines, for example, is classified as “Occasional Habitat.”

![Discriminant Analysis Graph](image)

**Figure 4.10:** Example of Discriminant Analysis Habitat Classification Procedure

### 4.6 Comparison of the Two Analyses

Wildlife managers have long been concerned with disturbances and destruction of riparian areas by beavers, emphasizing a critical need to define landscape-beaver
colonization trends as they apply to conservation and nuisance avoidance objectives (Jackson and Decker, 2004). This study presents two empirically developed multivariate statistical approaches with which to evaluate such beaver-habitat dynamics: a multiple logistic regression model and a discriminant analysis. These two ecological models both evaluate beaver habitat preferences by utilizing a comprehensive beaver census dataset. Additionally, both analyses employ the common, user-friendly and relatively easy to learn ArcGIS 10.1 software as an essential tool for the analysis of beaver ecology. Representative (or average) conditions from a range of beaver habitat types are ultimately used to provide input data and parameters for each model, with an emphasis given to those primary environmental attributes which modulate the physical processes and biological responses of beavers-habitat dynamics. Although both ecological models incorporate similar parameterization techniques, the methodologies and outputs of each analysis have been developed at two spatial scales to serve different purposes for different wildlife management needs.

The purpose of the MLR model is to evaluate the probability that a given habitat is currently being occupied by beavers throughout a large geographic extent. The MLR model is additionally capable of identifying those locations not currently occupied by beavers that are most susceptible to becoming newly colonized. This GIS-based MLR model is best served for land managers possessing GIS resources and processing capabilities who would like to identify the degree of beaver habitat suitability throughout a landscape. Alternatively, the discriminant analysis method offers a predictive, systematic technique for classifying specific sections of riparian forests into three habitation classes: preferred, occasionally preferred, or non-
preferred by beavers. This local scale method requires fieldwork in the form of a targeted vegetation survey and is best suited for property owners and land managers concerned with assessing the habitat attributes that dictate beaver colonization behavior at a specific site. In summary, the discriminant analysis produces a predictive model of local habitation, while the multiple logistic regression analysis generates a cartographic model of regional habitat suitability. These two models may ultimately be made readily available to land planners and managers as tools, in singularity or in tandem, through the medium of a GIS to help guide and modify beaver management strategies to be proactive and adaptive to the ever-evolving landuse dynamics of beavers.
Chapter 5

RESULTS

5.1 Beaver Habitat Preference Analysis Using a Multiple Logistic Regression

Results of Statistical Analyses

A principal component analysis (PCA) was performed on all 11 environmental variables considered by the MLR model (displayed in Figure 4.3) to alleviate the problem of collinearity and evaluate the degree to which each variable contributes to differentiating between various habitat quality types. The PCA retained all 11 components, indicating that very little bias was introduced through the procedure (Table 5.1 shows the final eigenvalues derived from the analysis). Principal components with a large associated variance best distinguish between varying degrees of habitat quality. Thus, the most informative principal component for distinguishing beaver habitat quality is the first, and the least informative is the last. With this in mind, the first three components are considered the most significant, as they explain over 70% of the variance amongst habitat variables (Table 5.1).

Furthermore, the component matrix derived from the PCA helped to identify the specific contributions of each environmental variable under consideration by the MLR model. Table 5.2 shows the coefficient matrix for the first three principal components derived from the PCA, which are the most informative. Specifically, those environmental variables that are associated with high coefficient values within the first three components are the most informative for distinguishing beaver habitat
quality. Following the environmental variables associated with high coefficient values in Table 5.2, the PCA found stream slope, along with the proportion of coniferous tree, grass, and deciduous tree/shrub cover to be the most helpful in distinguishing between habitats with varying degrees of beaver activity. A habitat’s average NDVI value, as well as its distance from the Quabbin Reservoir coastline, were additional variables which helped identify historically preferred beaver habitats, but to a lesser degree (Table 5.2). Conversely, the environmental variables of soil drainage class, as well as the proportion of riparian grass cover, for example, contributed little in explaining the variation between beaver habitat types (Table 5.2).

Table 5.1: Total Variance Explained by Principal Components

<table>
<thead>
<tr>
<th>Principal Component</th>
<th>Eigenvalues</th>
<th>% of Variance</th>
<th>Cumulative %</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>4.056</td>
<td>36.876</td>
<td>36.876</td>
</tr>
<tr>
<td>2</td>
<td>2.516</td>
<td>22.876</td>
<td>59.752</td>
</tr>
<tr>
<td>3</td>
<td>1.259</td>
<td>11.443</td>
<td>71.195</td>
</tr>
<tr>
<td>4</td>
<td>1.025</td>
<td>9.314</td>
<td>80.509</td>
</tr>
<tr>
<td>5</td>
<td>0.556</td>
<td>5.052</td>
<td>85.561</td>
</tr>
<tr>
<td>6</td>
<td>0.531</td>
<td>4.830</td>
<td>90.391</td>
</tr>
<tr>
<td>7</td>
<td>0.396</td>
<td>3.598</td>
<td>93.989</td>
</tr>
<tr>
<td>8</td>
<td>0.262</td>
<td>2.377</td>
<td>96.366</td>
</tr>
<tr>
<td>9</td>
<td>0.192</td>
<td>1.749</td>
<td>98.115</td>
</tr>
<tr>
<td>10</td>
<td>0.128</td>
<td>1.168</td>
<td>99.283</td>
</tr>
<tr>
<td>11</td>
<td>0.079</td>
<td>0.717</td>
<td>100.000</td>
</tr>
</tbody>
</table>
Table 5.2: Component Matrix from PCA

<table>
<thead>
<tr>
<th>Variable</th>
<th>Component</th>
</tr>
</thead>
<tbody>
<tr>
<td>Avg. Slope (°)</td>
<td>0.741</td>
</tr>
<tr>
<td>Avg. Elevation (m)</td>
<td>0.301</td>
</tr>
<tr>
<td>Soil Drainage Class</td>
<td>-0.178</td>
</tr>
<tr>
<td>NDVI</td>
<td>0.667</td>
</tr>
<tr>
<td>Watershed Area (m²)</td>
<td>0.441</td>
</tr>
<tr>
<td>Distance to Reservoir (m)</td>
<td>-0.045</td>
</tr>
<tr>
<td>Riparian Grass Cover (%)</td>
<td>-0.328</td>
</tr>
<tr>
<td>Coniferous Cover (%)</td>
<td>-0.903</td>
</tr>
<tr>
<td>Decid./Shrub Cover (%)</td>
<td>0.857</td>
</tr>
<tr>
<td>Cornus spp. Cover (%)</td>
<td>0.625</td>
</tr>
<tr>
<td>Grass Cover (%)</td>
<td>0.874</td>
</tr>
</tbody>
</table>

Table 5.3 shows the results of the regression analysis performed on the resulting 11 components. Coefficient (bp) and intercept (b0) values were ultimately used as inputs to derive the logistic regression function (Equation 3a in Section 4.4). Equation 4 shows the final multiple logistic function used in the model, which was derived by applying the Coefficient (bp) and intercept (b0) values found in Table 5.3 to the logistic regression function presented in Equation 3a. Thus, the final MLR model used to predict the likelihood of beaver presence throughout the continuous Prescott Peninsula is represented in Equation 4:

\[ P_z = \frac{1}{1 + e^{-(0.261 + 1.467 \times X_1 + 1.319 \times X_2 + 1.008 \times X_3 + 0.729 \times X_4 + 1.497 \times X_5 - 1.698 \times X_6 + 1.910 \times X_7 - 1.235 \times X_8 - 2.867 \times X_9 - 3.351 \times X_{10} + 4.706 \times X_{11})}} \]
where $P_z$ represents the odds, or probability of beaver presence in a given location with a discriminant function value of $Z$, and $X_n$ represents the principal component values associated with each of the 11 environmental variables displayed in Table 5.2.

