Ecological and hydrological consequences of beaver activity in Riding Mountain National Park, Manitoba.

by

Peter Sinkins

A thesis presented to the University of Manitoba in partial fulfillment of the requirements for the degree of Master of Science in the Faculty of Graduate Studies

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ABSTRACT

Landscape and community level effects of beaver disturbance were investigated over a 60-year period in the boreal forest of Riding Mountain, Manitoba. Two sites were studied; both currently support high beaver populations, following reintroduction of the species in 1947. Beaver affect landscapes in two ways: (a) selective harvesting of aspen, altering forest stand structure, composition, and dynamics; (b) beaver damming, creating new wetland habitat. Beaver foraging distance ranged from 24 m to 40 m. Large amounts of timber were harvest by beaver, ranging from 16.4 m2/ha to 20.7 m2/ha (basal area). The number of beaver dams at one site increased from 12 in 1964 to 324 in 2004, resulting in a doubling of wetland habitat to 10% of the landscape. In addition, beaver were found to potentially affect 21-26% of the forested landscape through their foraging activities.

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CHAPTER 1

BIOLOGY AND ECOLOGY OF THE NORTH AMERICAN BEAVER

1.1 BEAVER BIOLOGY

1.1.1 Life History

The North American beaver (*Castor canadensis* Kuhl) is the largest member of the Order Rodentia endemic to the North American continent (Baker and Hill 2003). The beaver belongs to the family Castoridae, which traces its origin to the Oligocene Epoch (part of the Tertiary Period in the Cenozoic Era, about 33.7 to 23.8 million years ago), and reached its highest diversity during the late Tertiary Period (Cahn 1932). The genus *Castor* dates back to the Pleistocene Epoch, which began about 1.65 million years ago (Baker and Hill 2003). Today only two very closely related species comprise the genus *Castor*, the European beaver (*Castor fiber* L.) and the North American beaver (*Castor canadensis*). The pre-European population of beaver in North America has been estimated at between 60 and 400 million animals (Seton 1929; Baker and Hill 2003). The beaver ranged across the entire North American continent, as far north as the arctic tree line and as far south as northern Mexico.

Both the range and abundance of beaver in North America declined quickly following the arrival of Europeans on the continent (Naiman et al. 1988). The harvesting of beaver was unregulated during an intense period of trapping during the 18th and 19th centuries (Bird 1961). The presence of a large network of trading companies on the continent, together with the European fashion for beaver fur hats, resulted in the rapid extirpation of the North American beaver from many areas of its original range (Naiman et al. 1988).

The combination of reintroductions and regulated trapping in the early 20th century resulted in the re-establishment and recovery of the beaver over much of its original range (Rosell et al. 2005). However, in many areas the density of beaver is strongly limited by habitat degradation and loss. This loss of habitat is largely attributable to agricultural, forestry and other human land-use practices (Naiman et al. 1988). While beaver now occupy nearly their entire original range, population densities in many regions are only about 10% of their pre-European levels (Butler 1995). The current population of beaver in North America is estimated at between 6 and 12 million animals (Naiman et al. 1988).

Castor canadensis is a large rodent, the average adult weighing between 15 and 30 kg and reaching an overall body length of over 100 cm with a tail measuring about 30 cm (Baker and Hill 2003). Growth of beaver is initially rapid, but begins to stabilize at 4 or 5 years of age and stops when the animal is approximately 9 years old (Hill 1982). Beaver typically live for approximately 10-12 years, but some individuals have been reported to survive for 21 years (Novak 1977).

Beaver are easily recognizable. Their heavily muscled body is covered with dark fur, and they have a distinctive paddle-like, dorso-ventrally flattened tail (Green 1936). The flattened tail is an important attribute, providing locomotion underwater, storing fat reserves, and aiding in heat exchange. In addition, beavers slap their flattened tail on the water surface to give warning of potential predators (Müller-Schwarze and Sun 2003).

Beavers have several adaptive traits that reflect their semi-aquatic habit. Their general shape has a fitness ratio of 4.8 (close to that of seals), which allows ease of movement through water (Reynolds 1993). The large and powerful flattened tail acts as a rudder to increase dexterity while swimming (Müller-Schwarze and Sun 2003). The large webbed hind feet of beaver increase propulsion while swimming, while the clawed forefeet are adapted for both feeding and dam construction (Green 1936). Valves close the ears and nostrils when the animal is swimming, and the lips are placed inside of the incisors to allow browsing under the water. Underwater vision is facilitated by transparent nictitating membranes that protect the eyes. The long, sharp and strong incisors, which grow continuously, allow beaver to fell very large trees that are used for dam building and food (Müller-Schwarze and Sun 2003).

