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Abstract:

The North American beaver (*Castor canadensis*) represents a quintessential example of an "ecosystem engineer." Yet the species' landscape-scale impacts on hydrology, geomorphology, and ecosystem ecology are not uniformly distributed through landscapes or time. Understanding beaver lodge site selection and lodge fidelity through time can help to predict where the greatest effects of beaver activity may occur. In this research project, I seek to understand the relationships between beaver habitat suitability, the habitat variables that currently define suitable areas, and lodge occupancy over time. Using Geographic Information Systems (GIS) to model habitat suitability, I use hydrologic, vegetative, and physiographic variables to determine the relationship between traditionally conceived suitable factors and their influence on both lodge site suitability and lodge occupancy at my study site in the Huntington Wildlife Forest (HWF) in the Central Adirondacks of New York state. The results confirm beaver habitat preferences for stable water sources, herbaceous wetland vegetation, and shallow topographic slopes. These habitat variables, however, did not influence occupancy at the lodge-scale over time. Furthermore, three different habitat suitability models showed no relationship between site suitability and lodge occupancy, thereby revealing that long-term occupancy is not a significant consideration when beaver select lodge sites. Together, this project demonstrates that factors promoting suitability for beaver settlement do not correspond to suitability for long-term lodge occupancy.

A GIS SUITABILITY MODEL EVALUATING HABITAT CHARACTERISTICS INFLUENCING BEAVER (*CASTOR CANADENSIS*) LODGE SITE SELECTION AND LODGE OCCUPANCY IN CENTRAL ADIRONDACKS, NEW YORK

by

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Thesis

Submitted in partial fulfillment of the requirements for the degree of

Master of Arts in Geography.

Syracuse University

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It takes a colony to build a lodge, but it takes a colony and a half to complete a thesis. Thank you to my advisor, Dr. Jacob Bendix, for your continued patience and suggestions through every winding turn of this thesis. Thank you for your encouragement, mentorship, and comic strips over the last several years. Thank you to my committee members, Dr. Jane Read and Ms. Stacy McNulty, for your flexibility, advice, and comments. Thank you to my friends and roommates for your countless hours of support, laughter, and necessary distractions. Your friendships have meant the world to me. Thank you to my family—Mom, Dad, David, Danielle, and Haleena—for everything that I am and everything that I can be. Your endless love and support never goes unappreciated, and I love you all the more for it. This thesis is the product of everyone's unwavering belief in me and I could not have done it without you all. Here's to doing the dam thing!

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Introduction:

The North American beaver (*Castor canadensis*) represents a quintessential example of an "ecosystem engineer." The species' natural instinct to improve an ecosystem's suitability for its occupation drastically alters the ecology and hydrogeomorphology at landscape and local scales. Beaver fell riparian trees, then interlay the wood, branches, and leaves with mud and stone to impound low-order, low-gradient streams (Woo and Waddington 1990; Pollock et al. 2014; Naiman et al. 1986). The dams impede stream flow and promote upstream flooding to form ponds and wetlands. Ponds serve primarily as protection against predation, serving as a buffer and concealment for lodge entrances and food caches. The ponds—expanded across floodplains and termed beaver wetlands or meadows—serve secondarily as food and building material transportation networks and additional security during foraging activities (Zurowski 1992). If channel conditions are optimal and preferred food remains available, beaver colonies may continue to occupy individual sites for many years, continuously or intermittently. The project here seeks to explore this relationship further by examining the habitat conditions that promote site occupancy through time.

Understanding of the environmental components that promote successful beaver occupation is important because beaver occupation in an area, specifically through engineering activities, alters ecosystem structure and function geomorphically, hydrologically, and ecologically. Studies (e.g. Butler and Malanson 1995, Meentemeyer and Butler 1999, Bigler et al. 2001) suggest that by reducing stream flow, beaver impoundments cause sediment deposition and accumulation within river channels. Sediment accumulation over time may restore incised streams and aggrade streambeds (Pollock et al. 2007, Polvi and Wohl 2012) or alter the longitudinal connectivity of river systems by increasing channel complexity or heterogeneity, thereby affecting channel and landscape morphology. Relatedly, beaver and their dams influence the hydrology within an area by improving lateral connectivity between river channels and their surrounding floodplains as well as improving vertical connectivity between ground and surface waters through inundation and infiltration, potentially raising water table levels in some areas (Wade et al. 2020, Majerova et al. 2015). Inundation may also alter nutrient cycling within aquatic systems, particularly nitrogen availability. Poor aeration resulting from inundation decreases oxidized nitrogen (NO3) levels while increasing reduced nitrogen (NH4) levels, leading to anaerobic conditions (Naiman et al. 1988).

Ecologically, beaver-mediated ponds and wetlands create new habitat for fish, amphibian, avian, invertebrate, and macrophyte species (Stringer and Gaywood 2015, Wright et al. 2002, Alza 2014). For riparian vegetation, however, beaver presence can reduce stand scale basal area and alter species composition. Beaver impoundment may serve as a disturbance agent wherein the inundation instigated from beaver impoundments could not only reduce terrestrial habitat for riparian species, but could also present a constant stress that leads to die-off for particular species (Bendix and Stella 2013). The inundation promotes the proliferation of water-tolerant species such as willow (*Salix spp.*) and aspen (*Populus spp.*) that beaver prefer for consumption.

Beaver foraging also affects terrestrial species composition, distribution, and structure. As central place foragers, beaver typically forage within 30-40 meters from their pond before returning to their central lodge, although foraging distances of up to 100 and even 200 meters have been reported in the literature (Allen 1983, Donkor and Fryxell 2000). Described as “picky generalists” (Gerwing et al. 2013) or “generalist herbivores” (Rosell et al. 2005), beaver will feed on the bark, shoots, and leaves of woody plants in addition to terrestrial herbaceous vegetation and aquatic macrophytes. Though beaver tend to prefer aquatic or herbaceous vegetation all year round when available, they also exhibit species preferences for riparian hardwoods species like aspen (*Populus tremuloides*), willow (*Salix spp.*), and cottonwood (*Populus deltoides*) when and where available; beaver will typically avoid coniferous species due to their poor nutrient load (Allen 1983, Rosell et al. 2005). This specialized herbivory can often deplete particular species—decreases of up to 40% of above ground biomass after 6 years of foraging—thereby increasing the coverage of less palatable species and decreasing the density of palatable species (Naiman et al. 1988, Johnston and Naiman 1990, Rosell et al. 2005).

As central place foragers, several studies (Gallant et al. 2004, Gerwing et al. 2013, Mahoney and Stella 2020) suggest that there is a negative relationship between stem size and species forage probability and distance from water's edge. Beaver exhibit stem size class preferences in addition to species preference and become more selective in both stem size and species with increasing distance from the central place. Stem class selectivity can impact vegetation structure, particularly in relation to canopy closure and light availability within foraging ranges, which can have down-scale impacts on early successional communities (Mahoney and Stella 2020).

The combined effects of beaver described above are not uniformly distributed throughout landscapes. Although landscape-scale changes—defined here on the scale of hundreds of meters to kilometers—have been observed, most consequences of beaver presence and activity are localized to their specific ponds and their upland foraging corridors on the order of tens of meters. Furthermore, these consequences are also not uniformly distributed throughout time. Greater ecosystem changes can be seen in areas where beaver activity persists for longer periods. Several studies (Slough and Sadlier 1977, Allen 1983, Suzuki and McComb 1998, Ritter et al.

2020) document the habitat preferences of beaver, particularly the habitat variables necessary to make an area suitable for beaver colonization; these details will be touched upon in greater detail below. Less understood, however, is how beaver habitat preferences influence site suitability in relation to lodge occupancy and longevity. Understanding site selectivity in relation to occupancy may challenge our traditional notions of how we define "preferable" or "suitable" beaver habitat to include parameters of lodge fidelity and occupancy through time.

Research Objectives and Questions:

In this research project, I seek to understand the relationships between beaver habitat suitability, the habitat variables that currently define suitable areas, and lodge occupancy over time. The unit of analysis for occupancy in this project is the lodge rather than the colony, pond, or territory. The lodge is a unique unit of analysis among beaver habitat suitability studies, but allows us to expand the qualifications for suitable areas while providing new insights on occupancy at a finer scale than the colony or territory. In doing so, I attempt to broaden our understanding of the role long-term lodge fidelity and occupancy could and should play in what we consider suitable habitat.

Using Geographic Information Systems (GIS) to model habitat suitability, I use hydrologic, vegetative, and physiographic variables to determine the relationship between traditionally conceived suitability factors and their influence on both site suitability and lodge occupancy at my study site in the Huntington Wildlife Forest (HWF) in the Central Adirondacks of New York state. In doing so, I address the following research questions:

1. What habitat factors—hydrologic, vegetative, or physiographic—most influence lodge occupancy?
2. Are the lodges on more preferable or suitable sites occupied longer?

3. How does beaver lodge site selection influence lodge occupancy?

Research Question 1 examines what conditions at a site are more important or influential in the relationship between the lodge site and its occupancy over time. In particular, I ask what variables, if any, better predict long-term occupancy for a lodge. The relative importance of each factor, in addition to their importance as described in the literature, helps frame suitability for Research Question 2. Research Question 2 is focused on the relationship between habitat suitability and lodge occupancy. I use a GIS habitat suitability model to see whether habitat preferences for certain characteristics correspond to longer lodge occupancy. This question helps to see what role, if any, long-term lodge occupancy should play in evaluating how we define suitable locations. The combined results of Research Questions 1 and 2 provide the material to answer Research Question 3 about the overall relationship between lodge site selection and lodge occupancy and the general decision process in both selecting sites for lodges and remaining or continuing to return to particular sites. Research Question 3 thus forms the broader framework for this project, and answering this question is the primary objective of this research. Intuitively, one would expect to see a positive relationship or association between lodge site and occupancy. In particular, locations with preferred habitat characteristics seem likely to be occupied for greater amounts of time with fewer instances of abandonment (Mumma et al. 2018). As described in further detail below, lodges in areas with more consistent water sources, gentle gradients and/or slopes, and dominant coverage of preferred vegetation like herbaceous wetlands or deciduous trees should be occupied longer.

Pertinent Literature:

GIS Habitat Suitability Modeling:

Habitat suitability models (HSM) and modeling stem from an extensive history of research examining the spatial distribution of species. Also known as species distribution models, HSMs use various techniques to predict the likely spatial distributions for a species based on known habitat variables or indices (Barella et al. 2021). Such indices develop from field observations of the environmental variables that directly or indirectly influence the presence of a species within a particular area (Guisan and Thuiller 2005).

Geographic Information Systems (GIS) is a readily applicable tool aptly suited to analyze and model the inherently spatial aspects of habitat suitability. GIS use is prominent in species distribution and habitat suitability modeling for a variety of taxa, including avian species (Lauver et al. 2002), mammalian species (Traill and Bigalke 2006, Imam et al. 2009), reptilian species (Dujsebayeva et al. 2019, Nekrasova et al. 2021), and plant species (Vargas et al. 2004, Torres-Meza et al. 2009, Rajan and Jayalakshmi 2017). Additionally, GIS and habitat modeling has extensive use in ecological management and conservation more broadly (e.g. Store and Jokimaki 2003, Liu et al. 2013).

In GIS model development, environmental predictors or habitat requirements are multiplied by coefficients representing their relative weight within the model (Maringer and Slotta-Bachmayr 2006). These coefficients, obtained from extensive surveys and field observations, thus determine how much a given factor influences habitat suitability; higher coefficients, or greater weights, provide more influence over suitability. HSMs, particularly those created with GIS, provide a general framework for how to develop a suitability model for beaver in HWF. The relative weights for beaver habitat variables are discussed below.

Beaver Natural History:

Beaver are a large, semi-aquatic rodent with a distribution across much of North America. Their habitat ranges across subtropical to semi-arid to subarctic areas (Rosell et al. 2005). Beaver live within a colony, defined as a group occupying a pond or common stretch of stream, utilizing a shared food supply, and maintaining a common dam or dams (Bradt 1938). The colony size varies across time and space, but typically ranges from two to eleven individuals (McTaggart and Nelson 2003). Average colony size was found to be 5.1 by Bradt (1938) in Michigan, 5.6 $\mp$ 2.5 by McTaggart and Nelson (2003) in central Illinois, and 5.2 $\mp$ 1.4 by Rosell & Parker (1995) in North America broadly. A colony typically consists of an adult breeding pair, the previous year's juveniles, and the current year's kits. Juveniles will often disperse from their birth colony at the age of two to form new colonies (Dieter and McCabe 1989). During dispersal, young beaver may occupy transient habitat temporarily, including territories previously vacated by others (Slough and Sadlier 1977). Colonies exhibit territoriality over occupied areas using scent markings so that colonies in similar areas do not overlap one another (Bradt 1938, Müller-Schwarze and Schulte 1999).

Within a colony's territory, one or more lodges may be constructed. In some instances, a colony will not build a lodge, but rather dig a bank burrow or a series of burrows in stable banks (Bradt 1938). Like burrows, lodges can be constructed against a bank but are generally surrounded by water for concealment and protection against predation. Lodges are the central shelter for means of escape, resting, thermal cover and insulation against weather elements, and reproductive activity (Jenkins and Busher 1979, Allen 1983). A colony may construct multiple new lodges within colonization of its site and subsequently rotate between a set of lodges over time. Colonies within a site usually prefer to reoccupy older, previously used lodges and will repair older lodges rather than build new ones. New lodge construction typically follows access to a new food source (Slough and Sadlier 1977).

Beaver colony activity and site occupancy varies temporally and regionally. A study by Scrafford et al. (2018) in Yellowstone National Park found colonies were active for 8.8 years on average and inactive for 4 years in main channels whereas colonies on secondary channels were active 12.9 years on average and inactive 2.3 years. Hyvonen and Nummi (2008) found average site occupation to be 2.6 years with a range of 1 to 9 years in southern Finland. Recolonization of sites occurred after 9 years on average following initial abandonment, with reoccupation ranging from 6 to 13 years after abandonment. These values diverge from those presented by Howard and Larson (1985) who found several instances of colonies who reoccupied sites and lodges after only 1 or 2 years of abandonment in Massachusetts. Harrison (2011) calculated average site occupancy in HWF to be 11.5 years across 14 sites. Using site tenancy—calculated as total number of active years/number of active periods—Harrison found tenancy values to range from 1 to 30, with an average of 5.4 years. A study from Hood (2019) found ponds in Alberta were occupied an average of 3.6 years and were unoccupied or inactive for 7.4 years on average. Many of these studies and others (Ritter et al. 2020) found colonies in less suitable or less optimal habitats to be more dynamic wherein the colonies are more likely to abandon sites and have lower occupancy rates. Ritter et al. (2020) argued that when habitat is less stable, the site is more difficult to occupy longer.

General habitat requirements for beaver are well understood within the literature. Most broadly, habitat requirements fall into three major categories that influence new settlement locations: hydrologic, vegetation, and physiographic. The suitability within each category and their relationships to site colonization and occupancy are described below.

Beaver Habitat Preferences: Hydrology

As semi-aquatic mammals, beaver require a permanent supply of water and consistent water levels year-round. Deep water levels in larger lakes or rivers or ephemeral streams with seasonal fluctuations that cannot be controlled by beaver may be partially or entirely unsuitable for beaver (Allen 1983). Yet Touihri et al. (2018) noted that quality habitat, especially for lodge construction, does not necessarily require dam construction so that stable water sources that do not necessitate beaver mediation to maintain stability may still be suitable sites.