Values under the “t” and “P” columns of Table 5.3 represent the two-sided $t$ statistic and corresponding significance values, respectively, and are used to assess the degree to which each component contributes to the regression equation. $P$-values less than 0.05 are considered to help significantly in predicting beaver habitat quality. Overall, components possessing high coefficient ($b_p$) values coupled with $P$-values less than 0.05 indicate a high correlation between that component and the predicted likelihood of beaver presence by the MLR model (Table 5.3). This regression analysis yielded a net correlation coefficient (Pearson’s $r$) value of 0.796, indicating a strong fit between empirically quantified beaver-habitat relationships and those relationships predicted by the multiple logistic regression function (Equation 4).
**Table 5.3:**  Regression Coefficients for Input into MLR Equation

<table>
<thead>
<tr>
<th>Principal Component</th>
<th>Coefficient (b&lt;sub&gt;p&lt;/sub&gt;)</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>(b&lt;sub&gt;0&lt;/sub&gt;)</td>
<td>-0.261</td>
<td>0.325</td>
<td>0.747</td>
</tr>
<tr>
<td>1</td>
<td>1.467</td>
<td>4.324</td>
<td>0.001</td>
</tr>
<tr>
<td>2</td>
<td>1.319</td>
<td>2.841</td>
<td>0.007</td>
</tr>
<tr>
<td>3</td>
<td>1.008</td>
<td>1.894</td>
<td>0.065</td>
</tr>
<tr>
<td>4</td>
<td>0.729</td>
<td>1.254</td>
<td>0.217</td>
</tr>
<tr>
<td>5</td>
<td>1.497</td>
<td>1.892</td>
<td>0.066</td>
</tr>
<tr>
<td>6</td>
<td>-1.698</td>
<td>1.799</td>
<td>0.079</td>
</tr>
<tr>
<td>7</td>
<td>1.910</td>
<td>2.005</td>
<td>0.052</td>
</tr>
<tr>
<td>8</td>
<td>-1.235</td>
<td>1.042</td>
<td>0.303</td>
</tr>
<tr>
<td>9</td>
<td>-2.867</td>
<td>2.015</td>
<td>0.050</td>
</tr>
<tr>
<td>10</td>
<td>-3.351</td>
<td>2.038</td>
<td>0.048</td>
</tr>
<tr>
<td>11</td>
<td>4.706</td>
<td>2.218</td>
<td>0.032</td>
</tr>
</tbody>
</table>

**Classification Results and Accuracy of the Multiple Logistic Regression Model**

To improve clarity and readability, all cartographic results derived from the MLR function that are presented in this section have been broken up into the three sub-regions within the Prescott Peninsula outlined in Figure 5.1. Specifically, regions A, B, and C encompass the northern, central, and southern thirds of the peninsula, respectively (Figure 5.1). Figures 5.2A-C display the mapped results of the multiple logistic regression function (which have been broken up into the three sub-regions displayed in Figure 5.1) throughout the stream network of the Prescott Peninsula. Following the map legends, the bluish colors represent low probabilities of beaver presence while the reddish colors represent locations likely to be occupied by beavers. Additionally, the purple dots overlaid on top of these maps represent the locations of
historic beaver colonies from 1988 to 2011, which were originally used to determine
the presence/marginal/absence (PMA) habitat regions outlined in Chapter 3. Overall,
the MLR model predicts the distribution of beaver habitat throughout the Prescott
Peninsula as expected, with the highest probabilities of beaver presence located at
ponds and low-gradient streams.
Figure 5.1: Sub-region designation of Prescott Peninsula
Figure 5.2a: Final MLR probability Map
Figure 5.2b: Final MLR Probability Map
Figure 5.2c: Final MLR Probability Map

Figure 5.2A shows the MLR results of region “A”, which contains the most frequently colonized areas by beavers within the Prescott Peninsula (Figure 5.2A). This high degree of beaver activity is likely a product of the local area’s favorable geomorphologic conditions, as region A’s vast network of interior, gradually sloping hydrologic features produces expanses of highly preferred pond habitats, which beavers tend to occupy on a semi-sustainable basis (Figure 5.1A). Moreover, a variety of different habitat quality types are found within region “B” (Figure 5.2B), which contains a high abundance of both poor (rarely colonized) and quality (frequently colonized) habits. Such varying degrees of habitat utilization by beavers are likely the
result of the area’s highly heterogeneous landscape, as region B contains a mixture of steeply sloping coastal streams, which are highly avoided by beavers, along with the strongly favored gradual sloping interior streams. The most frequently colonized habitats within this region occur along the interior stream network that flows in the North-South direction (Figure 5.2B). Lastly, region “C” contains the most sparsely occupied beaver habitat within the Prescott Peninsula, as small, steep and coastal streams dominate the hydrology of the local area, which inhibit beaver colonization.

To determine how well the modeled logistic regression equation represented the likelihood of beaver presence, an independent test of the MLR model’s accuracy was carried out by evaluating the model’s predicted probability of beaver presence within the 18 habitats that were occupied by beaver colonies in 2012. As described in Chapter 4, habitats that are assigned predicted probabilities of 70% or greater by the MLR model are classified as quality beaver habitat. Therefore, in order for the MLR model to achieve 100% accuracy, all 18 habitats that were occupied by beavers in 2012 would have to have been classified as quality habitats (i.e., receive a score ≥ 0.70) by the model.

The ensuing classification results of the MLR model are presented in Table 5.4, which presents the model’s assigned probability of beaver presence within each of the 18 active 2012 colony habitats. Correspondingly, Figures 5.3A-C present the locations of active 2012 colonies, which have been overlaid onto the final MLR cartographic results. Again, probabilities within these habitats correspond to the classification results presented in Table 5.4. Specifically, the classification values found in the 3rd column of Table 5.4 were calculated as the average predicted probability within a 100 meter radius (i.e., the local habitat) of each active beaver
colony in 2012 (Figures 5.3A-C). These 100 meter buffer areas used to evaluate the model are symbolized in bright yellow within Figures 5.3A-C. Through this evaluation process, the MLR function successfully predicted 72.2% (13/18) of the habitats colonized by beavers in 2012 (Table 5.5).