The North American beaver is a monogamous species that breeds during the winter and gives birth late the following spring (Baker and Hill 2003). Litter size is commonly 4 to 6 kits. Kits usually remain with the parent for about two years, aiding with parenting and lodge care. After two years or so they leave their parents to establish their own colony (Müller-Schwarze and Sun 2003). A beaver colony is a closed extended family unit typically consisting of two adult parents, 4-6 first-year kits, and (sometimes) second-year kits. A typical colony has 4 to 8 family members (Jenkins and Busher 1979), with a mean of 5.7 beaver per colony reported from Canada (Frey and Avery 2004). Beavers spend most of their lives in colonies with their kits: once a colony has been established,

the adults will remain at the pond site for the rest of their lives unless driven out by drought, food/habitat loss, or predators (Svendsen 1989; Baker and Hill 2003).

Beaver colonies have well-established territories that are regularly marked and defended. The primary mode of territory marking is based on scent (Aleksiuk 1968; Müller-Schwarze and Sun 2003). Beavers excrete castoreum and/or anal gland secretions onto the tops of constructed scent mounds to ward off other beavers. These scent mounds ring the colony territory (Müller-Schwarze and Sun 2003). Castoreum has other functions as well: it aids in night navigation, and is used as a general indicator of physiological status within the family unit (Butler and Butler 1980). Castoreum may also serve as an "enhancer", elevating the confidence of colony residents while suppressing that of invasive beavers (Svendsen 1980). Beavers are able to distinguish among family members, near-neighbours and far-neighbours based on scent mounds, and will spend much time over-marking the scents of foreign intruders (Schulte 1998).

1.1.2 Population Dynamics

When older (about two year-old) kits disperse from their parent colony, they must locate an environment that can support a new colony. The dispersal of sub-adults is the principal mode of population expansion in beavers (Müller-Schwarze and Sun 2003). Sub-adults may move upstream, downstream and even across land to new watersheds in their search for a new home, but most dispersing sub-adults search downstream (Sun et al. 2000).

Beaver density is usually reported as the number of colonies per km (or other unit length) of stream, or alternatively as the number of colonies per unit area (km^2). Densities vary greatly with topography, the availability of favourable habitat, depredation, human trapping intensity, water quality and permanence, and various other factors (Baker and Hill 2003; Naiman et al. 1988). In Canada, beaver densities range from a mean of 0.33 colonies per km^2 in New Brunswick to a high of 3.51 colonies per km^2 in central Alberta. The maximum mean density in the boreal region of Canada is 1.0-1.2 colonies per km^2 (Broschart et al. 1989; Müller-Schwarze and Sun 2003).

The carrying capacity of beaver in a given habitat is dependent primarily on food availability and water level fluctuations, i.e. inter-annual variability in precipitation levels (Müller-Schwarze and Sun 2003). A natural population (i.e. one not subject to trapping) is considered to have reached its climax or carrying capacity when the habitat is saturated and a major increase in the number of colonies is not sustainable. A number of specific characteristics are associated with beaver populations at carrying capacity: new beaver colonies are established in sub-optimal habitats such as streams with faster moving water on steeper gradients; two-year-old sub-adults remain with their parent colony longer; less-preferred food items are browsed and harvested; and individuals forage further from the edge of water bodies. However, body weight, population density and family size do not vary significantly between climax and non-climax beaver populations (Müller-Schwarze and Sun 2003).

1.1.3 Disease

The most common disease affecting beaver is type B tularemia, a water-borne disease caused by the bacterium *Francisella tularensis* (Baker and Hill 2003). This disease, which is common in semi-aquatic mammals such as muskrat and beaver, has been described as "plague-like" (Davis et al. 1970). Infections can usually be traced to feces or infected corpses within waterbodies inhabited by beaver, since the bacteria contaminate the entire water column (Müller-Schwarze and Sun 2003). Human infections are rare and non-fatal, with type B tularemia accounting for only 5-10% of the total human tularemia infections (Davis et al. 1970). The disease can be spread to humans through contact with infected corpses, ingestion of contaminated water, or from biting insects such as mosquitoes and ticks that have previously fed on an infected animal (Davis et al. 1970).