In examining different types of water bodies, one study found that 50% of 28 colonies were in riverine habitat, 32% were in lacustrine habitat, and 18% were in drainage ditches (McTaggart and Nelson 2003). The same study found that although the number of colonies within these habitats differed, the colony size between the three did not significantly differ, though riverine and lacustrine colonies averaged more individuals per colony than drainages (5.6, 6.3, 4.0 respectively). King et al. (1998) discovered similar frequencies for lodges with 49.3% of lodges located in open water and 30.7% located in edge habitats. Touihri et al. (2018) argued that between water habitats lakes are more a transitional or temporary habitat compared to streams as the superior habitat. This argument is in keeping with the colony frequency by habitat found by McTaggart and Nelson, but less so with the findings of King et al.

In examining water body habitat in relation to settlement and occupancy, Holland et al. (2019) described beaver as more likely to occupy sites with increased water availability, such as areas with larger streams. Bergman et al. (2018) support this claim, finding that lakes, with greater water availability, were occupied more persistently over time compared to rivers or wetlands. Another study found that the probability of settlement sharply declines with the proportion of stream in wetland waterbody type (Ritter et al. 2020). As water enters a wetland, the availability of water may decrease, making the area less suitable for settlement. One study found four variables—including gradient, soil drainage, stream width, and watershed size—associated with water reliability helped explain the variation between short-term occupancy (<5 years) and long-term occupancy (≥5 years) (Howard and Larson 1985). Another variable positively associated with occupancy was pond area according to Hood (2019). As pond area increases, its stability and water reliability also increases, potentially explaining its positive association with occupancy. Pond area, however, did not explain variation in length of occupancy. Touihri et al. (2018), on the other hand, found hydrologic variables such as water body type to be less important in settlement and occupancy than other habitat factors.

Beaver Habitat Preferences: Vegetation

Beaver are picky generalist or generalist herbivores in that organisms will feed on the bark, shoots, and leaves of woody vegetation, as well as terrestrial herbaceous vegetation, forbs, ferns, and aquatic macrophytes (Rosell et al. 2005). Though aquatic and terrestrial herbaceous vegetation may constitute the greatest volume of beaver diet—and often be preferred (Lapointe St. Pierre et al. 2017)—Boyce (1981) contends that the biomass of herbaceous vegetation in an area may not limit the ability of an area to support beaver whereas woody plants may be limiting (Allen 1983). Beaver modifications to landscapes promote the rapid growth of herbaceous vegetation in beaver's wetlands, whereas altering the biomass of woody tree species takes more time given the greater (re)generation period of woody stems or branches (Brenner 1962).

Within woody tree species, beaver exhibit selective foraging. Rosell et al. (2005) described quaking aspen (*Populus tremuloides*), poplar (*Populus spp.*), willow (*Salix spp.*), alder (*Alnus spp.*), ash (*Fraxinus spp.*), birch (*Betula spp.*), maple (*Acer spp.*), and some oak (*Quercus spp.*) as preferred species due to their digestibility and high energy yield. Within the Adirondack region of New York state, Mahoney and Stella (2020) found preferences for speckled alder (*Alnus incana*), red maple (*Acer rubrum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*), as well as coniferous species like balsam fir (*Abies balsamea*) and red spruce (*Picea rubens*). The penchant for the latter two species, however, more likely corresponds to beaver's size selectivity in foraging as balsam fir and red spruce produce more branches in the preferred 2-10 centimeter size range. While beaver will forage on conifer species, conifers' poor digestibility and lower energy output make them less preferable than deciduous woody species (Gallant et al. 2004). Other species preferences for beaver that have been observed within HWF include striped maple (*Acer pennsylvanicum*), American beech (*Fagus grandifolia*), white ash (*Fraxinus americana*), and yellow birch (*Betula alleghaniensis*) (Harrison 2011). Naiman et al. (1988) noted that beaver annually cut nearly a metric ton of woody stems and branches within 100 meters of their pond.

All foraging by beaver occurs within a limited radius surrounding the central lodge or pond. Central place foraging theory describes how organisms, like beaver, will forage at various distances from a fixed location—the pond—to return and store food in the fixed location (Jenkins 1980). The theory also suggests that central place foragers seek to "maximize net rates of energy intake per unit feeding time" (Jenkins 1980, 740) and will modify foraging accordingly (Fryxell 1992). Therefore, we would expect to see greater concentration of foraging near the central place and a greater degree of selectivity with increasing distance from the fixed location (Jenkins 1980, Fryxell 1992). Such is the case with beaver, who cut more selectively in both size and species with increasing distance from the lodge and pond. Gerwing et al. (2013) reported a negative relationship between distance and stem forage probability, indicating beaver reduce foraging with greater distance. A study from Gallant et al. (2004) found a negative coefficient between distance and stem diameter, suggesting beaver selected bigger stems further from the pond. Raffel et al. (2009) supported both claims, finding beaver cut preferred species proportionally more compared to avoided species in addition to a significant positive interaction between distance from pond and stem size wherein larger stems were foraged further from lodge.

Though it is well understood that foraging changes with distance, there is some variance in the literature regarding the distance measurements themselves. One study recorded 50% of foraging occurring less than 10 meters from water's edge and less than 7% occurring more than 40 meters away (Donkor and Fryxell 2000). Several studies (Jenkins 1980, Suzuki and McComb 1998, King et al. 1998, Maringer and Slotta-Bachmayr 2006) used between 20-30 meters at the optimal foraging distance for beaver, with one study (Francis et al. 2017) extending optimal foraging up to 60 meters. Many other studies (Howard and Larson 1985, Naiman et al. 1988, Lapointe St. Pierre et al. 2017, Ritter et al. 2020) extended maximum beaver foraging distance to 100 meters from water, and foraging distances of up to 200 meters have been reported (Bradt 1938). Maximum foraging distance recorded at HWF was 85 meters according to Harrison (2011). Although distance exerts a selective pressure on beaver foraging habits, other factors such as beaver density, time since establishment for both plants and beaver colonies, predator activity, flood regimes, and other disturbance may impact foraging decisions as well (Gerwing et al. 2013, 84).

Many studies agree that vegetation variables may be important for dam and lodge construction during site colonization but may be less important in site suitability associated with long-term occupancy. One study made note that vegetation for food had the greatest effect on the number of colony sites on streams (Slough and Sadlier 1977). This distinction is reasonably intuitive in that areas with greater quantities of food can support more colonies and that colonies would choose areas with greater quantities of food species. However, Petro et al. (2018) and Howard and Larson (1985) both argued that it is unlikely beaver use the presence of food species as a cue for dam establishment and site settlement.

Other studies, like Barnes and Mallik (1997), found that beaver built dams based on vegetation structure rather than species type, choosing woody vegetation with small stem diameters. This corroborates earlier reports (Gallant et al. 2004, Gerwing et al. 2013, Mahoney and Stella 2020) that stem size may be more influential than species preferences. Another study stated that the probability of settlement in an area increased with woody canopy cover, agreeing with Barnes and Mallik that structure may be more vital to settlement than species preferences for food (Ritter et al. 2020). These studies described the importance of woody vegetation availability for construction materials during colonization, but other studies (Howard and Larson 1985, Holland et al. 2019) suggested that these variables become secondary to other factors in habitat suitability over time.

When examining vegetation in relation to occupancy, most studies concur that most vegetation parameters did not correlate with occupancy. Holland et al. (2019) found neither percent cover of forest nor woody vegetation as dominant land-cover type to predict beaver occupancy. Percent deciduous forest cover from another study was also not a predictor of occupancy (Hood 2019). Touihri et al. (2018) found that any vegetation factor alone could not predict suitable dam sites nor occupancy duration. In explaining the variation between long-term and short-term occupancy groups, Howard and Larson (1985) discovered food availability and vegetation variables alone were not significant. Only Harrison's (2011) study found that models including deciduous stand basal area better explained site occupancy. These models, however, also included other variables such as forage area and dam volume, so the contribution of quantity of woody vegetation alone to explain variance was unclear. One study that did demonstrate a relationship between vegetation and occupancy was that of Bergman et al. (2018). Their study, like others, showed terrestrial vegetation had no significant relationship to colony density or persistence, but they found that aquatic vegetation did. Specifically, total macrophyte cover was the strongest predictor for colony persistence and percent cover of floating macrophytes was the strongest predictor of colony density.

Beaver Habitat Preferences: Physiography

Physiography is frequently cited as the most important factor in beaver habitat use. Given beaver's ability to manipulate hydrology and vegetation variables to better suit their needs, but their inability to greatly alter physiographic conditions, it is unsurprising that physiography is important to colony settlement and occupancy (Allen 1983, Beier and Barrett 1987). The most prominent physiographic variable described in the literature related to beaver habitat is stream gradient. Stream gradient is the major component of stream morphology and is often argued to be the most important factor determining suitable habitat (Slough and Sadlier 1977, Allen 1983, Beier and Barrett 1987). Steep topography and gradients prevent beaver from establishing food transport systems (Slough and Sadlier 1977) and the risk for dam breach or blowout increases with steeper topography (Woo and Waddington 1990) so lower stream gradients are more preferable. When reporting stream gradients, however, many studies use topographic slope interchangeably with gradient. This is important to note as it results in topographic slope values often being reported as stream gradient values. Specifically, Touihri et al. (2018) singled out gradients between 3-4% as being most optimal. Suzuki and McComb (1998) showed this to be true with more frequent dams on gradients less than 4% near the central Oregon coast.

Additionally, Retzer et al. (1956) reported 68% of colonies within their Colorado study were on gradients less than 6%, 28% were on gradients between 7-12%, 4% on gradients between 13-14%, and none on gradients greater than 15%. Ritter et al. (2020) calculated that beaver settlement odds at a site declined by 51% for every 1% increase in stream gradient. Their study also reported that dispersing beavers never settled stream segments with gradients larger than 5%. Yet the same study uses the metric reported by Retzer et al. of 15% gradient as the threshold between suitable and unsuitable habitat for beaver.

Other important physiographic variables reported in the literature include valley floor width and shoreline or riverbank slope. Along with stream gradient, Suzuki and McComb (1998) found valley floor width to be wider at dammed sites compared to random unoccupied sites. More dams were found in valleys between 15-65 meters wide. Similarly, another study found known dam sites had wider valley floors than hypothesized sites (Petro et al. 2018). Dieter and McCabe (1989) argued instead that riverbank slope was the most important physical factor over valley width or stream gradient. Their study found riverbank slope to be significantly greater at lodge sites compared to random sites. Both Suzuki and McComb and Petro et al. reported similar results, with shallower shoreline slopes at known dam sites than unoccupied (Suzuki and McComb) or predicted sites (Petro et al.). Only one study (Hood 2019) examined slope in relation to occupancy. The study found the standard deviation of slope at active ponds was higher compared to abandoned ponds or never occupied ponds, contradicting previous studies that increasing slope would negatively affect suitability through occupancy. Put together though, all physical variables—stream channel gradient, valley floor width, and riverbank slope—have the greatest predictive power for identifying dam sites, correctly classifying 83% of dam sites in one study (Suzuki and McComb 1998).

However, it is important to note that physical variables vary in importance between dam and lodge sites as well as different water habitats. Slough and Sadlier (1977) found physical variables to be more important in stream models relative to lake models. This may be because of the stronger topographic influence on shaping stream morphology and its valleys compared to lacustrine habitats. Touihri et al. (2018) also noted a distinction between dam and lodge sites. Stream gradient, they said, is more important for dam construction whereas topographic slope is more so for lodge location. Their argument stands to reason given that dams are largely constructed in river systems where stream gradient would play a more pivotal role and that lodges can be constructed along banks making shoreline slope a greater variable for lodges.

Beaver habitat suitability modeling:

Many studies have modeled suitable beaver habitat, but several only consider suitability in relation to colony settlement and dam construction potential. Those that do examine suitability in relation occupancy, however, often consider occupancy at the colony or site-scale rather than at lodges. What follows is a general overview of how previous studies have modeled beaver habitat suitability with a particular emphasis on the characteristics defining suitability.

Rosenberg and McKelvey (1999) argued that any models for central place foragers, like beavers, need to consider distance from central place as a crucial factor. Only two studies considered distance as a variable in suitability. One study (Bonner 2005 and Bonner and Anderson 2014) actually incorporates foraging distance on land and distance from water as a variable in their GIS suitability analysis. Distances less than 50 meters were more suitable whereas distances over 100 meters were least suitable and distances greater than 200 meters were unsuitable. Foraging distance was weighted at 35%. Other variables included stream gradient weighted at 50% and available woody food sources at 15%. Gradients less than 2% were most favorable, 12-20% were least favorable, and gradients above 20% were unsuitable. Aspen specifically was the most suitable food resource, conifers were least suitable, and no food source was considered unsuitable. The other (Hood 2019) used varying distances of 30, 50, and 100 meters within the many regression models. Other variables within the models included combinations of pond area, distance to other active ponds, percent grasslands within the chosen distance, and standard deviation of the slope within chosen distance. The results of these models are discussed more below.

Other studies (e.g. Slough and Sadlier, 1977, Ritter et al. 2020, Harrison 2011) categorize habitat requirements into three major categories. Slough and Sadlier considered water size, water stability—as characteristics of lake outlets, stream gradient, flow rates, and stream width—and food availability both quality and quantity. Ritter et al. considered wetland type, stream geomorphology—as stream channel and geologic conditions—and vegetation, both quantity and distribution of forage and construction materials. Harrison divided categories based on landscape capacity, forest composition, and site maintenance cost. Landscape capacity included impoundment area, upland forage area, and down-valley stream slope; forest composition included total stand basal area and basal area for deciduous and conifer stands; site maintenance cost included the number of dams, total dam volume, and cross-valley slope.

Of the studies modeling beaver habitat suitability, two developed detailed suitability indexes. Suzuki and McComb's (1998) suitability index for *Castor canadensis* classified gradients less than 3% as optimal (1) and gradients greater than 10% unsuitable (0), stream width between 3-4 meters as optimal (1) and widths less than 2 meters or greater than 10 meters unsuitable (0), and valley widths greater than 25 meters as optimal (1) and widths less than 10 meters unsuitable (0). Maringer and Slotta-Bachmayr's (2006) suitability index for *Castor* *fiber*—the European species of beaver who share similar habitat requirements—included elevation, channel gradient/slope, minimum water level, land use, woodland coverage, and minimum habitat area. Their index, like Suzuki and McComb, used a 0-2 scale to determine suitability with 0 being unsuitable, 1 being acceptable, and 2 being optimal. Elevation greater than 900 meters was 0, between 700-900 meters was 1, and less than 700 meters was 2; gradient/slope greater than or equal to 15% was 0 and below 15% was 1; minimum water level below 50 centimeters was 0 and greater than or equal to 50 centimeters was 1; land use with continual disturbance was 0, with temporary disturbance was 1, and limited disturbance was 2; conifer woodlands were 0, other land cover was 1, and deciduous or mixed woodlands were 2; and minimum forest area less than 3.2 hectare was 0 while areas greater than or equal to 3.2 hectare was 1.

In studies examining habitat factors and suitability with site occupancy or colony persistence, there were no clear trends regarding best habitat variables for occupancy. One study by Howard and Larson (1985) in Massachusetts found stream width, stream gradient, soil drainage class, hardwoods within 100 meters and 200 meters, and abandoned fields within 100 meters significantly related to colony site longevity in a linear regression. Another study in California determined stream gradient, stream width, and stream depth to appear most frequently in the logistic functions and with the greatest coefficients when examining colony persistence versus abandonment (Beier and Barrett 1987). A generalized model predicting active beaver colonies from Mumma et al. (2018) found habitat quality to be the best predictor. Habitat quality variables included vegetation-class richness and the proportions of open water, nutrient-rich fen, deciduous swamp being positively correlated to colony activity and upland deciduous being negatively correlated. Hood's (2019) models for a study area in Alberta performed best at all foraging distances when they included pond area, distance to other active ponds, and percent grasslands within 30 meters. These habitat factors were better able to explain persistent pond occupancy over time. Lastly, best models from Harrison (2011) in HWF consisted of combinations of upland forage area, dam volume, and deciduous stand basal area. Such combinations revealed longer site occupancy given greater forage and impoundment areas, greater amounts of desirable woody forage species, and low site maintenance costs.