Figures 5.4A-C, as well as Tables 5.4 and 5.5, display the classification results of the habitats likely to be newly colonized in 2012 which were not occupied by beavers in 2011 (see Section 4.6 for details on methodology). Following the legend of Figures 5.4A-C, habitats that were occupied by beavers in 2011 are drawn in red, while high-quality areas that were predicted by the MLR model to be newly colonized by beavers in 2012 are drawn in green. A total of eight habitats were identified by the model as highly likely to be newly colonized in 2012, though some regions were predicted to experience far more relocation events than others. As expected, the MLR model identified seven habitats which are likely to harbor a new colonization event within the highly active territories of region A; conversely, only one such habitat was identified in region B and no such habitats were identified on the streams of region C (Figures 5.4A-C). The 2nd column of Table 5.4 shows that a total of 8 such relocation events into new habitats occurred in 2012. Overall, the MLR model accurately predicted five (62.5%) of the eight identified habitats that were newly colonized by beavers in 2012 (Table 5.5).

In summary, Table 5.4 shows the MLR model’s final classification results of the known active habitats from the 2012 beaver census. Table 5.5 summarizes these results and presents the overall classification accuracy of the MLR model. In general, the MLR model predicted that the most likely locations to be inhabited by
beavers are interior pond and low gradient stream habitats containing a vegetative species structure that is indicative of long-term selective foraging by beavers.
### Table 5.4: MLR Model Classification Results for Active 2012 Habitats

<table>
<thead>
<tr>
<th>Colony ID</th>
<th>Relocation?</th>
<th>Avg. Posterior Probability</th>
<th>Correct?</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>Y</td>
<td>2.16%</td>
<td>N</td>
</tr>
<tr>
<td>1</td>
<td>Y</td>
<td>2.70%</td>
<td>N</td>
</tr>
<tr>
<td>5</td>
<td>Y</td>
<td>12.07%</td>
<td>N</td>
</tr>
<tr>
<td>2</td>
<td>N</td>
<td>50.59%</td>
<td>N</td>
</tr>
<tr>
<td>13</td>
<td>N</td>
<td>59.43%</td>
<td>N</td>
</tr>
<tr>
<td>15</td>
<td>N</td>
<td>74.12%</td>
<td>Y</td>
</tr>
<tr>
<td>6</td>
<td>Y</td>
<td>77.51%</td>
<td>Y</td>
</tr>
<tr>
<td>9</td>
<td>Y</td>
<td>79.66%</td>
<td>Y</td>
</tr>
<tr>
<td>11</td>
<td>N</td>
<td>85.37%</td>
<td>Y</td>
</tr>
<tr>
<td>7</td>
<td>Y</td>
<td>91.34%</td>
<td>Y</td>
</tr>
<tr>
<td>8</td>
<td>N</td>
<td>91.97%</td>
<td>Y</td>
</tr>
<tr>
<td>16</td>
<td>N</td>
<td>92.00%</td>
<td>Y</td>
</tr>
<tr>
<td>14</td>
<td>N</td>
<td>92.03%</td>
<td>Y</td>
</tr>
<tr>
<td>0</td>
<td>N</td>
<td>92.78%</td>
<td>Y</td>
</tr>
<tr>
<td>10</td>
<td>Y</td>
<td>96.41%</td>
<td>Y</td>
</tr>
<tr>
<td>12</td>
<td>N</td>
<td>97.15%</td>
<td>Y</td>
</tr>
<tr>
<td>17</td>
<td>Y</td>
<td>99.78%</td>
<td>Y</td>
</tr>
<tr>
<td>3</td>
<td>N</td>
<td>100.00%</td>
<td>Y</td>
</tr>
</tbody>
</table>

### Table 5.5: Accuracy of the Summarized MLR Model Classification Results

<table>
<thead>
<tr>
<th>MLR Model Accuracy</th>
<th>Fraction (Correct/Total)</th>
<th>Percentage of Correctly Classified Habitats</th>
</tr>
</thead>
<tbody>
<tr>
<td>Classification of all Habitats</td>
<td>13/18</td>
<td>72.22%</td>
</tr>
<tr>
<td>Classification of Relocated Habitats</td>
<td>5/8</td>
<td>62.50%</td>
</tr>
</tbody>
</table>
Figure 5.3a: Locations of Active Beaver Colonies in 2012
Figure 5.3b: Locations of Active Beaver Colonies in 2012
Figure 5.3c: Locations of Active Beaver Colonies in 2012
Figure 5.4a: Predictive Map of Habitats Likely to be Newly Colonized in 2012
Figure 5.4b: Predictive Map of Habitats Likely to be Newly Colonized in 2012
Figure 5.4c: Predictive Map of Habitats Likely to be Newly Colonized in 2012
5.2 Discovered Trends within Presence/Marginal/Absence Habitats Using Correlation Analysis

A correlation analysis was used to determine the significance of relationships between all 11 environmental variables considered by the MLR model (independent variables) and beaver habitat preference (dependent variable). Habitat preferences were evaluated from the same 54 presence/marginal/absence (PMA) regions used to develop the MLR model (identified in Chapter 4). A fundamental assumption of this study is that habitats (along with their associated environmental characteristics), which have been most frequently occupied by beavers are considered to be of higher quality than sparsely occupied habitats. That is, frequently colonized areas are likely to share common ecological traits which separate them from beaver habitats of lesser quality. Because PMA regions were established based on their historic rates of local colonization, beaver-ecology trends were further discovered from the regression analysis to provide additional insights as to which environmental variables are most strongly associated with habitat quality. Furthermore, environmental variables that were determined to be statistically significant with beaver presence likely modulate the physical processes and the associated biological responses of beavers to their habitats.
Correlation statistics (presented in Table 5.6) were calculated based on the relationship between the average environmental variables within the 54 PMA regions and each region’s associated average probability of beaver presence, as predicted by the MLR model. Of the 11 environmental variables considered by the MLR model in this correlation analysis, most proved to have statistically significant relationships with beaver colonization behavior (Table 5.6). Stream slope and the proportion of deciduous trees and shrubs contained within a given habitat exhibited the two strongest relationships by far, yielding Pearson’s r-values of -0.695 and -0.687, respectively, as well as having two-tailed p-values less than 0.001 (Table 5.6). Two other environmental variables displaying highly significant relationships with beaver colonization behavior are the proportion of coniferous trees and grass cover within a habitat. Conversely, two environmental variables had no statistically significant relationships with beaver colonization at the 0.10 level: elevation and the proportion of riparian grass cover.
Results from Table 5.6 indicate that, on average, habitats with more intense beaver usage had flatter stream gradients, lower NDVI values (and, therefore, less vegetation productivity), greater areas of upstream watershed, higher proportions of coniferous trees, Cornus spp. and grass cover, lower proportions of deciduous tree and shrub cover, and were further inland from the Quabbin Reservoir coastline. Conversely, habitats associated with little to no beaver activity exhibited opposite ecological trends.