During 1939 and 1940 in Montana, several hundred beaver were found dead due to a tularemia outbreak (Jellison et al. 1942). Many animal species in the Riding Mountain National Park region can carry tularemia, including domestic animals, rodents, deer, and various bird and predator species. Although the biological requirements for a type B tularemia outbreak are met in Riding Mountain, the effects of the disease have been minimal during the 20th century. A few isolated incidents of the disease occurred in the 1970s, mainly outside the National Park boundary. The dense beaver population in Riding Mountain is a cause for concern, however, and careful monitoring of disease in both muskrat and beaver is recommended.

There is some historical evidence of tularemia epidemics in the past. John Tanner, an early inhabitant of the Clear Lake region, reported an outbreak of beaver "distemper" in 1801 in the Fort Dauphin area:

> "*Afterward I directed my attention more to the hunting of beaver, I knew of more than twenty gangs of beaver in the country about my camp, and I now went and began to break up the lodges, but I was much surprised to find nearly all of them empty. At last I found that some kind of distemper was prevailing among these animals which destroyed them in vast numbers. I found them dead and dying in the water, on the ice, and on the land. Sometimes I found one that, having cut a tree half down, had died at its roots; sometimes one who had drawn a stick of timber half way to his lodge was lying dead by his burden. Many of them which I opened, were red and bloody about the heart. Those in large rivers and running water suffered less. Almost all of those that lived in ponds and stagnant water, died. Since that year the beaver have never been so plentiful in the country of Red River and Hudson's Bay, as they used formerly to be*".

According to Dr. R.D. Bird, this description is entirely consistent with a type B tularaemia epidemic (Parker 1978).

1.1.4 Depredation and Dam Construction

Beavers will go to great lengths to protect themselves from the various predators that share their habitat. Beaver are slow-moving and awkward on land, and they move about

in cautious, ambling steps (Green 1936). In boreal regions such as Riding Mountain National Park, beaver are an attractive prey for predators such as the black bear (*Ursus americanus*), wolf (*Canis lupus*), lynx (*Lynx canadensis*) and fisher (*Martes pennanti*). Although beavers are large and powerful enough to haul harvested stems for up to 200 m over land, the majority of their foraging efforts occur within 20 m of a major water body (usually an impounded wetland). This is thought to be a predator-avoidance strategy, since high predator densities in the vicinity of a beaver pond result in less time spent on land (Barnes and Mallik 2001). Unfortunately for beavers, densely forested regions such as Riding Mountain contain mostly small-order streams that offer very limited protection. An aquatic rodent such as the beaver has only one option to increase its rate of survival: to turn the forest itself into an aquatic environment. To accomplish this, beavers have evolved to do what no other animal (expect humans) can: they dam moving water.

Beaver are generalist herbivores, feeding on wide variety of vegetation ranging from macrophytes and herbaceous vegetation to tree branches. However, deciduous woody vegetation is the principal component of their diet (Donker and Fryxell 1999). Surprisingly, the availability of food is not the primary reason for selecting a site for a new colony (Barnes and Mallik 1997). Instead, beaver select a dam-building site based on the proximity and availability of woody vegetation required for dam construction. The presence of deciduous woody vegetation close to the shoreline ensures quick construction of the dam and lodge, and minimizes the time spent on land exposed to predators (Barnes and Mallik 1997). Although some riparian woody species (e.g. poplars, willows) are palatable to beaver, other species such as alder are used only for

construction purposes. It appears that beaver do not differentiate between palatable and unpalatable species in selecting a new dam site (Barnes and Mallik 1996).

Through the construction of dams, beaver are able to alter low-order stream flow and thus modify and increase their preferred wetland habitat. It is for this reason that the beaver is sometimes referred to as an "ecosystem engineer" (Jones et al. 1997; Meentemeyer and Butler 1999). Beavers will use nearly any available material to construct their dam, but tend to maximize the use of mud and unpalatable woody stems and branches (Baker and Hill 2003; Müller-Schwarze and Sun 2003). Dam construction by beaver is initiated by a critical environmental cue: water running down a gradient (Barnes and Mallik 1997). Dams are constructed by first finding or creating a ridge perpendicular to the flow of water, and then by using woody stems, rocks, mud and any other available substrata to add structure (Baker and Hill 2003). The bulk of the dam consists of woody stems and branches oriented parallel to the flow of water and jammed into the stream bottom for added support, with additional material intertwined and weaved perpendicularly into the main support structure (Baker and Hill 2003).