Put together, previous studies clearly demonstrate the importance of hydrologic, vegetative, and physiographic habitat characteristic requirements for beaver. Where these studies diverge, however, are in which specific habitat variables were examined and their relative importance to habitat suitability and/or colony persistence in an area. Furthermore, the studies that do examine suitability and occupancy do so at the site or colony-scale, thereby leaving room for further examination about relative influence(s) of site selection, suitability, and occupancy at the lodge-scale.

Methods:

Study Area:

The Huntington Wildlife Forest (HWF) is a 6,000-hectare experimental forest owned and operated by the State University of New York College of Environmental Science and Forestry. HWF (latitude 44° 00” N, longitude 74° 13” W) sits in the central Adirondack region of New York state within the boundary of the 2.5-million-hectare Adirondack Park (Figure 1). The forest—donated to the college with the explicit intent of investigation, experimentation, and research on the ecology of the region—now operates as an ecological field station with over 100 monitoring programs on the biological, chemical, and physical processes of the region (Bulletin of the Ecological Society of America, 2006). The Adirondack Ecological Center (AEC) operates as the forest’s research station and is responsible for the monitoring programs, including the Adirondack Long-Term Ecological Monitoring Program (ALTEMP). Specifically, the ALTEMP-1 dataset records nearly 50 consecutive years of beaver (*Castor canadensis*) colony lodge location and activity. This dataset was possible, in part, due to the lack of both historical and current beaver trapping and harvesting on the property. Though populations were once nearly extirpated from the central Adirondack region due to harvesting at the turn of the 20th century (Johnson 1922), their colony numbers have since recovered so as to maintain much of their pre-settlement range.

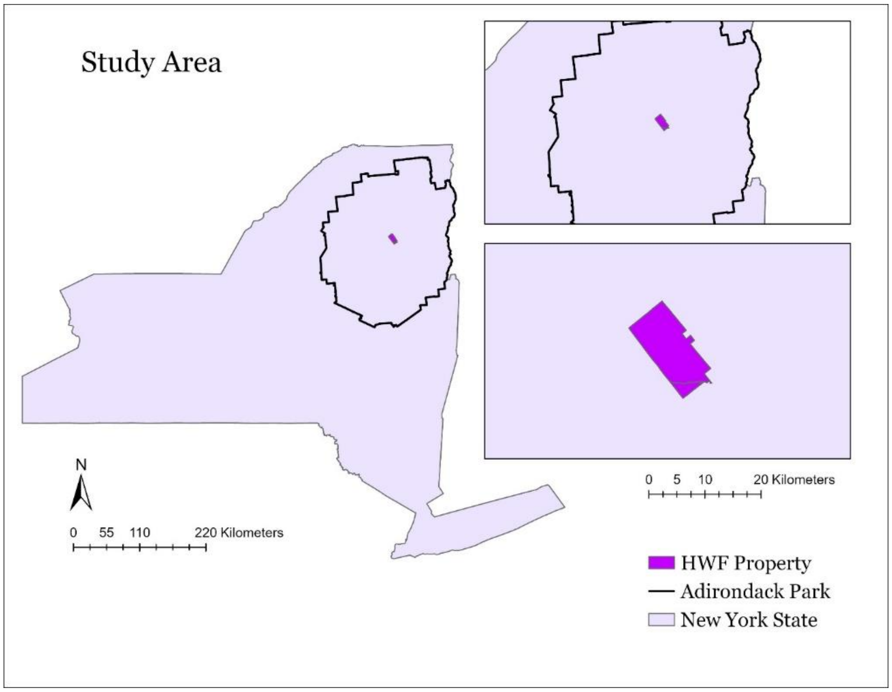

Figure 1: *Study Area Map*. Map shows Huntington Wildlife Forest located within Adirondack Park boundary and New York state.

The topography of HWF is mountainous with elevations ranging from 457 meters up to 823 meters (Bulletin of the Ecological Society of America, 2006). Northern hardwoods dominate the vegetation on the property (72%), though mixed hardwood-conifer stands and conifer stands make up 18% and 10%, respectively, of the forest vegetation. Dominant hardwood species include American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), yellow birch (*Betula alleghaniensis*), and white ash (*Fraxinus americana*); dominant conifer species include red spruce (*Picea rubens*), balsam fir (*Abies balsamea*), Eastern hemlock (*Tsuga canadensis*), Northern white cedar (*Thuja occidentalis*), and white pine (*Pinus strobus*). Mean annual temperature is 4.4° Celsius with mean monthly temperatures ranging from -10° Celsius in January to 18° Celsius in July. Annual precipitation in rain and snowfall is about 100 centimeters (Bulletin of the Ecological Society of America, 2006). Major hydrologic features on the property include five lakes ranging in size from 38 to 217 hectares as well as several ponds and many low-order streams.

Beaver Lodge Surveys:

Research staff at HWF commence field surveys in mid-October once beaver caching activity begins. The presence of fall food caches constitutes evidence of an active lodge, whereas lodges without caches are inactive and are omitted from the yearly summary. Surveyors walk drainages or use small watercrafts to navigate lake shores, major streams, and tributaries; aerial flight surveys substitute only if necessitated by on-ground constraints. Surveys continue until all available waterways are accounted for or until winter snowfall hinders survey abilities.

Researchers record the GPS coordinates at each active lodge—or as close to the lodge as safely possible—and assign the lodge to a colony ID. The colony ID is linked to historical knowledge of colony location, in addition to topography and hydrography, to determine colony territory and occupancy. Researchers also assign each lodge a unique lodge ID separate from the colony ID. Unique lodge IDs help researchers understand temporal use or occupancy by each colony.

To date, there have been approximately 45 colonies recorded throughout HWF. During a given year, however, researchers typically find between 20 and 30 active colonies with between 20 and 30 active lodges. Records indicate that occasionally there will be two active lodges inside a colony boundary where a single colony uses more than one lodge at a time.

The yearly surveys add to the ALTEMP-1 beaver colony dataset. The ALTEMP-1 dataset thus contains the colony ID (as site_ID), the unique lodge ID (as lodge_ID), the individual point ID (as point_ID), x-coordinate, y-coordinate, year, and additional survey notes including observer comments, aerial or ground survey, distance from lodge, GPS date (Charlotte Demers, personal communication).

<u>GIS Layers:</u>

Property boundary, vegetation, and hydrology layers were provided by staff at the Adirondack Ecological Center (AEC). All AEC shapefiles were digitized in the mid-1990s from source material of hand-drawn maps dating back to the 1940s. Features were cross-referenced in the early 2000s using remotely sensed imagery at a 30-meter scale and updated accordingly. These shapefiles, however, represent the specific conditions of a particular point in time and may not reflect the exact conditions in a given (subsequent) year. In particular, stream sinuosity and vegetation coverage are likely to change through time, though all digitized files were cross-referenced to field surveys during their creation. These conditions are unlikely to have changed significantly over the past 20 years, though, so the GIS data still provides an appropriate representation of the on-ground characteristics. Digital Elevation Model (DEM) layers were obtained from the New York State GIS Clearinghouse at a 10-meter scale. The DEM was used to calculate slope and stream gradient. The ALTEMP-1 beaver colony dataset provides the GPS coordinates for all lodge locations, which were converted from standalone tables to vector point data. All data are projected in the NAD 1983 UTM Zone 18N mercator projection. All analyses were done using Esri ArcGIS Pro 2.9.0.

Hydrology:

Each water feature was classified into one of five categories: lakes, ponds, major streams, minor streams, or wetlands. Permanent, larger order rivers within HWF were considered major streams whereas smaller tributaries or intermittent streams were classified as minor streams. AEC staff initially classified and processed rivers into separate shapefiles and I retained their classifications. I grouped major stream segments together based on location and labeled accordingly within their layer; the same process was applied to minor stream segments as well.

Lakes and ponds were provided as a single shapefile by AEC with the distinction between the two being ponds are smaller in area compared to lakes. I next converted the lakes and ponds layer from polygon to polyline so that all water features could be combined into a single layer, entitled hydrology. Stream segments overlapping portions of lakes or ponds were erased from the combined hydrology layer.

I then selected wetlands from the vegetation layer and exported them as a new polygon feature. Overlapping segments within lakes were erased from the wetlands layer before converting the feature to line data. The wetlands lines layer had intersecting stream segments erased so that it could be merged with the previously created hydrology layer to form an entirely new all waters layer. From here, a 100-meter buffer was constructed around the all waters layer. 100 meters reflects the maximum probable foraging distance for beaver, a central place forager, reported in the literature and the greatest distance used in most beaver suitability modeling studies (Naiman et al. 1988, Lapointe St. Pierre et al. 2018, Hood 2019, Ritter et al. 2020). The buffer was used to clip all vegetation and slope layers to when developing suitability models.

I used the distance accumulation tool to calculate probable foraging potential and suitable distance from water availability. The merged hydrology layer was used as the initial input so that wetland areas were not weighted twice when developing the suitability model later given that wetlands were also included in the vegetation stands layer. The 100-meter buffer was used as the barrier when calculating distance. The resulting suitability output was scaled so that areas within 30 meters were given a higher value—and thus suitability score—while areas within 50 meters were given moderate values and areas between 50 and 100 meters were least suitable (Ritter et al. 2020).

I again used the distance accumulation to calculate the distance for the merged hydrology layer, this time with no barrier. Raster calculator was then used to select areas less than 100 meters from the water's edge; areas less than 100 meters were reclassified with a value of 1 whereas areas greater than 100 meters were reclassified with a value of 0. The reclassified distance layer was subsequently clipped so as to not exceed the property boundary. This process was repeated using each individual hydrology type—lakes and ponds, major streams, and minor streams—as the input layer for the distance accumulation function. Calculating distances for all hydrology layers combined and separately allows the distance from water body type to be weighted differently in one suitability model and equally in another.

Vegetation:

The vegetation layer derives from the stands shapefile from the AEC. The shapefile was pre-classified into principal stand types: hardwoods (HWD), softwoods (SWD), mixed hardwood-conifer forests (HC), and non-commercial (NC). Using the principal sub-type attributes, I selected only wetlands from the NC principal type and removed all other non-commercial areas from the stands layer. Principal stand type represents the dominant forest coverage in an area being either deciduous hardwoods, coniferous softwoods, or a mixture of both hardwoods and conifers. I then converted the stands shapefile from polygon to raster and symbolized the layer according to the principal stand type.

Physiography:

I obtained four DEM shapefiles from the NYS GIS Clearinghouse for full coverage of the HWF property. I used the mosaic tool to merge the four pieces together into a single shapefile which was then extracted to the property boundary. The DEM served to profile stream gradient as well as to calculate slope. Using the slope tool, slope was calculated based on percent rise, but was subsequently reclassified into six categories: 0-3%, 3-6%, 6-10%, 10-15%, 15-20%, and >20%. These uneven breaks between categories were automatically generated by ArcGIS Pro, but I reclassified them to include any slopes with greater than 20% rise into a single category. Furthermore, these breaks were largely unaltered in reclassifications as their values match the general breaks reported previously in the literature. Reclassification necessitates a new value be assigned to each category, so 0-3% became 5, 3-6% became 4, 6-10% became 3, 10-15% became 2, 15-20% became 1, and >20% became 0; these values mirror the suitability score discussed below. The resulting reclassified slope layer was at a 10-meter scale as determined by the scale of the DEM.

The profile tool from the ready-to-use elevation toolset uses the elevation contained in the DEM to profile the terrain along line features to determine stream gradient. Using the hydrology lines, profiles of each stream or lake containing lodges was created. The profiles describe the change in elevation (Δelevation) in meters in relation to the total horizontal distance of the stream. Because the streams' line features created by the AEC are segmented as separate attributes, certain streams contain multiple stream segments whose horizontal distance was added together to get the total horizontal distance of the stream. Due to the short length of many segments, the total stream length was rounded to the nearest 25 meters. The minimum and maximum elevation was taken from the combined stream segment; minimum elevation was rounded down to the nearest 0.5 meters and maximum elevation was rounded up to the nearest 0.5 meters due to the inexact selection along the profile at the precise highest and lowest points. Stream gradient was then calculated for each stream or lake by finding the change in elevation and dividing it by the total horizontal distance. Stream gradient is presented in Table 1 in m/m.

Stream Name	Gradient	Years/100m
Big Sucker Brook	0.0181	16.800
Corner Stream	0.0241	1.250
Catlin Tributary 1	0.0355	7.111
Catlin Tributary 2	0.0520	2.057
Catlin Tributary 3	0.0012	5.555
Deer Stream	0.0107	11.607
Fishing Brook	0.0050	20.833
Flat Brook	0.0052	3.130
Little Sucker Brook	0.0400	7.579
Military Stream	0.0200	0.421
Rich Stream	0.0187	1.600
Shattuck Stream 1	0.0341	9.412
Shattuck Stream 2	0.0095	6.316
Trucka Stream	0.0100	2.824
Wolf Pond Outlet	0.0118	9.836
Wolf Stream	0.0342	6.316

Table 1: *Stream Gradient and Occupancy.* Table shows stream gradient and number of years occupied per 100 meters of stream for 16 different streams in HWF.

Lodges:

The ALTEMP-1 beaver colony dataset from the AEC, presented in Microsoft Excel, contained all 479 lodge sightings from 2001 through 2021. I reorganized all lodges based on their geographic coordinates to assess occupancy based on individual lodges. This analysis yielded 233 individual or unique lodges constructed by beavers during the 21-year period. I subsequently divided unique lodges into six categories of site occupancy, defined as the total number of active years per total years within the study (# active years/total # years). Categories were: single-year occupancy (1/21 years), two-years (2/21), three-years (3/21), four-years (4/21), five-years (5/21), and greater than six-years (6-16/21). An additional subcategory was added to each lodge to further label whether total years occupied were consecutive, or continuous, or reoccupied over multiple, non-consecutive years; reoccupied lodges include any number of abandonments and reoccupation. The purpose of this categorization was to easily identify and analyze lodges based on occupancy using GIS.

I then added the six occupancy categories as six separate tables to GIS. I used the display x-y data feature to convert the y-coordinate and x-coordinate of each unique lodge from the tables to vector point data, thus creating six lodge layers based on occupancy. Further analysis within GIS, however, revealed 13 lodges existed outside the HWF property boundary and were therefore excluded from the study, resulting in 220 unique lodges. A 50-meter buffer was also constructed around every lodge to understand relative distance from water's edge and probable foraging distance.

All 220 lodges were overlain against the hydrology, vegetation, and slope layers, respectively, to understand the specific characteristics of each factor at every lodge (Figures 2-4). The type of water body—pond, lake, major stream, minor stream, or wetland—was recorded at every lodge as well as the name of the water body, such as Arbutus Lake. This was important in understanding colony dynamics and territoriality. Lodges occurring outside 50 meters from any type of water, including wetlands, were recorded as having no water. Dominant vegetation type—wetland, deciduous, coniferous, and mixed—at each lodge was determined by visually assessing the largest type within a 50-meter buffer of each lodge. Although multiple types of vegetation may exist within a 50-meter range, only the type with the greatest cover percentage was recorded. Lodges centrally located within ponds or lakes and more than 50 meters from water's edge were recorded as having no dominant vegetation. Lastly, slope was assigned using the reclassified slope layer, resulting in values ranging from 0-5.