5.3 Classification of Beaver Habitation using Discriminant Analysis

Results of Discriminant Analysis PCA

Eigenvalues derived from the PCA are displayed in Table 5.7, ordered from highest to lowest explained variance. The first four components are considered the most significant, explaining over two thirds of the variance amongst habitat variables. The principal components analysis found that habitat type, high proportions of preferred understory, and gradual stream slopes best separate preferred beaver habitats from non-preferred. High proportions of occasionally preferred tree species, as well as greater amounts of canopy closure and tree density were also found to be good indicators of quality beaver habitat, but to a lesser degree. Conversely, the presence of preferred tree species and the upstream watershed area variables contributed little to identifying beaver habitat quality. The most unexpected aspect of these PCA results is the counterintuitive contributions of the two tree cover classes: the presence of occasionally preferred trees by beavers was a far better identifier of habitat quality than the presence of preferred tree species (refer to section 6.1 for explanation).
Table 5.7: Total Variance Explained by Principal Components Analysis

<table>
<thead>
<tr>
<th>Principal Component</th>
<th>Eigenvalue</th>
<th>% of Variance</th>
<th>Cumulative %</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>3.011</td>
<td>23.160</td>
<td>23.160</td>
</tr>
<tr>
<td>2</td>
<td>2.009</td>
<td>15.456</td>
<td>38.616</td>
</tr>
<tr>
<td>3</td>
<td>1.906</td>
<td>14.658</td>
<td>53.274</td>
</tr>
<tr>
<td>4</td>
<td>1.741</td>
<td>13.390</td>
<td>66.664</td>
</tr>
<tr>
<td>5</td>
<td>1.111</td>
<td>8.548</td>
<td>75.212</td>
</tr>
<tr>
<td>6</td>
<td>0.978</td>
<td>7.524</td>
<td>82.736</td>
</tr>
<tr>
<td>7</td>
<td>0.809</td>
<td>6.223</td>
<td>88.959</td>
</tr>
<tr>
<td>8</td>
<td>0.552</td>
<td>4.244</td>
<td>93.203</td>
</tr>
<tr>
<td>9</td>
<td>0.247</td>
<td>3.787</td>
<td>96.990</td>
</tr>
<tr>
<td>10</td>
<td>0.215</td>
<td>3.010</td>
<td>100.000</td>
</tr>
</tbody>
</table>

Results of Discriminant Functions

All 10 principal components were implemented into the discriminant analysis to explain the total variance between the three habitat quality groups. The final standardized canonical discriminant function coefficients appear in Table 5.8, which show the relative contribution of each principal component (uncorrelated habitat variable) to the discrimination between the three habitat quality groups based on the magnitude of each variable’s coefficient. Additionally, Table 5.9 displays the values of the two discriminant functions evaluated at the center of each habitat quality group’s centroid. These values help indicate the direction and degree to which each of the two discriminant functions contribute to assigning a given habitat into one of the three quality classes (non-preferred, occasional, and preferred). The discriminant function coefficients found in Table 5.8 are used to calculate the discriminant score for a given survey plot (Equations 5 and 6), which is calculated in the same manner as a predicted value from a linear regression. The resulting discriminant score for each
case is then plotted alongside the two discriminant functions, and is then assigned into one of the three habitat quality groups based on its relative location with respect to the two discriminant functions (see figure 4.10 for a graphical representation).

Ultimately, the corresponding habitat quality group assigned to a given habitat was determined by using the two discriminant functions (represented by Equations 5 and 6) derived from the discriminant analysis. Following Table 5.9, the two higher function #1 values at group centroids are associated with non-preferred and occasionally preferred habitat groups, while the larger function #2 value is associated with the preferred habitat group. As a result, function #1 clearly distinguishes non-preferred and occasionally preferred beaver habitats from preferred habitats, while function #2 best distinguishes preferred habitats from the two habitat types of lesser quality. Following this logic, habitat variables associated with large function #1 coefficients should be considered good indicators of poor and marginal beaver habitat. For example, following Table 5.8, the presence of higher counts of preferred tree species, lower counts of occasionally preferred tree species, higher proportions of occasionally preferred understory species, and steeper stream gradients are all strong indications of lesser quality beaver habitat because these environmental variables all have large coefficient values associated with function #1. Likewise, habitat variables associated with large function #2 coefficients are good indicators of quality beaver habitat. For instance, following Table 5.8 once again, the presence of sparse canopy cover, as well as high proportions of preferred species within the understory are both strong indications of higher quality beaver habitat, as these two environmental variables each have large coefficient values associated with function #1.
### Table 5.8: Standardized Conical Discriminant Function Coefficients

<table>
<thead>
<tr>
<th>Variable</th>
<th>Function 1</th>
<th>Function 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat Type (Boolean)</td>
<td>-0.380</td>
<td>0.402</td>
</tr>
<tr>
<td>Canopy Cover (%)</td>
<td>0.564</td>
<td>-0.571</td>
</tr>
<tr>
<td>Tree Density (#/m²)</td>
<td>-0.110</td>
<td>0.213</td>
</tr>
<tr>
<td>Preferred Tree Count</td>
<td>1.185</td>
<td>0.062</td>
</tr>
<tr>
<td>Occ. Preferred Tree Count</td>
<td>-0.948</td>
<td>0.019</td>
</tr>
<tr>
<td>DBH (cm)</td>
<td>-0.317</td>
<td>0.348</td>
</tr>
<tr>
<td>Pref. Und. Cover (%)</td>
<td>0.575</td>
<td>0.819</td>
</tr>
<tr>
<td>Occ. Und. Cover (%)</td>
<td>0.997</td>
<td>0.196</td>
</tr>
<tr>
<td>Watershed Area (m²)</td>
<td>0.055</td>
<td>-0.021</td>
</tr>
<tr>
<td>Stream Slope (°)</td>
<td>0.872</td>
<td>-0.097</td>
</tr>
</tbody>
</table>

**Note:** Function 1 identifies non-preferred/marginal habitat  
Function 2 identifies preferred habitat

### Table 5.9: Functions at Group Centroids

<table>
<thead>
<tr>
<th>Habitat Quality Group</th>
<th>Function 1</th>
<th>Function 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-Preferred</td>
<td>3.553</td>
<td>0.923</td>
</tr>
<tr>
<td>Occasional</td>
<td>2.252</td>
<td>0.887</td>
</tr>
<tr>
<td>Preferred</td>
<td>0.036</td>
<td>-1.673</td>
</tr>
</tbody>
</table>

\[
F(1) = -0.380 \times \text{HabitatType} + 0.546 \times \text{CanopyCvr} - 0.110 \times \text{TreeDensity} + 1.185 \times \text{PrefTreeCnt} - 0.948 \times \text{OccTreeCnt} - 0.317 \times \text{DBH} + 0.575 \times \text{PrefUndCvr} + 0.997 \times \text{OccUndCvr} + 0.055 \times \text{WatershedArea} + 0.872 \times \text{StreamSlope}
\]

\[
F(2) = 0.402 \times \text{HabitatType} - 0.571 \times \text{CanopyCvr} + 0.213 \times \text{TreeDensity} + 0.062 \times \text{PrefTreeCnt} + 0.019 \times \text{OccTreeCnt} + 0.348 \times \text{DBH} + 0.819 \times \text{PrefUndCvr} + 0.196 \times \text{OccUndCvr} - 0.021 \times \text{WatershedArea} - 0.097 \times \text{StreamSlope}
\]
Classification Accuracy and Case Wise Statistics of Discriminant Functions