The building of a dam alters the geomorphology of a stream in many ways: water velocity is slowed, discharge regimes and nutrient outputs are altered, and rates of sediment and organic matter loading are greatly increased (Pinay and Naiman 1991; Butler 1995; Rosell et al. 2005). In addition, the amount of permanently flooded soil in the area is greatly increased. The large ponds created by these impoundments afford beaver colonies a measure of protection from predators (Naiman et al. 1988). Since

beavers tend to forage on riparian vegetation, the impoundment also greatly increases the potential food supply by expanding the shoreline length (Ray et al. 2001). The ponds created by beaver activity produce a wetland patchwork within a topographically complex landscape. These wetlands have geomorphic and vegetative features that can persist for decades or even centuries (Naiman 1988; Shaw 1993).

Maintenance of active beaver dams is carried out during the spring and summer in northern climates, and year-round in more southerly locations (Baker and Hill 2003). Both sub-adults and adults inspect and maintain the dam, although adults undertake most of the serious maintenance. The entire colony works as a group to undertake major maintenance such as repairing a breached dam (Baker and Hill 2003). The work required to maintain and repair a functioning dam can be considerable: a dam may be up to 600 m in length, 2 m in height, and over 1m in width at its crest (Butler 1995).

Beaver will establish a lodge or beaver house in the deepest portion of the impounded wetland (Baker and Hill 2003). The lodge provides a permanent residence for the colony, protecting them from both predators and inclement weather. In northern climates, the lodge is a warm, well-insulated home that increases winter beaver survival beneath the snow and ice. Beavers may also build a bank den as a temporary residence while the main lodge is being built. Bank dens may be used as permanent residences when the water body is very large (lake or large river) or the water is very fast-moving (Baker and Hill 2003).

A beaver colony will generally remain at a single location for the duration of the lives of the parents: this undoubtedly reflects the considerable time and effort required to establish and maintain a dam and lodge. It is for this reason that the beaver is generally described as a central-place forager (McGinley and Whitman 1985; Johnston and Naiman 1990a; Wheatley 1997a,b,c).

1.1.5 Browse Selection

The central-place foraging activity of beaver has a tremendous impact on the vegetation adjacent to a beaver-impounded wetland. Because beavers forage close to their established pond habitats for years or even decades, their long-term impact on riparian vegetation is considerable when compared to ungulate herbivores that forage over much wider areas (Barnes and Mallik 2001). The long-term herbivorous activity of beavers within a small area greatly intensifies their local effect on riparian forests and wetlands.

Unlike any other animal (with the notable exception of humans), beaver are able to harvest whole mature trees. Beaver harvest far more biomass than they actually use for food (Johnston and Naiman 1990a). In northern Minnesota, a beaver population at carrying capacity harvests an estimated 1.3 Mg/ha of woody biomass each year. This is 15-4300 times the amount browsed by moose populations in the same area, and more than twice the amount consumed by a herd of ungulates in Africa's Serengeti Plains (Johnston and Naiman 1990a). Unlike these large ungulates, however, beavers are very "wasteful" and consume only a fraction of the woody biomass that they harvest (Johnston

and Naiman 1990a). In a second study from northern Minnesota, it was found that all harvested woody tissue greater than 1.3 cm in diameter, and two-thirds of all edible trembling aspen biomass, remained unconsumed by beaver (Aldous 1938). Given this high rate of tree loss, it is not uncommon for a beaver colony to eventually deplete its primary food source (mature trees). When this occurs the colony may be forced to relocate, or alternatively, to rely entirely on macrophytes as a source of food (Müller-Schwarze and Sun 2003). Aquatic vegetation has been found to sustain high levels of beaver activity even in the absence of preferred early-succession woody species such as trembling aspen (Fryxell 2001).

During the winter, beavers are much less apt to forage on land, particularly in cold climates where the impounded pond remains frozen during winter. Instead, beavers build a food cache near their lodge for winter foraging. The food cache is created by first floating coarse woody material to deep water near the lodge, and then placing more palatable branches beneath the initial raft (Baker and Hill 2003). These palatable branches become water-logged, and so remain under the ice for feeding during the winter.