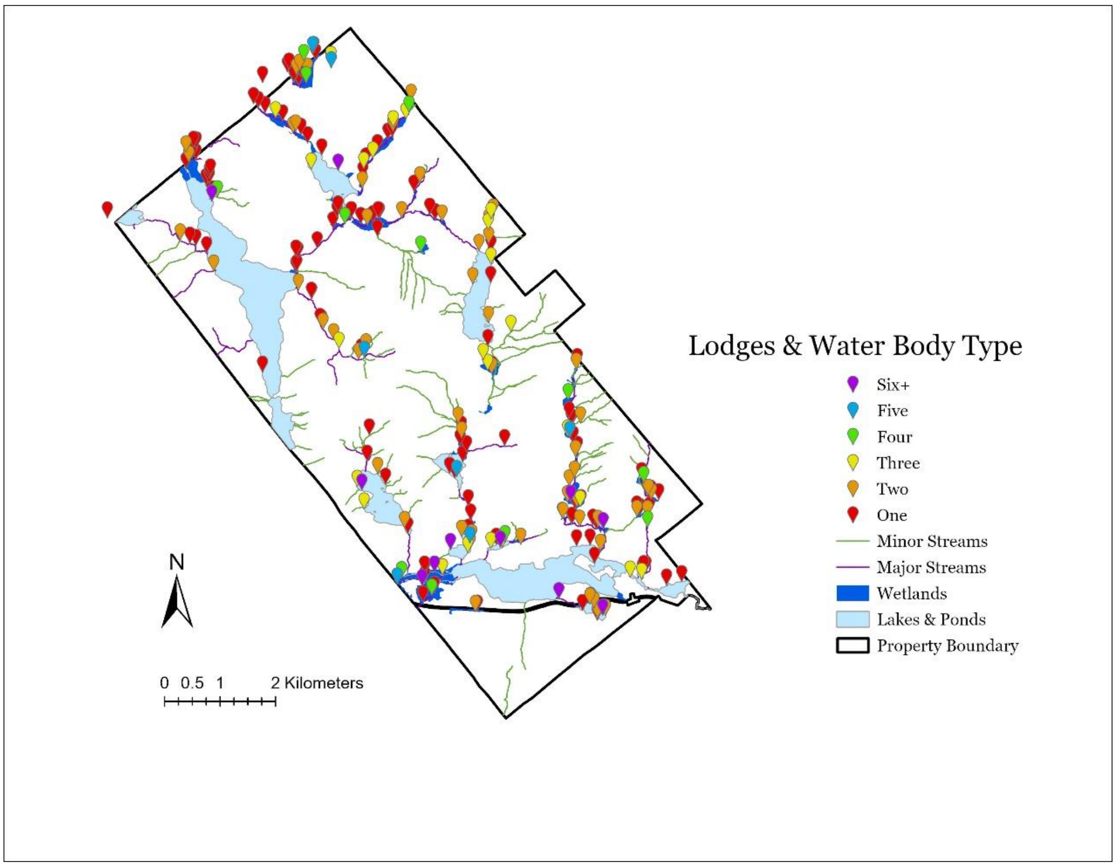

Figure 2: *Lodges and Water Body Type Map.* Map shows lodges, categorized by years of occupancy, overlaid against water body type, categorized as major streams, minor streams, lakes and ponds, and wetlands.

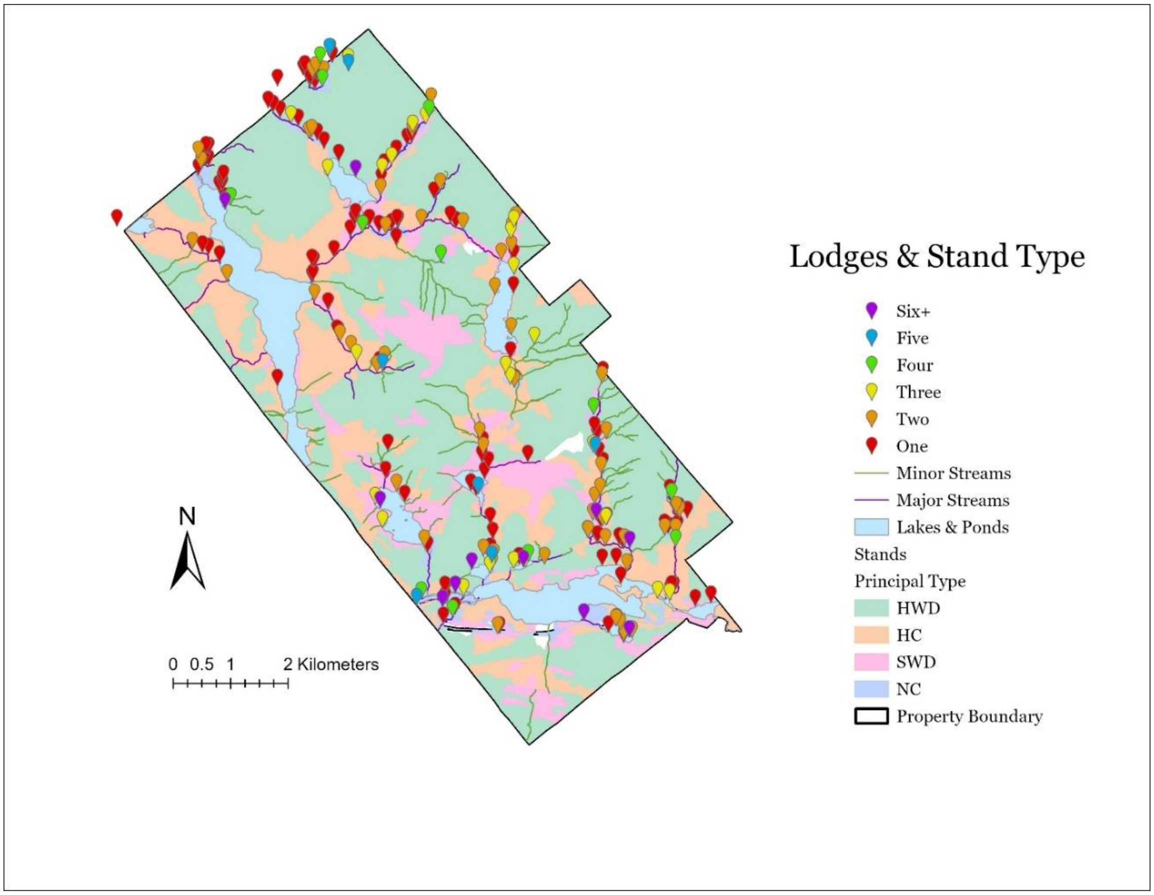

Figure 3: *Lodges and Stand Type Map*. Map shows lodges, categorized by years of occupancy, overlaid against vegetation type, categorized as deciduous hardwoods (HWD), mixed hardwood-conifer (HC), coniferous softwoods (SWD), and non-commercial wetlands (NC).

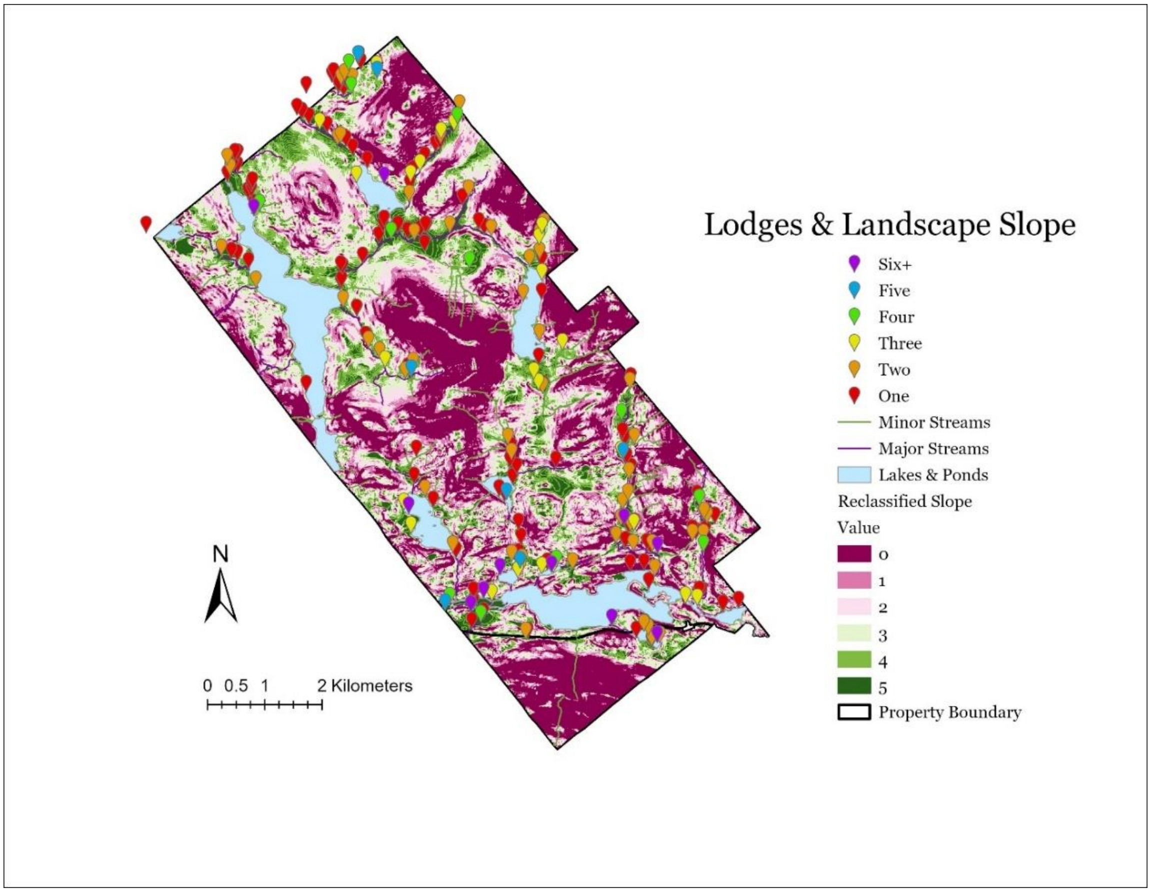

Figure 4: *Lodges and Landscape Slope Map*. Map shows lodges, categorized by years of occupancy, overlaid against landscape slope, categorized by reclassified values. 5 is 0-3% rise, 4 is 3-6%, 3 is 6-10%, 2 is 10-15%, 1 is 15-20%, and 0 is >20%.

GIS Suitability Model:

ArcGIS Pro's Suitability Modeler tool was used to develop the suitability model. The reclassified slope raster, stands raster, and distance accumulation rasters were added to the suitability modeler with weights, determined by percentage, being assigned based on previous habitat suitability studies. Suitability scores ranged from 1 to 9 with 1 being extremely low-quality or unsuitable habitat and 9 being the highest-quality or most suitable habitat for beaver.

Vegetation Suitability Scoring:

For the vegetation raster, I assigned wetlands the highest suitability of 9. According to Wright (2009) and Wright et al. (2002), all large, open-canopy wetlands and nearly 25% of the herbaceous plant species within them in HWF are associated with active or abandoned beaver dams. Bergman et al. (2018) also argued that aquatic vegetation associated with open water and their surrounding wetlands constitute more preferable food sources, particularly during the summer season. Others, including Brenner (1962), Allen (1983) and Lapointe St. Pierre et al. (2017), and Wang et al. (2019) noted that beaver appear to favor herbaceous vegetation found in existing or created wetlands over woody vegetation when and where available. Although fall food caches of predominantly woody stems signify active lodges, wetland vegetation supplements greater proportions of beaver diet throughout the year.

I assigned deciduous coverage the second highest score of 8 for their importance in fall food caches, dam and lodge construction materials, and preferred food species. Species preferences include trembling aspen (*Populus tremuloides*), willow (*Salix spp.*), cottonwood (*Populus deltoides*), alder (*Alnus spp.*), birch, (*Betula spp.*), maple (*Acer spp.*) (Allen 1983, Barnes and Mallik 1997, Mahoney and Stella 2020). In HWF specifically, species preferences include striped maple (*Acer pennsylvanicum*), American beech (*Fagus grandifolia*), white ash

(*Fraxinus americana*), and yellow birch (*Betula alleghaniensis*) (Harrison 2011). Additionally, many studies (Naiman et al. 1988, Ritter et al. 2020) demonstrated the importance of woody deciduous canopy and coverage in increasing the probability of beaver settlement in an area.

Coniferous areas were given the lowest suitability score of 1 for their poor nutritional quality (Brenner 1962, Allen 1983). Though beaver can subsist on coniferous species, conifers are typically less foraged, especially relative to abundance or coverage (Harrison 2011, Stella and Mahoney 2020). Lastly, mixed deciduous-conifer forests were given an intermediate score of 5. Mixed deciduous-conifer forests dominate many areas in the mountainous Adirondack State Park and contain both preferred and nonpreferred forgeable vegetation; therefore, these areas received a mixed suitability score of 5 being between deciduous' 9 and conifers' 1.

Physiography Suitability Scoring:

Within the suitability model, the slope raster acts as both topographic slope and a proxy for channel gradient. Using slope interchangeably with channel gradient is common within beaver suitability studies, particularly GIS suitability modeling studies (Barnes and Mallik 1997, Bonner 2005, Maringer and Slotta-Bachmayr 2006, Anderson and Bonner 2014, Hood 2019). As such, these studies often present values as stream or channel gradient, though the values likely reflect topographic slopes underlying gradient calculations. Furthermore, Touihri et al. (2018) emphasized that stream gradient is more important in dam construction whereas landscape slope could be a better predictor for lodge sites. With the focus of this project being on lodge site selection rather than dam construction location, using slope within the suitability model rather than stream gradient alone is preferable.

For the slope raster, I assigned the reclassified raster value of 5, representing slopes between 0-3% rise, the highest suitability of 9. Studies from Suzuki and McComb (1998), Touihri et al. (2018), and Petro et al. (2018) describe slopes less than 3% specifically as most suitable. Slopes between 3-6% were given the next highest suitability score of 8. Allen (1983) describes how 68% of colonies in one study were located on streams with gradients less than 6%; this value includes slopes between 0-3% as well. Relatedly, Ritter et al (2020) found that the odds of beaver settlement declined by 51% for every 1% increase in stream gradient with sites on stream segments with gradients greater than 5% never being occupied by dispersing beaver populations. Barella et al. (2021) argue that beaver researchers and managers most often selected slopes between 3-6% as the most critical habitat variable for beaver. This study by Barella et al., however, is the only to signify this specific range from 3-6%, so although this range is important, it was given the second highest suitability rather than the first.

I assigned slopes between 6-10%, with a reclassified value of 3, a suitability score of 6. The incrementally smaller score reflects Ritter et al.'s point from above that a 1% increase in gradient decreases odds of beaver settlement by 51%. This score also reflects a point from Allen (1983) stating that 28% of beaver colonies in the study site were on slopes between 7-12%. I gave slopes between 10-15% the same incremental decrease in suitability, resulting in a suitability score of 4. Slopes above 20% were given the lowest suitability score of 1. This unsuitable score reflects the cutoff value presented by Anderson and Bonner (2014). Though many studies (Allen 1983, Maringer and Slotta-Bachmayr 2006, Ritter et al. 2020) dictate that slopes or gradients greater than 15% are never colonized by beaver and are wholly unsuitable, the mountainous terrain of HWF may force beaver into areas with steeper than average slopes. To account for these values, though, slopes between 15-20% were also rated highly unsuitable, receiving a suitability score of 2.