Table 5.10 displays the final classification results and associated case wise statistics of each plot from the discriminant analysis, where groups 1, 2 and 3 represent non-preferred, occasionally preferred and preferred beaver habitats, respectively. The overall classification accuracy of the two discriminant functions is additionally summarized in Table 5.11, which was calculated using the empirical method. Explicitly put, the proportion of survey plots incorrectly classified into each habitat quality group was derived by applying the two discriminant functions to the same 20 survey plots used for deriving it. The results from this empirical method show that the discriminant analysis model correctly classified 90% (18/20) of the survey plots into their respective habitat quality groups. Furthermore, 100% (5/5) of the non-preferred surveyed habitats were correctly classified by the model, while 87.5% (7/8) of occasionally preferred and 85.7% (6/7) of preferred surveyed habitats were classified correctly.
### Table 5.10: Classification Results and Case Wise Statistics of Discriminant Analysis

<table>
<thead>
<tr>
<th>Plot #</th>
<th>Actual Group</th>
<th>Predicted Group</th>
<th>( P )</th>
<th>Mahalanobis Distance</th>
</tr>
</thead>
<tbody>
<tr>
<td>18</td>
<td>1</td>
<td>1</td>
<td>1.000</td>
<td>1.998</td>
</tr>
<tr>
<td>4</td>
<td>1</td>
<td>1</td>
<td>0.997</td>
<td>0.752</td>
</tr>
<tr>
<td>19</td>
<td>1</td>
<td>1</td>
<td>0.979</td>
<td>4.170</td>
</tr>
<tr>
<td>20</td>
<td>2</td>
<td>2</td>
<td>1.000</td>
<td>0.251</td>
</tr>
<tr>
<td>16</td>
<td>2</td>
<td>2</td>
<td>0.994</td>
<td>0.900</td>
</tr>
<tr>
<td>17</td>
<td>2</td>
<td>2</td>
<td>1.000</td>
<td>1.033</td>
</tr>
<tr>
<td>8</td>
<td>3</td>
<td>1*</td>
<td>0.753</td>
<td>3.718</td>
</tr>
<tr>
<td>6</td>
<td>3</td>
<td>3</td>
<td>0.999</td>
<td>0.537</td>
</tr>
<tr>
<td>7</td>
<td>3</td>
<td>3</td>
<td>0.997</td>
<td>0.205</td>
</tr>
<tr>
<td>14</td>
<td>3</td>
<td>3</td>
<td>0.941</td>
<td>1.052</td>
</tr>
<tr>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1.000</td>
<td>1.869</td>
</tr>
<tr>
<td>15</td>
<td>1</td>
<td>1</td>
<td>1.000</td>
<td>2.809</td>
</tr>
<tr>
<td>2</td>
<td>2</td>
<td>2</td>
<td>0.999</td>
<td>0.225</td>
</tr>
<tr>
<td>5</td>
<td>2</td>
<td>3*</td>
<td>0.888</td>
<td>1.404</td>
</tr>
<tr>
<td>9</td>
<td>2</td>
<td>2</td>
<td>0.993</td>
<td>0.490</td>
</tr>
<tr>
<td>10</td>
<td>2</td>
<td>2</td>
<td>1.000</td>
<td>2.543</td>
</tr>
<tr>
<td>3</td>
<td>2</td>
<td>2</td>
<td>0.998</td>
<td>1.012</td>
</tr>
<tr>
<td>12</td>
<td>3</td>
<td>3</td>
<td>0.998</td>
<td>0.050</td>
</tr>
<tr>
<td>11</td>
<td>3</td>
<td>3</td>
<td>0.999</td>
<td>0.435</td>
</tr>
<tr>
<td>13</td>
<td>3</td>
<td>3</td>
<td>0.996</td>
<td>1.219</td>
</tr>
</tbody>
</table>

* = Misclassified

### Table 5.11: Summarized Classification Results of Discriminant Analysis

<table>
<thead>
<tr>
<th>Group</th>
<th>Non-Preferred</th>
<th>Occasionally</th>
<th>Preferred</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Non-Preferred (1)</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>Occasional (2)</td>
<td>0</td>
<td>7</td>
<td>1</td>
<td>8</td>
</tr>
<tr>
<td>Preferred (3)</td>
<td>1</td>
<td>0</td>
<td>6</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Non-Preferred</td>
<td>100.0%</td>
<td>0.0%</td>
<td>0.0%</td>
<td>100.0%</td>
</tr>
<tr>
<td>Occasional</td>
<td>0.0%</td>
<td>87.5%</td>
<td>12.5%</td>
<td>100.0%</td>
</tr>
<tr>
<td>Preferred</td>
<td>14.3%</td>
<td>0.0%</td>
<td>85.7%</td>
<td>100.0%</td>
</tr>
</tbody>
</table>
Posterior probabilities, designated as “P” in Table 5.10, represent the probability that each survey plot was correctly classified into its proper habitat quality group. Plots containing posterior probability values greater than 0.95 are highly likely to have been correctly classified by the model, while habitat classifications of plots with lower P-values should be viewed with more skepticism. Overall, the two discriminant functions performed extremely well; however, the model did a superior job at classifying certain types of beaver habitat over others, as demonstrated in Table 5.12. Specifically, non-preferred habitats, which possessed the highest average posterior probability of 0.995, were most successfully classified by the model. This means that 99.5% of non-preferred beaver habitats are likely to be accurately classified by the two discriminant functions. On the other hand, the discriminant functions were least successful at classifying preferred beaver habitats, which yielded an average posterior probability value of 0.955, the lowest of the three Groups. Still, these values are all relatively high and indicate an outstanding classification performance by the discriminant analysis model.

Table 5.12: Average Posterior Probability and Mahalanobis Values of each Habitat Quality Class

<table>
<thead>
<tr>
<th>Habitat Quality Class</th>
<th>Average P</th>
<th>Average Mahalanobis Distance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-Preferred</td>
<td>0.995</td>
<td>2.320</td>
</tr>
<tr>
<td>Occasional</td>
<td>0.984</td>
<td>0.982</td>
</tr>
<tr>
<td>Preferred</td>
<td>0.955</td>
<td>1.031</td>
</tr>
<tr>
<td><strong>Total:</strong></td>
<td><strong>0.977</strong></td>
<td><strong>1.334</strong></td>
</tr>
</tbody>
</table>

The other case wise statistic presented in Table 5.10 is the squared Mahalanobis distance to centroid. These values measure the graphical distance
between the canonical discriminant function of each survey plot and the canonical
discriminant function at its associated group centroid (displayed in Table 5.9).
Mahalanobis distances indicate the degree to which the discriminant functions can
discriminate each survey plot into one of the three habitat quality groups. A smaller
Mahalanobis distance indicates that a survey plot is like a typical habitat within that
habitat quality group and hence probably belongs in that group. Therefore, it has been
determined that survey plot numbers 4, 2, and 12, which have the smallest
Mahalanobis distances of each of the three groups, are most representative of preferred
(plot 4’s distance = 0.752), occasionally preferred (plot 2’s distance = 0.225), and non-
preferred habitats (plot 12’s distance = 0.050), respectively (Table 5.10). Moreover,
Table 5.12 shows that non-preferred habitats (average Mahalanobis distance: 2.320)
are more than twice as difficult for the model to discriminate amongst the three groups
as occasionally preferred (0.982) and preferred (1.031) habitats. This phenomenon
likely occurs because the environmental characteristics associated with non-preferred
habitats are much more variable and broad than those of habitats which can support
beaver populations.
Chapter 6
DISCUSSION AND CONCLUSION

6.1 Explanation of Discovered Trends from Statistical Analyses

After performing three statistical analyses (multiple logistic regression, correlation analysis and discriminant analysis), this study has found that several significant relationships exist between beaver presence and habitat variables within the Prescott Peninsula. The strength of these relationships was determined based on the magnitude of various statistical indicators of correlation (e.g., Pearson’s r, p-value, posterior probability, classification matrix). Many of these discovered beaver-habitat trends were intuitive and consistent with past literature; however, a few were rather surprising.