Although beaver are considered generalist herbivores, they are very selective in their harvesting of mature trees. It is this selective harvesting behaviour that complicates their impact on riparian forest stands. Beaver can potentially haul cut stems at least 200 m over land, but the majority of harvesting activity takes place close to water. In northern Ontario, half of all stems felled by beaver were less than 10 m from the pond edge, and

over 90% were within 20 m (Barnes and Mallik 2001). Furthermore, almost all the foraging for dam construction (mainly species of alder) took place within 20 m of the pond (Barnes and Mallik 1996). A possible explanation of why beaver forage close to the water is that they are unable to directionally fell trees: because trees growing near water have a greater amount of biomass (branches and foliage) on their water-side where light availability is greater, they are more likely to fall towards or into the water when felled (Barnes and Mallik 2001). In addition, beavers foraging close to open water have a quick route of escape from potential predators (Müller-Schwarze and Sun 2003).

Beaver often increase their foraging range by digging canals, or "beaver runs", gaining easier access to food and construction material and reducing the dragging distance of woody material over land. These canals can persist for an extended period of time following pond abandonment (personal observation).

Over much of the Canadian boreal forest, trembling aspen (*Populus tremuloides*) is the preferred forage of beaver and is harvested in preference to other tree species (Barnes and Mallik 2001). White birch (*Betula papyrifera*) and willow (*Salix* spp.) are of secondary importance, as are other poplar species (e.g. balsam poplar, *P. balsamifera*). Beavers will also consume many woody shrub species, including choke cherry (*Prunus virginiana*), red osier dogwood (*Cornus stolonifera*), and beaked hazelnut (*Corylus cornuta*). Healthy beaver populations can also be found in stands of maple (*Acer* spp.) and beech (*Fagus* spp.) if trembling aspen is not available (Müller-Schwarze and Sun 2003). Alders (*Alnus spp.*) and other riparian shrubs, and occasionally coniferous trees,

are used exclusively for dam construction (Barnes and Mallik 2001). Although beaver have been shown to browse on pine bark (*Pinus* spp.) when food is scarce, they generally avoid coniferous trees. With a few rare exceptions, spruce (*Picea* spp.) are avoided altogether (Müller-Schwarze and Sun 2003). Selective browsing of tree species by beaver has the potential to strongly influence the composition, structure, and dynamics of riparian forest stands (Barnes and Dibble 1988; Barnes and Mallik 2001; Rosell et al. 2005).

1.2 BEAVER ECOLOGY

1.2.1 Drainage Alteration

Beaver alter the drainage network of small-order streams by creating dammed impoundments. These impoundments are often dispersed along the length of the stream, creating a "stair-step" profile. Undisturbed beaver populations have the potential to influence 20-40% of the length of second to fifth order streams (Ford and Naiman 1988). The retention of sediment and organic matter, the flooding of uplands, and the general reduction in stream velocity resulting from beaver activity all play a role in dramatically altering the hydrologic and biogeochemical processes governing stream ecology (Shaw 1993; Naiman et al. 1994).

The reduced slope of the stream channel following beaver impoundment decreases the transport of sediment downstream. This results in sediment infilling of beaver ponds as suspended particles settle in slower-moving water (Butler 1995). The sediment of a typical beaver pond consists of typical stream sediment material intermixed with organic

debris, and bound together by emergent vegetation (Ives 1942). By minimizing erosion, the emergent macrophyte vegetation "locks" the accumulating sediment into the pond environment. The amount of sediment material accumulated by beaver damming activity can be very high: an average-sized dam containing 4-18 m^3 of wood accumulates up to 6,500 m^3 of sediment in its impoundment (Naiman et al. 1986). In Voyageur National Park in northern Minnesota, an area of 673 km^2 was estimated to contain 3.2×10^6 m^3 of accumulated sediment in small order streams dammed by beaver (Naiman et al. 1986). In an abandoned beaver pond in Glacier National Park, Montana, sediment accumulation rates were estimated at 10 cm/yr in depth, and 171 m^3/yr in volume (Butler 1995).

The decrease in water velocity attributable to beaver damming activity greatly impacts the carbon budget of a stream community. While carbon inputs are much higher into a non-dammed stream than an adjacent beaver impoundment, the standing stock of carbon and total carbon is much higher in the pond (Naiman et al. 1988). Although the pond receives less carbon overall, carbon retention is much higher: carbon turnover increases from 24 years in an unimpeded stream to 161 years in a beaver impoundment (Naiman et al. 1988).

The pond environment is also anoxic, greatly reducing decomposition rates and turning the pond into a net carbon sink (Müller-Schwarze and Sun 2003). However, the anaerobic soil conditions created by a higher water table and flooded conditions result in the development of a community of methane-producing organisms in the pond sediment (Naiman et al. 1986). As a result, methane evasion rates in beaver ponds are over 30

times higher than in a non-dammed stream environment of equivalent surface area (Ford and Naiman 1988). This increases the impact of beaver activity on carbon cycling, since methane evasion is an important vector for carbon flux into the atmosphere.