Hydrology Suitability Scoring:

Distance from a suitable water source was scored based on the suitability model being constructed. The first and third suitability models assume all water bodies have equal potential to support beaver settlement and occupancy. The reclassified distance layer from all merged streams and lakes had values of 1, or areas within 100 meters of water, and 0, or areas outside of 100 meters of water. Given that all waters have equal potential to support beaver, values of 1 were scored as 9 and values of 0 were scored as 1 due to their unsuitable distance from water's safety. The second suitability model, however, assumes different bodies of water have varying degrees of potential to support beaver occupation and therefore received varying suitability scores. Like the merged hydrology layer, distances within 100 meters from a specific type of water body were calculated as 1 and distances greater than 100 meters from that water type were calculated as 0. For lakes and ponds water type, values of 1 were given a suitability score of 9 whereas values of 0 were considered unsuitable and given a score of 1. Beaver require consistent sources of water supply for protection and material transport, which lacustrine environments provide with less fluctuation compared to streams. Additionally, researchers found lodges were most frequently, 49.3%, located in open water (King et al. 1998) and that colony size in lacustrine environments averaged 6.3 individuals, more than riverine or drainage areas, respectively (McTaggart and Nelson 2003). Most notably, Touihri et al. (2018) remarks that quality lodges locations do not necessarily require dam construction and areas that do not require dams may be better correlated to long term occupancy since the site maintenance cost is reduced (Harrison 2011).

For major streams—streams of higher orders and with more consistent water supply—distances valued at 1 were scored as 8 and distances valued at 0 were scored 1. Riverine environments are most strongly associated with beaver presence as beaver modify streams through dam construction to control water levels. In riverine systems, beaver are more likely to occupy larger streams for their increased water availability and increased pond area (Holland et al. 2019). Due to the energetic cost of maintaining dams within major rivers, distance from major streams ranked second in suitability. Lastly, minor streams—those with greater water fluctuations and intermittent periods as well as small order tributaries—with values of 1 were scored with a 6 and values with 0 were scored 1. The less consistent water supply for these minor streams reduces their suitability compared to lakes, ponds, and major streams, but the reduced energetic cost of maintaining smaller dams helps to partially offset low water levels.

Suitability Models:

The first suitability model weighed the vegetation, physiographic, and hydrologic layers equally (Figure 5). The vegetation and distance from merged waters rasters each contributed 33% to the output Even Suitability model and slope contributed 34% influence. With each of these factors weighted evenly, we can see what suitability looks like in relation to occupancy without the greater influence of one factor over another. The Even Suitability thereby creates a base with which to compare the Weighted Suitability model. For the Weighted Suitability model, slope was weighted at 40%, vegetation at 30%, and distance from lakes or ponds, major streams, and minor streams at 10% each, bringing the total to 30% for water bodies (Figure 6). Several researchers (Slough and Sadlier 1977, Allen 1983, Suzuki and McComb 1998, Anderson and Bonner 2014) argue that physiographic characteristics like slope and stream gradient are the most significant factors in determining suitable habitat for beaver. Steep topography prevents the establishment of food transportation networks (Slough and Sadlier 1977) and increases the likelihood of dam breach or blowout following major storm events (Woo and Waddington 1990).

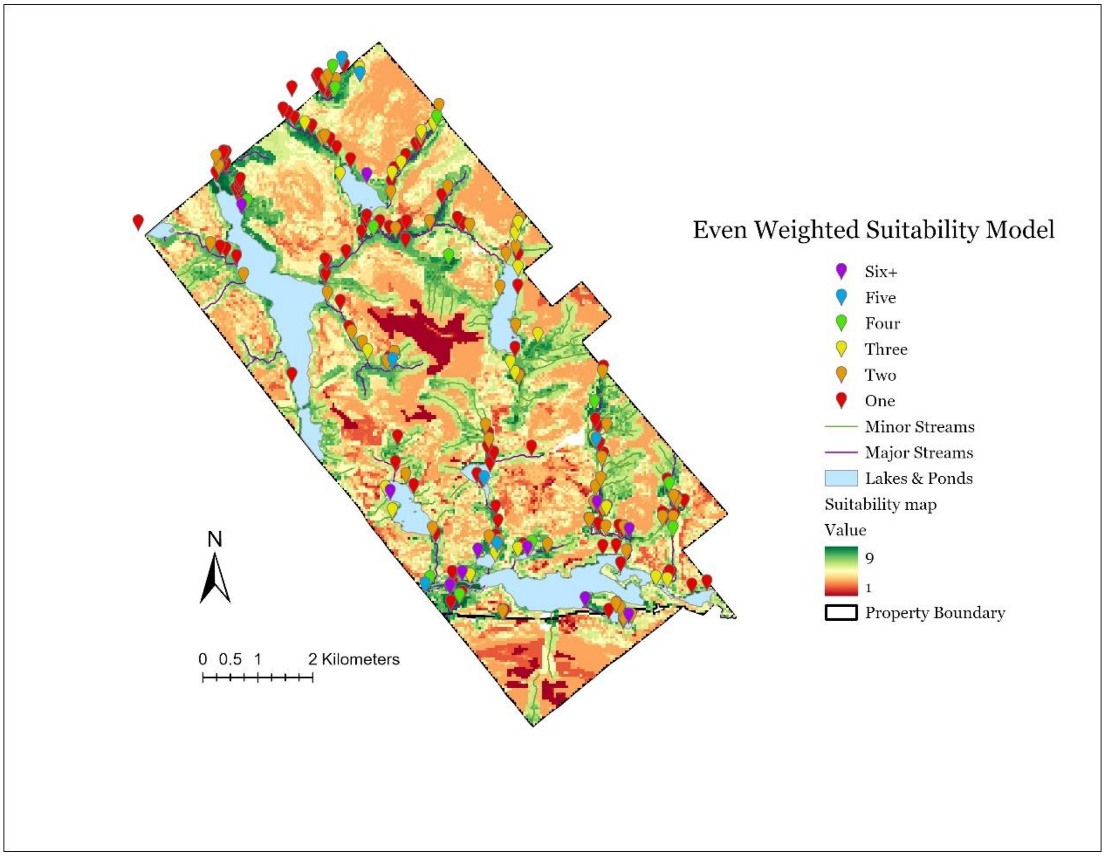

Figure 5: *Even Weighted Suitability Model*. Map shows lodges, categorized by years of occupancy, overlaid against the even-weighted suitability model. Suitability scores range from 1 with poor suitability to 9 with high suitability.

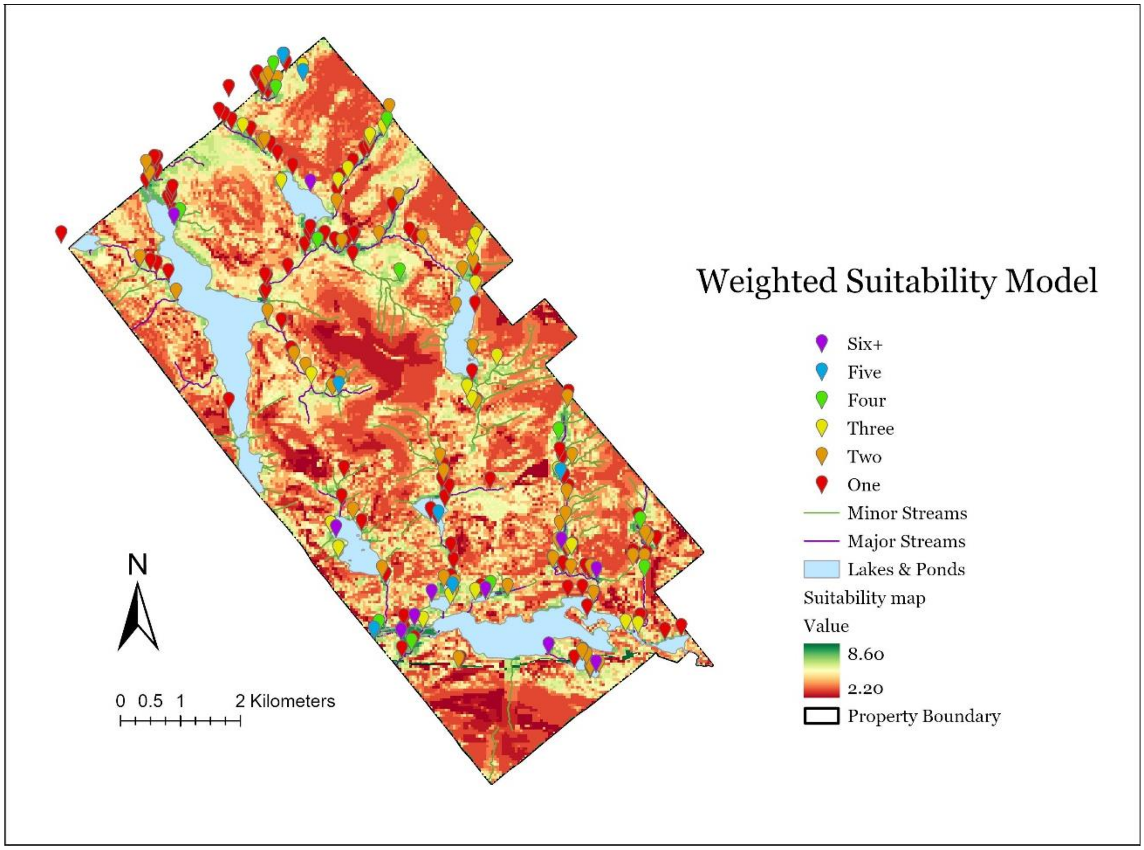

Figure 6: *Weighted Suitability Model*. Map shows lodges, categorized by years of occupancy, overlaid against the weighted suitability model. Suitability scores range from 2.20 with poor suitability to 8.60 with high suitability.

Furthermore, vegetation factors, particularly woody vegetation coverage or availability, may be of secondary importance to other habitat variables for many reasons. As Holland et al. (2019) and Howard and Larson (1985) both establish, woody vegetation is more important in site colonization for its role in dam and lodge construction material. Over time, however, this variable becomes less important as percent woody cover becomes a poor predictor of occupancy (Holland et al. 2019, Hood 2019). Secondly, beaver can alter the vegetation composition at the stand scale over time through pond formation and selective foraging. Not only does inundation from beaver ponds promote the proliferation of water-tolerant and preferred riparian tree species, but the formation of wetlands also promotes preferred food sources like herbaceous and aquatic species' coverage as well. Terrestrial foraging can also deplete above ground biomass of desirable species, especially in areas with long term beaver presence and occupation (Naiman et al. 1988, Johnston and Naiman 1990, Rosell et al. 2005). Due to its dynamism over time, in addition to beaver's foraging as a "picky generalist," vegetation (at least at the spatial and temporal scales recorded in the GIS layers) is less influential in suitability than physiographic characteristics.

Distance from water body type was given the least influence in the model because it plays the least significant role in previous beaver habitat studies. Although studies like McTaggart and Nelson 2003, King et al. 1998 and Touihri et al. 2018 examine the relative placement of lodges and colonies on water body type, few suitability models take into consideration its significance because beaver will occupy any type of water body so long as the water supply is available. In examining long term occupancy as I do here, however, water availability and consistency may play a more significant role, so that it should be included as a variable in a suitability analysis. The relative weights for each water body type within the second model remain equal to one another for the type's potential for colonization while the suitability score within each layer differs according to the water body's potential to support long term occupancy.

A third suitability model was constructed to understand the role foraging potential plays in site suitability (Figure 7). Rosenberg and McKelvey (1999) argue that habitat models for central place foragers, like beaver, must incorporate distance from the central place, among others, as a factor. For this reason, all potential suitable sites for beaver must be within 100 meters of the water's edge. 100 meters was chosen because several studies like those by Naiman et al. (1988), Hood (2019) and Ritter et al. (2020) use the 100-meter benchmark as the maximum foraging distance for beaver. Harrison (2011) corroborates this distance for beaver in HWF specifically, acknowledging the maximum distance with evidence of beaver foraging was less than 85 meters from water's edge.

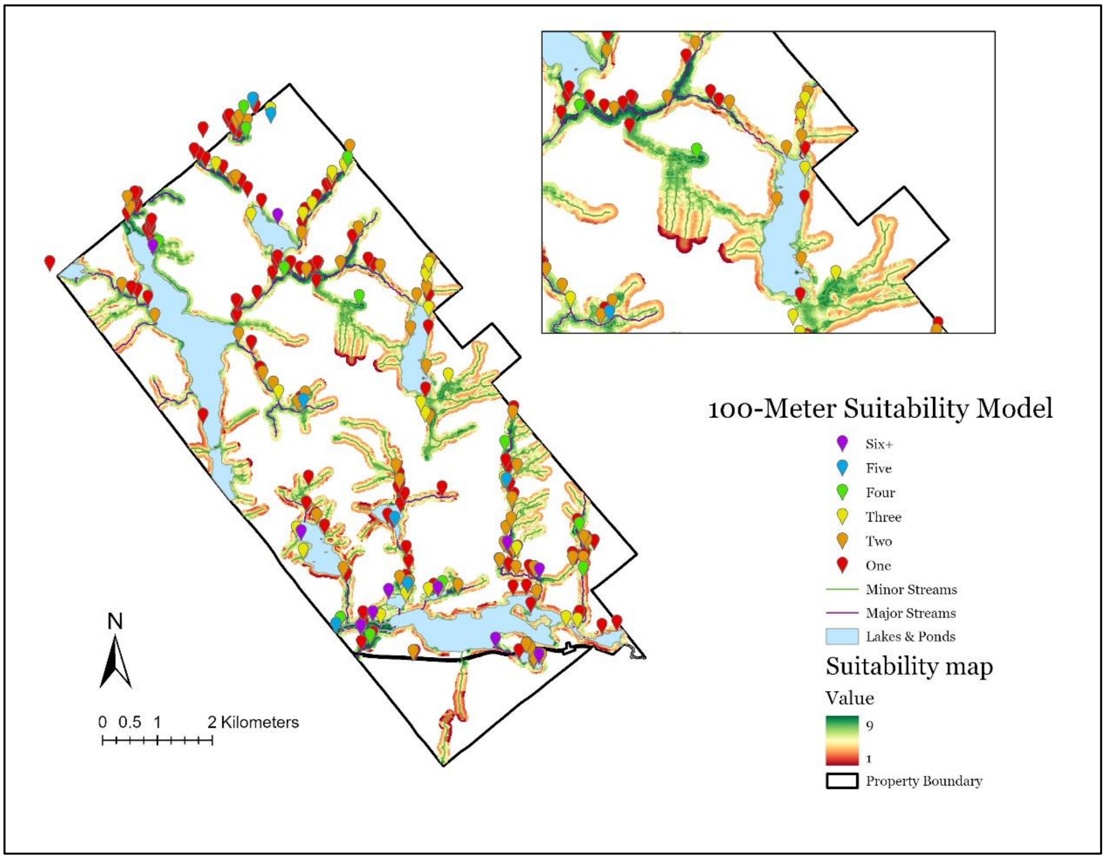

Figure 7: *100-Meter Suitability Model*. Map shows lodges, categorized by years of occupancy, overlaid against the 100-meter distance suitability model. Suitability scores range from 1 with poor suitability to 9 with high suitability.

The 100-meter distance layer was previously scaled so that areas within 30 meters were given a higher suitability score, areas between 30 and 50 meters were given moderate scores, and areas between 50 and 100 meters were least suitable, receiving lower scores (Ritter et al. 2020). The slope and vegetation rasters were then clipped to this extent and scored according to the previous models. Like the weighted suitability model, slope was weighted most heavily at 50%, vegetation at 30%, and foraging distance weighted least heavily at 20%. The purpose of this suitability model is to reduce the influence of water body type and increase the influence of foraging probability near water's edge, regardless of type. The suitability scores from all three models will be compared to one another as well as their respective relationships to occupancy.

To assess the suitability score from each lodge, the six lodge categories were overlaid against the suitability outputs of the three models. By clicking on the raster cell in which each lodge was located, a resulting suitability score ranging from 1 to 9 was visible in the pop-up dialogue box. The score was recorded for each of the 220 unique lodges for each of the three suitability models. For the third model, lodges located outside the 100 meters from water's edge failed to meet suitability requirements and were therefore excluded from the analysis. This brought the total number of lodges for the third suitability model to 205 unique lodges as the other 15 lodges were located greater than 100 meters from lakes or streams, or were in wetlands which were excluded from the initial merged hydrology layer buffered to 100 meters.