The strongest and most consistent relationship was also the least surprising: beavers tended to prefer habitats with gradual stream slopes. Slough & Sadlier (1977) and Howard and Larson (1985), among others, similarly found that stream gradient was the most important physical variables related to beaver activity on streams. Simply put, the force created by streamflow can be too great for beavers to build and maintain dams on higher-gradient streams. Gradual stream gradients are additionally important because they allow beavers to greatly increase their safe foraging area through dam construction, as steep topography hinders the establishment of a food transportation system (Beier and Barret, 1987).

A second highly significant environmental variable was the distance from a given habitat to the Quabbin reservoir shoreline: beavers tended to colonize habitats
that were located further inland of the Prescott Peninsula. There are likely two explanations for this phenomenon. First, the reservoir water level fluctuates throughout the year, making it more difficult for beavers to maintain and regulate stable flow. Second, coastal habitats are much more out in the open compared to inland habitats, which provide better concealment due to surrounding dense riparian vegetation. Both factors cause beavers to be more easily noticed by predators, as lower reservoir water levels may also help to expose a beaver colony. As a result, beavers prefer the peninsula’s more concealed inland habitats.

A lower amount of grass cover, as well as an abundance of preferred understory vegetation within the understory also was positively associated with preferred beaver habitats. Explanations for these two trends are relatively straightforward. Areas dominated by grass offer less food and cover to beavers and are, therefore, a less preferred habitat. Moreover, Jenkins (1981) found that beavers show a clear preference for cutting and eating trees of smaller dbh and tend to avoid trees of larger diameter, which are more difficult to fell. Thus, the increased likelihood of beaver colonization of habitats containing a high abundance of smaller woody vegetation within the understory likely reflects this phenomenon.

Although some previous studies have concluded that vegetative variables added little explanatory value to beaver habitat models (Beier and Barret, 1987; Suzuki and McComb, 1998), the results from this study seem to suggest that local vegetation structure can be used as an excellent indicator of preferred beaver habitat. However, the vegetative trends detected in this study are initially counterintuitive, but make sense after some thought. Results from the correlation and MLR analyses show that areas with high beaver activity tend to have high coniferous tree cover, which
consist of non-preferred species, and low deciduous tree, shrub, and Cornus spp. cover, which are preferred by beaver. The discriminant analysis also found the presence of occasionally preferred tree species to be a far better identifier of habitat quality than the presence of preferred tree species. However, it should be noted that beavers do in fact cut, eat, and use conifers when necessary, but usually as an alternate option behind more preferred vegetation. Still, these results are surprising because, if a relationship between vegetation cover and habitat quality exists at all, it would be expected that the presence of preferred species would be positively correlated. These results display the exactly opposite trend. These unexpected relationships in vegetation cover (Table 6.1), can likely be explained precisely as a result of beaver food preferences.

**Table 6.1:** Vegetation-Cover Dynamics Associated with Abundant Beaver Colonization

<table>
<thead>
<tr>
<th>Presence</th>
<th>Preferred Species</th>
<th>Relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coniferous</td>
<td>No</td>
<td>(+)</td>
</tr>
<tr>
<td>Deciduous/Shrub</td>
<td>Yes</td>
<td>(-)</td>
</tr>
<tr>
<td><em>Cornus</em> spp.</td>
<td>Yes</td>
<td>(-)</td>
</tr>
</tbody>
</table>

Trends of decreased preferred species cover within highly preferred habitats are likely responses to beaver occupancy, rather than factors in which beavers respond to when selecting habitat. This is because beavers alter the species composition of riparian plant communities by removing preferred species and subsequently stimulating the growth of avoided species (Johnston and Naiman, 1990). Through decades of selective foraging, areas of high beaver activity are likely to be more devoid of preferred species, leaving non-preferred species, such as coniferous trees, in
greater numbers. Therefore, areas that have an abnormal amount of coniferous tree cover (compared with the rest of the Prescott Peninsula) are more likely to indicate preferred beaver habitat. Of course, these vegetative relationships can only hold true in regions that have had an established, highly dense beaver population for quite some time.

This explanation can be empirically verified by comparing the surrounding vegetation structure of habitats that were newly colonized in 2012 with the vegetation structure of quality habitats, which have been continually occupied by beavers for the past several decades (Tables 6.2 and 6.3). Table 6.2 shows the direct comparison in site longevity and MLR performance between the 3 least successful colonized habitats in 2012 (all of which are new colonization events) and the 3 most successful colonized habitats (which are continuously occupied habitats).

Table 6.3 goes on to compare the average environmental variables within newly colonized habitats and continually occupied habitats. In particular, a ratio of the average environmental variables for each habitat type has been calculated to create an index with which to directly compare between the two habitat types (displayed in the 2nd column of Table 6.3). These ratio values show that the 3 newly colonized habitats have, on average, 10.19% less coniferous tree cover than the 3 most continually occupied habitats. These newly colonized habitats also contain 8.98% more deciduous/shrub cover and 11.98% less Cornus spp. than habitats that are continually occupied by beavers. Overall, results from Table 6.2 and 6.3 support the conclusion that the observed trends between vegetative structure and habitat preference are a result of long-term selective foraging by beavers.
Table 6.2: Comparison of Site Longevity and MLR Model Performance between Newly and Continually Colonized Habitats

<table>
<thead>
<tr>
<th>Colony ID</th>
<th>Newly Colonized Habitats</th>
<th>Continually Occupied Habitats</th>
</tr>
</thead>
<tbody>
<tr>
<td>% Occupied Since 1988</td>
<td>4 1 5</td>
<td>12 17 3</td>
</tr>
<tr>
<td>MLR Model Probability (%)</td>
<td>2.16 2.70 12.07</td>
<td>97.15 99.78 100.0</td>
</tr>
</tbody>
</table>

The local depletion of deciduous/shrub species within the most heavily utilized beaver habitats indicates that selective beaver foraging likely has a strong negative impact on these species, though past and present grazing by deer may also be a contributing factor. Similarly, the abnormally high abundance in local coniferous tree cover within newly colonized habitats is likely a vegetative artifact left from generations of prior beaver avoidance of non-preferred species. On the other hand, continually occupied habitats on average have 11.98% more Cornus spp. than newly colonize habitats. These results indicate that, unlike most other plant species, Cornus spp. are able to sustainably regenerate themselves while simultaneously being heavily foraged by beavers. In fact, Zhu et al. (2010) found that the regenerated sapling density of Cornus controversa within more intensely thinned stands of forest was two times greater than densities in less intensely thinned stands. The authors attribute their findings to the seed dispersal and shade tolerant characteristics of Cornus spp. during its early establishment. In addition to quickly recovering from anthropogenic thinning, these two regenerative characteristics certainly must aid Cornus spp. in prolific sapling regeneration from beaver herbivory, ultimately supporting this thesis’ results. Therefore, the presence of a large Cornus spp. population is likely indicative of a quality habitat which can be recurrently colonized by beavers on a semi-sustainable basis.
Table 6.3: Comparison of Environmental Variables between Newly and Continually Colonized Habitats