Statistical Analysis:

All statistical tests were run using Microsoft Excel data analysis extension. Several Chi-Square goodness of fit tests were used to test the differences in water body type, vegetation type, and landscape slope within single-use lodges and within multi-use lodges. The Chi-Square test was also used to test the differences in the three habitat variables between single-use and multi-use lodges. Additionally, a single-factor analysis of variance (ANOVA) test was used to test the influence of each habitat factor on occupancy. Here, occupancy was continuous rather than categorical and was the dependent variable while water body type, vegetation type, and landscape slope category were each respectively the categorical independent variable.

To calculate the relationship between stream gradient, as an additional physiographic variable, and occupancy, a new continuous variable was created to account for the total number of lodges, their respective occupancy, and stream length. The new variable multiplied the total number of lodges on a river by the total number of years all lodges were occupied to create a variable conveying total years occupied per 100 meters of stream. A simple correlation analysis was run between stream gradient as the independent variable and years occupied per 100 meters as the dependent. All 3 statistical tests help to answer Research Question 1 about which habitat factors—hydrologic, vegetation, or physiographic—better influence occupancy.

To answer Research Question 2 and determine whether more suitable sites are occupied longer, a t-test assuming unequal variance comparing the average suitability scores for lodge occupancy categories was conducted. Lodges were categorized into two occupancy categories: lodges occupied only once (single-year) or lodges occupied more than once (multi-year). A scattergraph was used to initially analyze the relationship, if any, between site suitability scores and lodge occupancy in total years occupied. If the visual analysis suggested a relationship between suitability, as the independent variable, and lodge occupancy, as the dependent variable, a simple correlation analysis was performed. Put together, the results of these tests combined helped answer Research Question 3 about how lodge site selection relates to occupancy, though in a descriptive, non-quantitative approach.

Results and Discussion:

Lodges and Occupancy:

A total of 220 unique lodges were occupied during the 21-year study period. Lodge occupancy ranged from 1 year to 16 years. Lodges were occupied for an average of 2.06 years, with a median of 1 year, and a standard deviation of 1.78 (Figure 8). The number of active periods averaged 1.59 for all lodges, ranging from 1 active period to 6. Site tenancy—defined as total number of active years/number of active periods—averaged 1.24 years. Average time of lodge inactivity, or average amount of time between active periods, was 8.08 years.

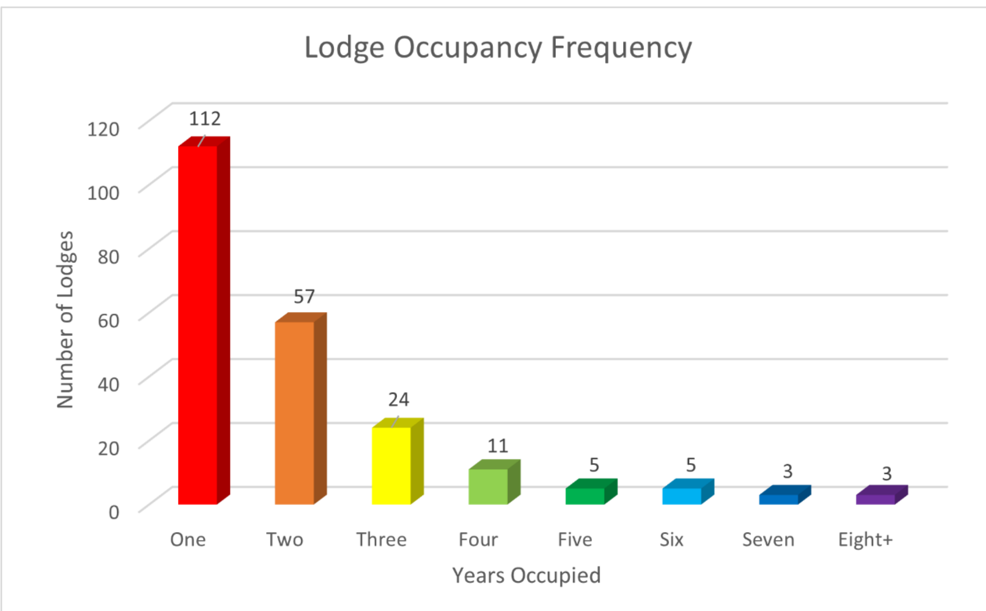

Figure 8: *Lodge Occupancy Frequency*. The graph shows the frequency of lodges by number of years occupied.

The lodge as the unit of analysis in this study is unique among beaver habitat suitability and occupancy studies. Given this, the mean lodge occupancy of 2.06 calculated in this study is exceptional among previous analyses. Only one other study, Hyonen and Nummi (2008), found average colony site occupancy (2.60) similar to the mean lodge occupancy in HWF. Many other studies also examined occupancy at the colony or site level but found higher occupancy averages. These higher averages likely result from colonies rotating between several lodges within a site or territory. When accounting for this difference in scale, an additional analysis of HWF colony occupancy revealed a mean site occupancy of 9.24 years. This value is within ranges presented by Scrafford et al. (2018) and Harrison (2011), albeit marginally lower. It is important to note, however, that the low lodge occupancy average exemplifies the highly skewed nature of lodge occupancy within HWF. This latter point will be touched upon further below.

Habitat Variables - Hydrology:

207 lodges were located within 50 meters of water's edge. 50 lodges (24.15%) were located on lakes or ponds, or lacustrine, environments, 110 (53.14%) were along major streams, 15 (7.25%) were on minor streams—totaling 60.39% in riverine environments—and 32 lodges were in wetlands (15.46%) (Figure 9). 13 lodges were not near water according to the digitized hydrology layers, which were digitized from hand-drawn maps dating back to the 1940s. These lodges were most likely located on new or intermittent streams that formed after the base maps were drafted. When examining the 207 lodges by occupancy and water type, 101 lodges were occupied more than once. Of these 101 lodges, 29 (28.71%) were in lacustrine areas, 55 were on major streams (55.45%), 6 were on minor streams (5.94%), and 11 were on wetlands (10.89%) (Figure 10). These frequencies indicated a definite preference for areas with consistent, more reliable water availability. Such results corroborate values presented by McTaggart and Nelson

(2003) and Holland et al. (2019) who both demonstrated higher colony frequency in riverine areas, followed by lacustrine areas.

For lodges occupied once (single-year), I performed a Chi-Square goodness of fit test to examine if observed frequencies of water body type selection matched expected frequencies. The Chi-Square revealed a significant relationship (χ^2=44.49, n=106, p<0.001) between water body type and lodge site selection within the single-use category. Likewise, the same Chi-Square for lodges occupied more than once (multi-year) revealed a significant relationship (χ^2=58.33, n=101, p<0.001) as well. These results indicated there is a clear preference for both single-use and multi-use lodges placement on water body type, in this case riverine environments. I then performed a Chi-Square test of homogeneity to test whether there was a difference between water type selection between single-year and multi-year lodges. This Chi-Square showed no statistically significant difference (p>0.05) between the two occupancy categories. A single-factor analysis of variance (ANOVA) also revealed water body type had no statistically significant (p>0.05) influence on lodge occupancy. This study is the first to report such findings regarding water body type and its relationship to occupancy at any scale.

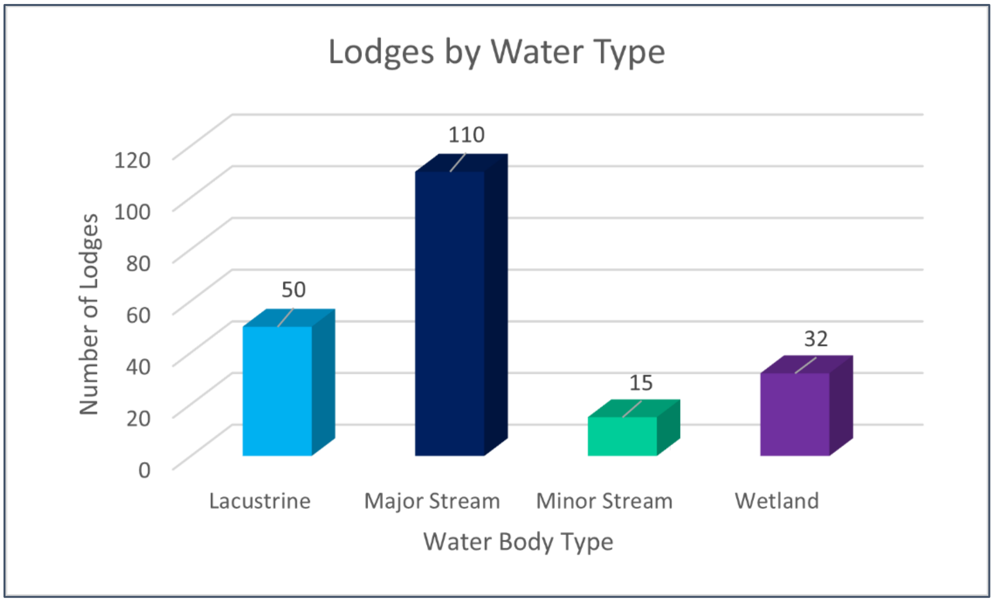

Figure 9: *Lodges by Water Body Type*. The graph shows the number of lodges within each water body category, lacustrine (lakes and ponds), major stream, minor stream, or wetland.

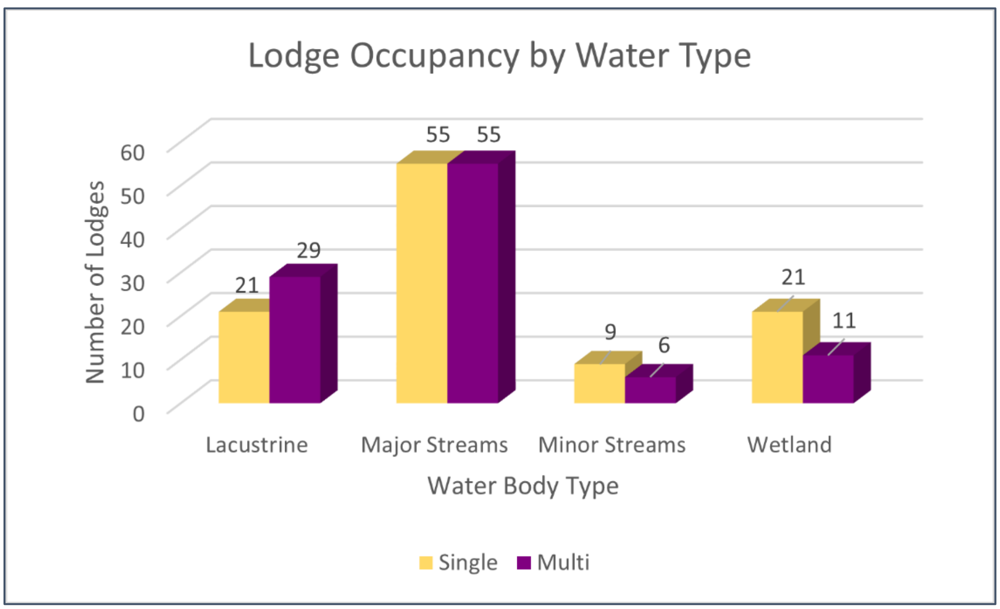

Figure 10: *Lodge Occupancy by Water Body Type*. The graph shows the number of lodges, categorized by single-year or multi-year occupancy, within each water body category, lacustrine (lakes and ponds), major stream, minor stream, or wetland.

Habitat Variables - Vegetation:

215 lodges had vegetation within 50 meters and 5 were so centrally located within a pond so as to be more than 50-meters away from water's edge. 39 lodges (18.14%) had deciduous trees as the dominant vegetation type, while 49 lodges (22.79%) were near mixed deciduous conifer forests, 86 (40%) were in wetlands, and 41 (19.07%) had conifers as the dominant vegetation within 50 meters (Figure 11). 103 of the 215 lodges were occupied more than once, with 19 lodges (18.45%) near deciduous coverage, 20 (19.42%) near mixed coverage, 42 (40.48%) in wetlands, and 22 (21.36%) near conifers (Figure 12). A Chi-Square goodness of fit test for both single-year and multi-year lodges showed a significant relationship (χ^2=14.36, n=112, p=0.002; χ^2=13.85, n=103, p=0.003) between vegetation and lodge site selection within both lodge categories. These results demonstrated a clear preference for wetland vegetation in both occupancy categories. A Chi-Square test of homogeneity revealed no statistically significant difference ($p>0.05$) between the two occupancy categories and site selection based on surrounding vegetation. ANOVA also indicated no significant influence ($p>0.05$) of vegetation on lodge occupancy.

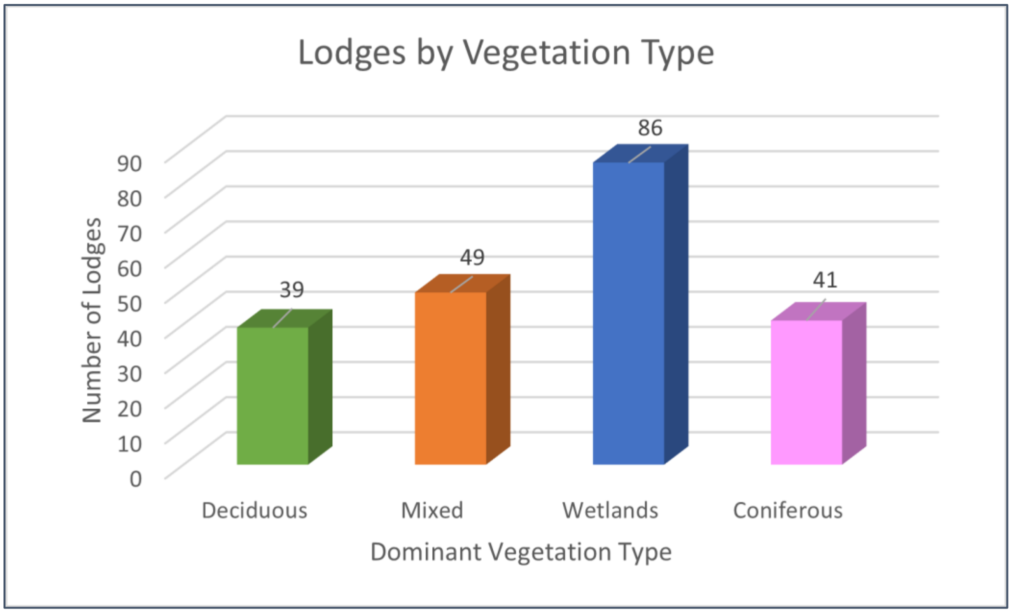

Figure 11: *Lodges by Vegetation Type*. The graph shows the number of lodges within each vegetation type category, deciduous, mixed deciduous-conifer, wetlands, and coniferous.

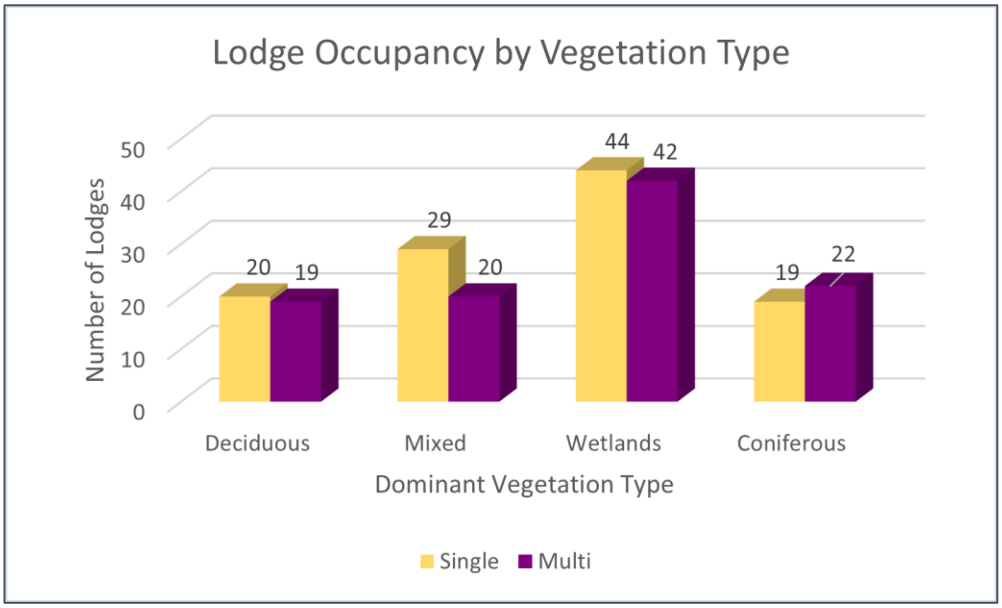

Figure 12: *Lodge Occupancy by Vegetation Type*. The graph shows the number of lodges, categorized by single-year or multi-year occupancy, within each vegetation type category, deciduous, mixed deciduous-conifer, wetlands, and coniferous.

Beaver's significant preference for wetland vegetation is unsurprising. Several studies (Allen 1983, Rosell et al. 2005, Lapointe St. Pierre et al. 2017) noted beaver's predilection for herbaceous vegetation when and where available. Furthermore, "all large, open-canopy wetland areas in the [HWF] landscape are associated with active or abandoned beaver dams" (Wright 2009, 3420) so the common occurrence of lodges within wetlands also points to beaver's ability to alter landscapes to develop preferred vegetation. Most surprising within these results, however, is the fewest number of lodges being located within 50 meters of deciduous forests relative to mixed conifer-deciduous or coniferous areas. Reported species preferences from Rosell et al. (2005), Harrison (2011), and Mahoney and Stella (2020) emphasized deciduous tree species as most palatable and foraged. Although other studies (e.g. Howard and Larson 1985, Touihri et al. 2018) suggested deciduous cover may only be important in colonization for construction materials, the results in this project demonstrated deciduous areas were not necessarily selected for during colonization. My findings here that vegetation type did not predict or influence occupancy, though, was supported by other studies (Touihri et al. 2018, Holland et al. 2019, Hood 2019) who found similar outcomes.

Habitat Variables - Physiography:

Of all 220 lodges, 83 (37.73%) were on landscape slopes less than 3% and between 3-6%, respectively, 34 (15.45%) were on slopes between 6-10%, 8 (3.64%) were on slopes between 10-15%, 9 (4.09%) were on slopes between 15-20%, and only 3 (1.36%) were on slopes greater than 20% (Figure 13). 108 lodges were occupied multiple years, of which 45 (41.67%) were on slopes less than 3%, 40 (37.04%) were on slopes between 3-6%, 16 (14.81%) were on slopes between 6-10%, 3 (2.78%) were on slopes between 10-15% and 15-20%, respectively, and only 1 (0.93%) lodge occurred on slopes greater than 20% (Figure 14). A Chi-Square goodness of fit test for single-use lodges showed a significant relationship (χ^2=85.56, n=112, p<0.001) between landscape slope and lodge site selection within the single-year category; a Chi-Square for multi-use lodges was also significant (χ^2=106.98, n=108, p<0.001). These results clearly demonstrated beaver's preference for shallow slopes within single-year and multi-year lodge site selection. A Chi-Square test of homogeneity, however, revealed no statistically significant difference (p>0.05) between slopes chosen for lodges occupied once or lodges occupied more than once. Though ANOVA also revealed no statistically significant (p>0.05) relationship between landscape slope and lodge occupancy, the Chi-Square and the ANOVA both produced the lowest p-values, indicating this variable may be more important than the others examined here.

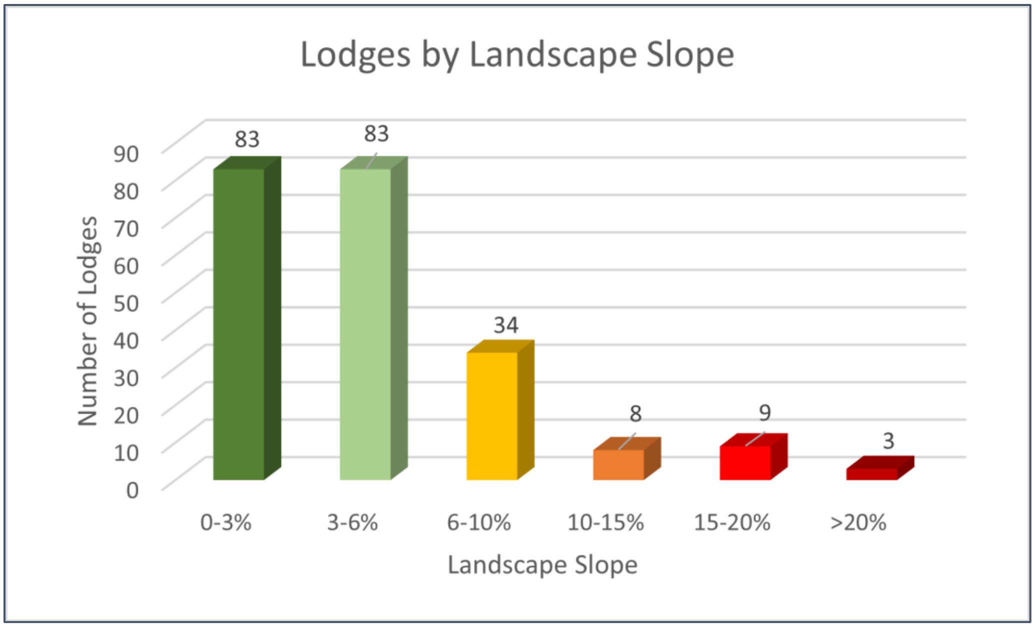

Figure 13: *Lodges by Landscape Slope*. Graph shows the number of lodges within each landscape slope category, 0-3%, 3-6%, 6-10%, 10-15%, 15-20%, and >20%.

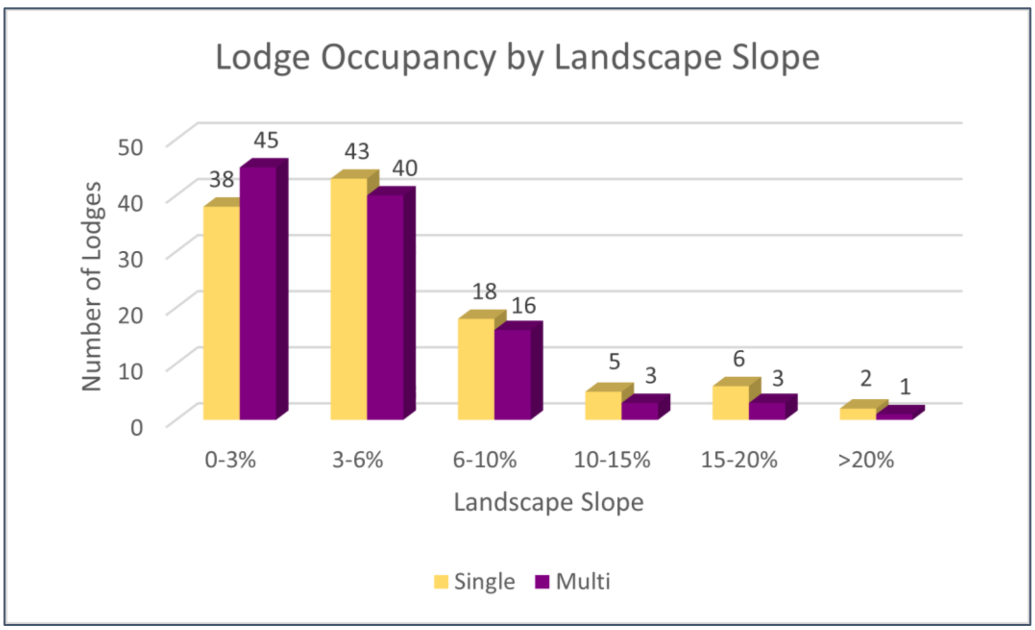

Figure 14: *Lodge Occupancy by Landscape Slope*. The graph shows the number of lodges, categorized by single-year or multi-year occupancy, within each landscape slope category, 0-3%, 3-6%, 6-10%, 10-15%, 15-20%, and >20%.

A Pearson's correlation analysis between stream gradient and occupancy—calculated as (number of years occupied x number of lodges)/100 meters of stream—gives a correlation coefficient of -0.2353 (Figure 15). The negative coefficient implies an inverse relationship between stream gradient and occupancy wherein shallow gradients promote longer occupancy, though this effect of stream gradient on occupancy is not statistically significant ($p>0.05$).

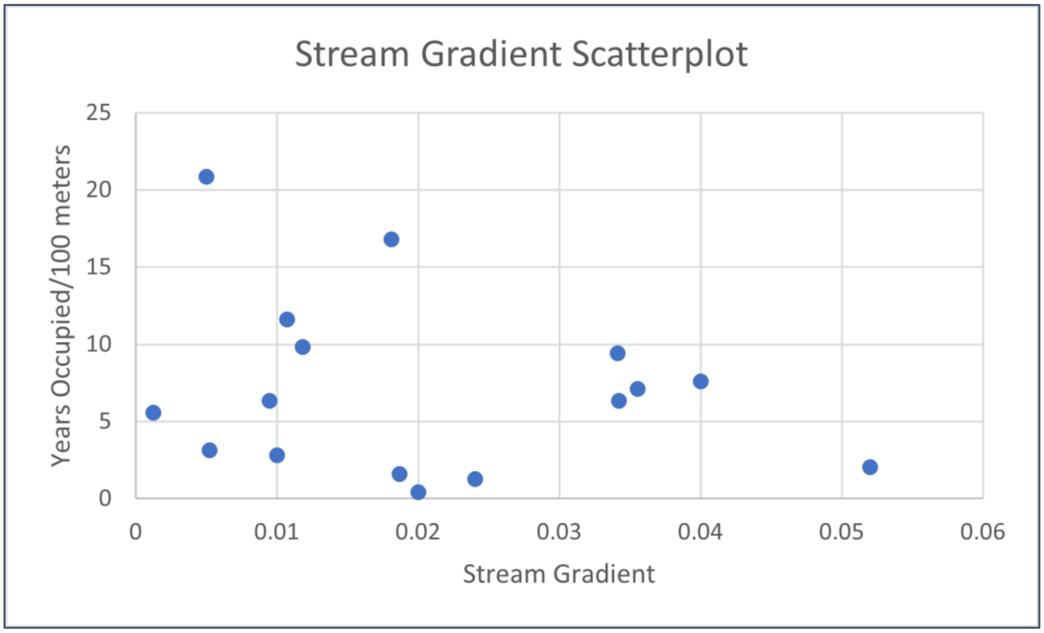

Figure 15: *Stream Gradient and Lodge Occupancy Scatterplot*. Graph shows a scatterplot comparing stream gradient to years occupied/100 meters of stream.

Distinct preference for shallower landscape slopes less than 6% was apparent in the results. These results are well-supported within the literature, where a few studies (Retzer et al. 1956, Suzuki and McComb 1998, Touihri et al. 2018) also pointed to the specific value of slopes—again, often reported as stream gradients—less than 6% as being optimal for dam establishment. Others (Dieter and McCabe 1989, Suzuki and McComb 1998, Petro et al. 2018) generally described shallow topographic slopes as better for beaver settlement. Because previous studies often misrepresent slope as stream gradient, it is difficult to compare my stream gradient results to theirs. I examined stream gradient as (*Δ*elevation)/total horizontal distance of the stream, which was separate from the percent rise values calculated for slope from the DEM. The landscape slope values I found matched those reported in the literature under both topographic slope and stream gradient. Therefore, my results comparing stream gradient and lodge occupancy are alone among these studies.

The importance of physiographic variables like landscape slope over water body or vegetation type, though, is supported in the literature. Studies (e.g. Slough and Sadlier 1977, Allen 1983, Beier and Barrett 1987, Touihri et al. 2018) suggested physical characteristics in the landscape were more influential in determining site settlement and occupancy. Hood's (2019) study determined higher standard deviations of slope better related to active pond occupancy, suggesting greater variance between preferred slope values at active sites. This result differs from my results reported here. I determined that more active (or more frequently occupied) lodges showed less variation in slopes, with distinct preference for shallower slopes, and that these shallower slopes better related to occupancy, though again not significantly. Regarding my research question as to which habitat factor best influences lodge occupancy, landscape slope would be the greatest influence of the variables selected in this study. Put together, however, these results demonstrate that no particular habitat variable—hydrologic, vegetative, nor physiographic—significantly impacts occupancy.

Suitability Models:

The even-weighted suitability model resulted in moderate-to-low suitability across much of HWF with suitable areas occurring only within 100-meters of water (Figure 5). A simple visual analysis shows how many of the more suitable sites to have or have had a lodge since 2001. The mean suitability score across all lodges was 7.544 (standard deviation=1.42). In comparing suitability to lodge occupancy, single-use lodges had a higher average of 7.61 in this model compared to multi-year lodges whose average was 7.48. A t-test showed no significant difference ($p>0.05$) between the mean suitability scores of single- and multi-year lodges. A scatterplot of the even-weighted suitability scores and lodge occupancy shown in Figure 16 clearly displays no relationship between the two variables. For this reason, no correlation analysis was performed as the results would more than likely be insignificant.

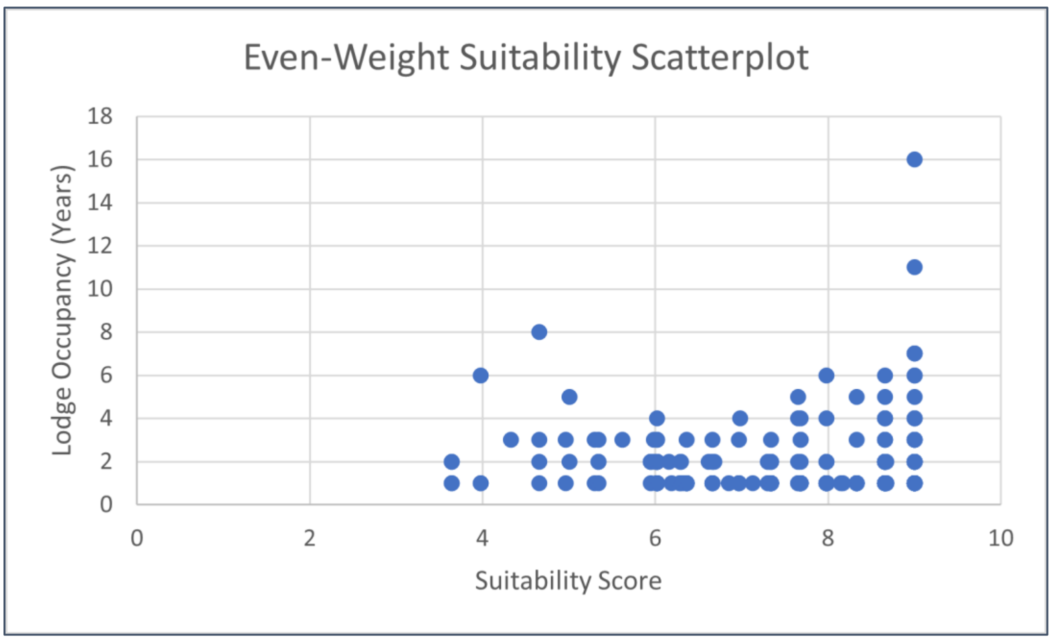

Figure 16: *Even Weighted Suitability and Lodge Occupancy Scatterplot*. Graph shows a scatterplot comparing the suitability scores from the even-weighted suitability model to lodge occupancy in total years occupied.