<table>
<thead>
<tr>
<th>Habitat Variable</th>
<th>Index</th>
<th>Comparison between New and Recurrent Habitats</th>
</tr>
</thead>
<tbody>
<tr>
<td>Avg. Steam Slope (°)</td>
<td>0.5645</td>
<td>↑ Stream Steepness (43.55%)</td>
</tr>
<tr>
<td>Coniferous Cover (%)</td>
<td>1.1019</td>
<td>↓ Coniferous Cover (-10.19%)</td>
</tr>
<tr>
<td>Deciduous/Shrub Cover (%)</td>
<td>0.9102</td>
<td>↑ Deciduous/Shrub Cover (8.98%)</td>
</tr>
<tr>
<td>Cornus spp. Cover (%)</td>
<td>1.1198</td>
<td>↓ Cornus spp. Cover (-11.98%)</td>
</tr>
<tr>
<td>Avg. Distance From Reservoir (m)</td>
<td>1.6171</td>
<td>↓ Avg. Distance between Habitat and Reservoir (-61.71%)</td>
</tr>
<tr>
<td>Avg. NDVI Value</td>
<td>0.9160</td>
<td>↑ Avg. NDVI Values (8.40%)</td>
</tr>
</tbody>
</table>

Note: 2nd Column values were calculated by dividing average variables from recurrently colonized habitats by average values from newly colonized habitats. Percent values in parentheses indicate the magnitude of the difference between the two habitat types, while the arrows indicate the direction of the trend.

Simply put, vegetative communities within continually occupied beaver habitats have a distinct species signature due to generations of selective beaver foraging. Therefore, it can be reasonably determined that habitats which exhibit this vegetative signature, in addition to possessing the necessary geomorphologic conditions, can sustainably harbor a beaver population over a long period of time. Such vegetative attributes can be easily detected when investigating ecosystems at the landscape scale. Because the observed differences in vegetative communities between preferred habitats and non-preferred habitats were the result of alteration by beaver, they can be utilized as good predictors of potentially active sites by the MLR model.

6.2 Insights gained from MLR Model

Based on 11 environmental variables investigated in this analysis, the MLR model has been developed to successfully evaluate the probability that stream and
pond habitats throughout a landscape are occupied by an active beaver colony. The MLR model is additionally capable of identifying habitats currently unoccupied by beavers that are likely to be colonized in the near future. Of course, this MLR function performs better when evaluating certain types of habitats over others, as is the nature of most models. In general, the MLR model was very successful at predicting habitats which are frequently colonized by beavers and exhibit those environmental characteristics which best modulate beaver survival on a semi-sustainable basis. Additionally, the MLR model was equally successful at predicting poor quality habitats which are rarely, if ever, colonized by beavers and possess those environmental characteristics which inhibit beaver survival. However, the MLR model struggled most at predicting habitats of marginal quality which are capable of harboring a beaver colony for a short period of time before becoming inhospitable soon thereafter.

Interestingly, studies by Nolet and Rosell (1974), Howard and Larson (1985), and Frantisek et al. (2010) discovered that expanding beaver populations exhibit different dispersal behavior than populations which have reached their home range’s carrying capacity. During the initial phase of expansion, they argue, beavers establish their colonies in optimal habitat first, before they occupy marginal habitats (Bushur and Lyons, 1999). During the later phase of population stability, all optimal sites become occupied and defended, forcing beavers to colonize sites in suboptimal/marginal habitats. Similarly, beaver ponds impounded first tended to have the greatest longevity within an expanding population (Howard and Larson, 1985). Ultimately, this habitat saturation hypothesis predicts that dispersers will be less successful in high-density populations.
As mentioned before, the Prescott beaver population reached the peninsula’s carrying capacity in 1988 and has stayed there ever since (refer back to Figure 3.5), though the total number of colonies have sometimes grown or shrunk slightly from year to year. Surprisingly, the interior Prescott beaver population has increased by four colonies in the past year, growing from 14 colonies in 2011 to 18 colonies in 2012. Because the number of active colonies has held steady at around 13.7 colonies since 1988, a population of 18 colonies is unusually high for recent times. In fact, the Prescott beaver population has exceeded this many colonies only once (2001) since 1988. As a result of this population growth, the number of dispersing beavers in search of a new habitat to colonize increased in 2012; however, their ability to find high quality, vacant habitat within the peninsula was likely compromised, as most if not all of the quality habitats that can be occupied on a long-term basis were already taken. In total, there were eight instances of beaver relocation into habitats that were previously unoccupied in 2011. Of these eight relocation events, three of them occurred in habitats that had very rarely, if ever, been utilized previously. As a result, the MLR model evaluated these habitats to be of poor quality when they were clearly of marginal quality, ultimately failing to predict all 3 of these extremely rare relocation events (see Table 6.2). The mapped MLR model results of the area surrounding colony #3 (a typical continually occupied habitat) are shown in Figure 6.1, while Figure 6.2 shows these mapped results over the area surrounding colony #4 (a typical newly colonized habitat). It should be noted that the purple dots in Figures 6.1 and 6.2 represent a year of occupation and not the actual focal point of a lodge. Colony ID numbers are provided in Table 6.2.
The large number of marginal habitats colonized in 2012 that was misclassified as poor quality habitat by the MLR model suggests that many of these newly colonized habitats are fundamentally different from quality habitats. To empirically verify this explanation, the environmental variables of habitats that were newly colonized in 2012 have been directly compared with those of quality habitats, which have been continually occupied by beavers for the past several decades (Tables 6.2 and 6.3). Compared with historically active beaver habitats, colonies in newly colonized habitats were, on average, located along 43.55% steeper-gradient streams and were 61.71% closer to the Quabbin Reservoir shoreline (Table 6.3). Because these two physical variables were strongly correlated to colony site longevity (see Section 6.1), it has been hypothesized that newly colonized habitats by dispersing beavers in 2012 were, on average, of poor overall quality and will be unable to sustain active occupation for more than a few years. Howard and Larson (1985) also found stream gradient to have a significant effect on colony site longevity, further supporting the hypothesis that colonization events within newly colonized habitats are likely to be short lived. Overall, the MLR model was most successful at predicting quality habitats that have been occupied by beavers on a relatively sustainable basis, but was less successful at predicting colonization events in more marginal, less frequently utilized habitats. Though these marginal habitats may meet the necessary ecological conditions to temporarily harbor beavers, they are often only occupied for a year or two due to local ecological pressures and will probably never support colonies on a sustainable basis. Thus, (1) the MLR model is a useful predictor of good and poor quality habitat; and (2) has the ability to indicate areas of short-lived beaver
colonization for those marginal habitats where the MLR model failed to identify a recolonization event.
Figure 6.1: Results of MLR Model: Colony #3 (Continually Occupied Habitat)
Figure 6.2: Results of MLR Model: Colony #4 (Newly Colonized Habitat)
6.3 Insights gained from DA model

The discriminant analysis found several significant beaver-habitat trends from the 20 survey plots (discussed in Section 5.3). Most notably, occasionally preferred tree species were found to be a far better identifier of habitat quality than preferred species. Lyons (1995) similarly observed within the Prescott Peninsula that beavers occupy a site until preferred food species are exhausted and leave stands of less preferred species behind, helping to explain the mechanism behind this relationship. Additionally, the DA analysis found an abundance of vegetation within the understory to be a great identifier of preferred beaver habitat. Beier and Barret (1987) also discovered this relationship within their study’s surveyed active dam sites, attributing the abundance of herbaceous vegetation to the removal of tree and shrub cover. Such observed relationships further validate this paper’s hypothesis (explained in Section 6.1) that decades of selective foraging likely creates a distinct signature within the local vegetative community of continually occupied habitats.

Due to the magnitude of such ecological relationships, the DA model proved to be quite successful at categorically evaluating beaver habitat preference based on local riparian characteristics. Overall, 90% of the total plots surveyed in this study were correctly classified into their respective habitat quality groups. Although the two discriminant functions performed slightly better when evaluating preferred and occasionally preferred habitat over non-preferred (as noted in Section 5.3), the classification accuracy for all 3 habitat quality groups was still satisfactory. In spite of such successful classification results by the DA functions, there is still one case of misclassification that requires further investigation (i.e. Plot #8 in Table 5.10).

Because plot #8 was surveyed adjacent to a pond habitat that had historically been frequently colonized by beavers, it met the criteria to be assigned into the
preferred habitat group and was, therefore, considered by the model as a quality beaver habitat. The model predicted this plot to be of poor quality based on the delineations of the two discriminant functions. Due to such a large discrepancy between the assigned habitat class and the predicted habitat class by the model, a closer inspection of this plot was needed. Upon visiting the site, there was substantial evidence of heavy amounts of beaver foraging of white pine, which is a non-preferred tree species by beavers (Figures 6.3 and 6.4). This is likely a sign of desperation, as beavers would likely only forage white pine as a last resort before starvation. Results from the 2012 census proved the DA model to be correct, as the colony that occupied the area in 2011 had either relocated or perished. Clearly, the DA model does an excellent job at assessing the degree of beaver habitation at a local scale.
Figure 6.3: Evidence of Pine Tree Foraging at Plot #8 by Beavers
6.4 Implications for Future Management of Beavers

As an ecosystem engineer, the beaver’s widespread ability to influence habitats and species can create important management opportunities. However, it is the beaver’s profound ability to cause significant damage to human property and water resources that justifies most management actions, especially in areas with both high beaver and human densities. Unfortunately, many areas throughout the Northeast are experiencing increases in both human and beaver population densities (Jackson and Decker, 2004). As a result, human-beaver conflicts are likely to increase, necessitating management of the species. Because nuisance beaver control management requires spatially significant information, ecological models capable of

Figure 6.4: Evidence of Pine Tree Foraging at Plot #8 by Beavers
assessing suitable and unsuitable habitats over a continuous landscape will be important going forward.

While detailed studies on foraging ecology are available (see Section 2.4), there currently are limited methods to quantify and map the degree of beaver habitat suitability, both at the local and landscape scale. The two ecological models presented in this study have the ability to function in beaver management by assessing habitat suitability. The ecological parameters selected for the two models were either selected from previous literature (outlined in Chapters 2 and 3), or were derived from field measurements and common geospatial datasets, such as a DEM and remotely sensed imagery.

Based on the environmental variables investigated in this study, the MLR model can be used to successfully evaluate the probability that stream habitats throughout a landscape are occupied by an active beaver colony. Alternatively, the DA model can be used to successfully classify local riparian habitats as either preferred, occasionally preferred, or not preferred by beavers. The MLR and discriminant function models can be utilized independently, but are best applied in tandem to streams of the Chicopee River drainage basin (where the models were developed); nevertheless, these models should be applicable for other streams in the Northeast region as long as geomorphology and hydrology are similar. Based on the beaver population dynamics observed on the Prescott Peninsula, these classification models should apply to other stream and pond habitats within the northeastern United States that have beaver populations at or near carrying capacity.

As mentioned before, flooding as a result of beaver dam building activity can pollute drinking water and cause damage to roads and domestic property. The
physical removal of these problem dams is often ineffective since dams at active sites are quickly rebuilt (Jenson et al., 1999). To complicate matters, kill trapping practices are now prohibited in Massachusetts due to the 1996 Wildlife Protection Act. Therefore, the most successful method for controlling water levels in flooded areas is the installation of a water flow device in a pond for drainage purposes. Wildlife managers can use these models to identify and inventory potential locations along the various stream networks throughout the Northeast region that could benefit from such flow device installations. Probabilistic maps of beaver presence produced by the MLR model can also play a major role in multiple land-use regions where a decision must be made as to which resource(s) should receive priority for preventative actions on nuisance beavers (Jenson et al., 1999). Ultimately, the utilization of the MLR model and discriminant analyses functions as tools can help land managers guide and modify beaver management strategies to be proactive and adaptive to the ever-evolving land-use dynamics of beavers.

6.5 Avenues for Future Research.

Insights gained from this study can provide a comprehensive understanding of land-use/landcover dynamics caused by beaver activity. The two ecological models presented in this paper can then utilize these empirically derived beaver-habitat relationships to systematically predict which habitats are most likely to be colonized by beaver at both the local and landscape scales. Land planners and managers, who have long been concerned with alterations and disturbances by beavers, can then use these models as tools, through the medium of a GIS, to help mitigate instances of nuisance beaver. Other modifications and avenues of related future research may:
1. Explore the role that *Cornus* spp. plays in continually occupied beaver habitats, specifically related to its regenerative properties.

2. Further explore the vegetation relationships that were found in this study within other study areas. Specifically, do these initially counterintuitive vegetative relationships hold true in other Northeastern regions within the United States which harbor beaver populations that have achieved carrying capacity?

3. Investigate the temporal relationships between habitat quality and site longevity within a newly colonized habitat by utilizing annually captured high-resolution remotely sensed imagery.

4. Evaluate road networks and LULC maps to find intersected areas of human property and highly preferred beaver habitats (as predicted by the MLR model) to identify likely locations of nuisance beaver.

These actions will increase the accuracy, precision and application of the two ecological models, which may allow land managers to better understand the ecological mechanisms that dictate the habitat selection behaviors of beavers and ultimately enhance their ability to predict and proactively mitigate instances of nuisance beaver.
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Appendix
PERMISSION LETTER

Alex,

I’d be happy to email you the Prescott Peninsula beaver survey data. The methodology is simple: all potential habitat is surveyed completely each fall (around November) and all active sites are documented. Activity is determined by the presence of active sign including: a food cache (established that year), mud on the lodge, well maintained dam with mud, etc., recent cuttings, or actual beaver sightings. The location of the active site is indicated with a GPS or estimated onto a paper map. This is typically the location of the lodge. Some notes on the food cache may be recorded.

The latest report is attached.

Dan

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