The weighted-suitability model also resulted in moderate-to-low suitability across HWF, including areas within 100-meters from water (Figure 6). A visual analysis reveals most lodges to be located on the few available suitable sites. The mean suitability score for all lodges in this model was 6.26 (standard deviation=1.24), considerably lower than the previous model. Single-use and multi-use lodges had near-even average suitability scores, 6.28 and 6.24, respectively. A t-test again showed no significant difference ($p>0.05$) between the suitability scores of the two occupancy categories. The scatterplot shown in Figure 17 visibly displays no relationship between suitability score and lodge occupancy, so no correlation analysis was performed here either.

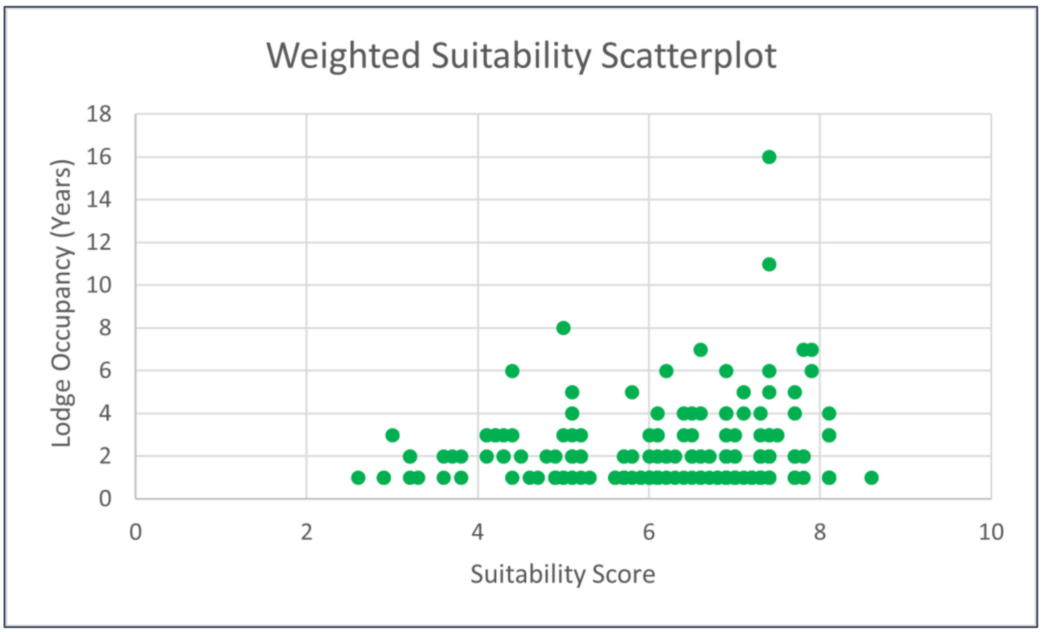

Figure 17: *Weighted Suitability and Lodge Occupancy Scatterplot*. Graph shows a scatterplot comparing the suitability scores from the weighted suitability model to lodge occupancy in total years occupied.

Unlike the previous models, the 100-meter distance suitability model more clearly demonstrates a distinction between suitable and unsuitable locations (Figure 7). Given the greater score assigned to sites closer to water's edge, it is unsurprising to see how suitability generally decreases with distance from water. More surprising is how landscape slope and vegetation type also visibly shape this model's suitability distributions; some areas closer to water are less suitable while sites 100 meters from water are still highly suitable. The average suitability score for all lodges in this model was 7.73 (standard deviation=1.3), the highest of the three models. This signifies that Rosenberg and McKelvey's (1999) point that models for central place foragers should include distance from the central place as a core tenet of said model is an important factor. The mean suitability score for single-year lodges was 7.67 and 7.8 for multi-year lodges. This was also the only suitability model where suitability was higher for multi-year lodges compared to single-year ones. The results of the t-test of unequal variance, however, revealed that this difference is not statistically significant ($p>0.05$). A scatterplot of 100-meter suitability scores and lodge occupancy again noticeably showed no relationship between the two, so no correlation analysis was conducted here as well (Figure 18).

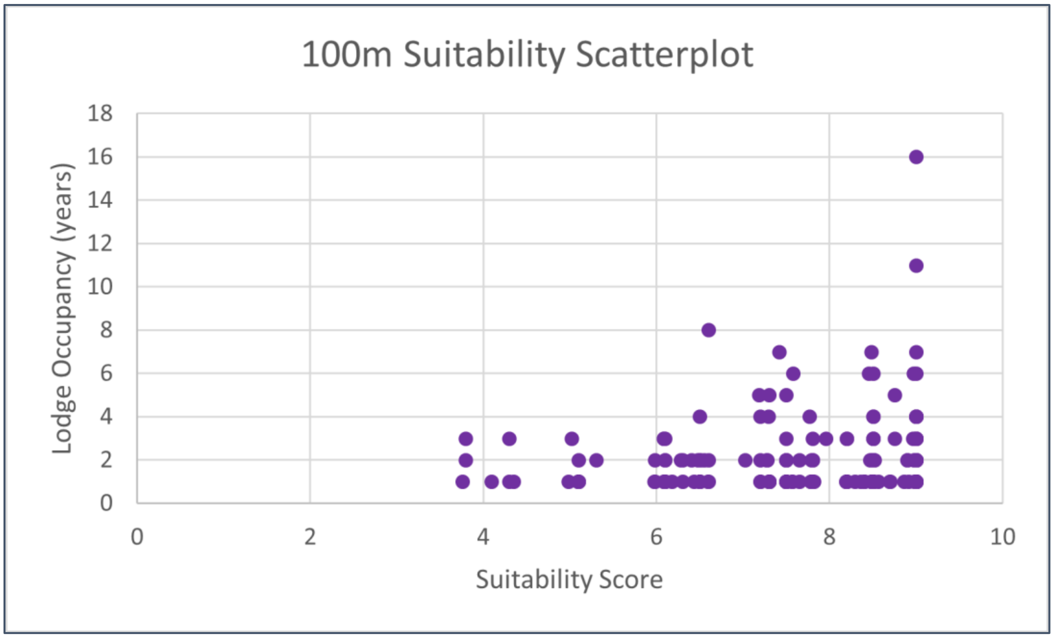

Figure 18: *100-Meter Suitability and Lodge Occupancy Scatterplot*. Graph shows a scatterplot comparing the suitability scores from the 100-meter distance suitability model to lodge occupancy in total years occupied.

The insignificant t-tests between single-use and multi-use lodges' suitability scores—in addition to the clear lack of relationship between suitability score and occupancy—across all suitability models demonstrates no relationship between lodge site suitability and lodge occupancy. Therefore, my answer to Research Question 2 is that more suitable sites are not occupied longer. From this, I reason that the factors that make suitable sites for settlement or colonization do not correlate to lodge occupancy.

Analyses for habitat variables' and suitability's influences on lodge occupancy both yield unsubstantial relationships. While beaver do exhibit selective preference for particular habitat characteristics, those characteristics alone do not define suitable sites for long-term lodge occupancy. Thus, in answering Research Question 3, I find no relationship between lodge site selection and lodge occupancy. I conclude that beaver do not consider suitability nor long-term occupancy when selecting lodge site locations.

In comparing the results of this study to those from other beaver occupancy studies, there are marked differences. Here I used the lodge as the unit of analysis for occupancy which resulted in no significant relationships between habitat variables, suitability, and occupancy. Other studies found various habitat parameters—such as stream gradient (Howard and Larson 1985, Beier and Barrett 1987), pond area and proportions of open water (Mumma et al. 2018, Hood 2019), and deciduous and/or herbaceous cover (Howard and Larson 1985, Beier and Barrett 1987, Broschart et al. 1989, Mumma et al. 2018, Hood 2019, Harrison 2011)—to significantly explain colony or territory occupancy or persistence. Given the difference in scale between a colony's entire territory and a single colony's lodge, it can be expected that other studies found more significant results for occupancy compared to mine here. This relates to my earlier point about the difference between mean occupancy time for the lodge (2.06 years) and the colony (9.24 years). Since the area for the colony is greater and often contains multiple lodges, the persistence or activity within an area can be greater as well. Examining the lodge, on the other hand, operates at a much smaller scale and may be too fine to produce significant relationships since mean occupancy is that much shorter.

Potential Explanations:

The insignificant results from this project highlight several key considerations. First, it is important to note the highly skewed nature of lodge occupancy in HWF (Figure 8). Most lodges were occupied for only one year and the number of lodges declined rapidly with each additional year of occupancy, giving considerable skew that favored shorter occupancy. The statistical analyses here did not transform the non-uniformly distributed lodge occupancy and that reason may explain why the habitat variables nor suitability showed any significant relationship to occupancy.

Second, the digitization of the GIS layers from hand-drawn maps from the 1940s may result in some inconsistencies. For instance, 13 of the 220 lodges were not located near a water source. The lodges—whose locations were determined via GPS—are accurately placed in GIS and are located near water in the field. The water sources for these lodges may have been mislocated on the original maps or developed in the decades after hand-drawing the maps, and thus are not reflected in the digitized GIS layers. Inclusion of these water sources could have slightly altered the results of the hydrology variable analysis in addition to the suitability analysis. If this problem is the case with the hydrology layers, there may be other inconsistencies in the digitized layers that could influence other results as well.

Third, as mentioned above, this project used the lodge as the unit of analysis which may be too fine a scale to develop significant relationships at. Other studies used the colony and/or its territory as the unit or scale for analysis which better reflects the species behavioral ecology. Beaver often abandon an individual lodge after 1 to 2 years but alternate between multiple lodges within their territory only to reoccupy the initial lodge at a later point. This behavior is most likely due to the depletion of vegetation within the immediate vicinity of the particular lodge after a few years as the result of beaver's central place foraging. Beaver may return to a particular lodge site once preferred vegetation or favorable stem sizes regenerate. The regeneration period for woody vegetation may likely match and explain the average inactive period of 8.08 years for lodges in HWF. But because beaver build multiple lodges within an area and abandon and reoccupy a series of lodges, analyzing individual lodges across all colonies may be too discrete a scale to understand beaver occupancy.

Fourth, suitability in this study only examined three characteristics, water body type, dominant vegetation type, and landscape slope. These variables were chosen as broad representations for the habitat categories—hydrologic, vegetation, and physiographic—that influence beaver suitability. Although the broadness of the variables may be beneficial in developing suitability models widely across regions and habitats, they may also be too broad, such that they do represent the area-specific characteristics that shape occupancy dynamics, specifically individual lodge use and longevity. More specific habitat variables like water level or percent vegetation cover—coupled with the colony-scale analysis—may be more practical in predicting occupancy, as other studies have shown. Furthermore, the three variables in this study alone may simply not be the most influential representatives of the hydrologic, vegetative, or physiographic conditions for occupancy at HWF.

Lastly, this project does not examine other factors outside habitat conditions that may influence occupancy. Water body type, distance to water body, dominant vegetation type, and landscape slope only accounted for less than 15% of the variance in lodge occupancy, leaving much space for external causes of occupancy. Other potential explanatory factors not considered here include: climate conditions and weather events, colony dynamics, and predation. While some studies (Müller-Schwarze and Schulte 1999, Lapointe St. Pierre et al. 2017, Touihri et al.

2018) also examined human presence (e.g. trappings, infrastructure) as a factor for colonization potential and colony presence, I believe such factors can be ruled out in HWF. HWF, as a designated field station, removes undue human influence like infrastructure that could otherwise impact beaver settlement and occupancy behavior.

At the lodge-scale, climate conditions and weather events could cause abandonment. Though Hood (2019) determined no relationship between total yearly precipitation and occupancy, the conditions may vary regionally so that yearly precipitation in HWF could require colonies to seek lodges with more stable water sources during years with less rainfall. Additionally, Hood's study does not account for individual storm events that could cause flooding resulting in dam breaches, which may prompt lodge abandonment as well.

Colony dynamics, such as territoriality or dispersal by juveniles, may also shape lodge site selection and occupancy. For instance, multiple colonies sharing larger streams may force lodge construction further apart so as to increase distance between territories (Müller-Schwarze and Schulte 1999). Distance to other lodges could also play a role not just between colonies, but within colonies as well. Proximity to additional functional lodges may reduce the occupancy at each individual lodge as beaver alternate between a series of lodges more readily. This proximity may also shape how and where beaver selection new lodge sites. When and how juveniles disperse from their parental colony might shape these factors as well. Delayed dispersal, wherein a juvenile stays with its parental colony for an additional season, could correspond to more consecutive and longer lodge occupancy. Dispersing beavers, at any age, may have to occupy marginal sites temporally before settling in more permanent areas, thereby resulting in lodges in poorer sites with shorter stints of occupancy (Müller-Schwarze and Schulte 1999).

Additionally, population characteristics over time, such as life history or predation and diseases, could be other factors shaping these lodge dynamics. Beaver lifespan is approximately 10-20 years, meaning the timespan of this study represents only 1-2 generations of beaver. As such, the lodge building and occupancy traits or trends found in this study only reflect the particular behaviors of select generations of beavers. Another factor could be predation. Though Petro et al. (2018) mentioned predation as a possible element that prevents dam establishment in certain areas, that same risk may apply to lodge establishment and lodge abandonment or persistence. Areas with increased predator presence may compel beaver to lodges in areas with deeper water levels or greater pond area to ensure safety in the expansive water. Predation could also generally reduce the total population of beavers in an area which has consequences for the number of individuals occupying lodges as well as dispersal rates and new lodge construction. Decreases in population sizes could also result from disease outbreaks or low birth rates in a region. Combined, the aforementioned factors may help to explain some of the variance not explained by the model's habitat conditions, but only represent a select number of plausible reasons.

Implications and Conclusions:

The project here examined what habitat factors, if any, best related to lodge occupancy, how these factors combined to determine lodge site suitability and its relationship to occupancy, and whether suitability for occupancy drives lodge site selection for beaver in an Adirondacks ecosystem. This study determined that certain factors, like water body type, dominant vegetation type, and landscape slope, are weak predictors of lodge site suitability and that lodge occupancy is not influenced by suitable conditions. Future studies should be cognizant of their scale of analysis (i.e. using lodges versus colony territory) as well as a wider range of habitat conditions that include both broad variables and fine-scale ones. Nonetheless, the project here provides a useful step in understanding occupancy at a fine-scale and how to develop generalized habitat suitability models appropriate for wide-use across spatial areas. Such an analysis may apply most readily to areas like eastern Canada, Minnesota, or other locations in the northeastern United States.

Understanding the habitat characteristics that shape beaver settlement and persistence in an area is vital to successfully understanding and managing the downscale impacts from beaver's engineering activities. Modeling suitable habitat through applications like GIS can be a great additional service for wildlife managers. GIS models can help be a predictive tool for visually representing and analyzing site colonization potential and successful resettlement sites. Broad suitability models like the one developed here can be helpful in their wide applicability across regions and landscapes. Their downside, however, is that broad models obscure the local and site-specific conditions that ultimately help shape suitability and occupancy dynamics in an area. Furthermore, when developing models that attempt to predict occupancy or persistence in relation to site settlement suitability, there are many factors outside the habitat that can influence such processes. Researchers creating habitat suitability models must continually weigh these considerations against one another. Thus, there is much room for additional predictive suitability models, especially those concerning occupancy or persistence through time, that push our understanding further by continuing to examine these different combinations.

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Teaching Experience

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Fall 2021 — Teaching Assistant | Department of Geography and the Environment
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Fall 2018 — Teaching Assistant | Renée Crown University Honors Program
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Honors & Awards

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August 2020 – May 2021 — University Fellowship
Department of Geography and the Environment

May 2020 — National Council for Geographic Education/American Association of Geographers Excellence of Scholarship Award
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Leadership & Service

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