Beaver impoundments are also net nitrogen sinks (Naiman and Melillo 1984). The sediment in beaver ponds is much richer in nitrogen-fixing microbes than the sediment of non-dammed streams. The accumulated nitrogen is lost mainly to emergent insects, and to the flow of water downstream. Even a single dam increases the nitrogen availability to the riparian ecosystem downstream (Naiman and Melillo 1984; Francis et al. 1985).

The effects of beaver damming activity on a small-order stream include a decrease in turbidity downstream, and nutrient accumulation in the impoundment. These effects lead to increased productivity, as well as a reduction in the variability of the discharge regime (Naiman et al. 1986). There is an overall shift of nutrients from the upland terrestrial riparian zone to the impoundment (Naiman et al. 1988). The accumulation of sediment and organic debris results in the pond becoming a sink for both carbon and nitrogen in the environment. One result of this shift in biochemical cycling is a decrease in the pH of impounded water (Muller-Schwarze and Sun 2003; Rosell et al. 2005). These indirect alterations to the aquatic system by beaver impoundment produce an aquatic patch that is sharply divided from the surrounding riparian forest, in terms of both habitat and nutrient availability (Johnston and Naiman 1987).

1.2.2 Beaver Disturbance Effects on Forest Structure and Composition

Beavers directly change the composition and structure of riparian forest stands through their selective harvesting of mature trees. In addition, the removal of canopy trees increases the amount of light available to non-harvested trees, and to the shrubs and understory plant species found beneath them. This increase in light availability results in higher net primary productivity of the forest understory (Johnston and Naiman 1990a). The removal of the mature trees also creates "gaps" in a continuous forest canopy, increasing the growth of canopy trees adjacent to the gap and promoting sapling regeneration within the gap itself. The selective harvesting of mature trembling aspen trees by beaver triggers a marked increase in root suckering and the subsequent development of a regeneration layer of rapidly-growing, light-demanding aspen saplings (Johnston and Naiman 1990a).

A long-term study of landscape change on the Kabetogama Peninsula in Voyageurs National Park, Minnesota, illustrates the role of beaver activity in dramatically altering forest stand composition and structure (Naiman et al. 1988). The beaver population in the region increased dramatically between 1940 and 1986, from 71 to 835 colonies. During this period the proportion of the Peninsula impounded by water increased from 1% to 13%. In addition, an estimated 12-15% of the forested uplands were directly affected by beaver browsing. Overall, by 1986 nearly 30% of the Peninsula was directly affected by beaver activity (Naiman et al. 1988). Notably, the Upland Plateau District of Riding Mountain National Park has seen a similar increase in beaver populations over the same time period (Frey and Avery 2004).

1.2.3 Beaver Effects on Forest Succession

Selective harvesting and browsing by beaver has the potential to impact boreal mixed-wood forest succession trends greatly. Beaver preferentially harvest mature trees of early successional species such as trembling aspen and willow. The consequent opening of the forest canopy increases light availability, promoting the regeneration of shade-tolerant species (Donkor and Fryxell 1999; Fryxell 2001) and releasing shade-intolerant species from competition (Pastor and Naiman 1992).

The preferred food for beaver is early successional, shade-intolerant deciduous trees, particularly trembling aspen (Fryxell 2001). The selective harvesting of trembling aspen by beaver, and their avoidance of conifer species, alter the composition and succession status of forest stands over time. Stands may undergo "accelerated" succession, in which shade-intolerant species more readily regenerate in beaver-created canopy gaps resulting in a rapid shift toward late-succession, conifer-dominated stands (Fryxell 2001). In boreal mixed-wood stands (e.g. the white spruce – trembling aspen forests of Riding Mountain National Park), mature coniferous trees and conifer saplings are generally left undamaged by beaver. Removal of trembling aspen by beaver increases the light available to shade-tolerant conifers, releasing them from aspen competition. As a consequence, non-browsed conifer species will increasingly dominate riparian habitats over time (Naiman et al. 1988). Over many years this produces a patchwork landscape of wetlands and conifer-dominated stands in an otherwise deciduous or mixed-wood boreal forest environment (Johnston and Naiman 1990a).

An alternative hypothesis is that beaver herbivory inhibits normal successional trajectories. In this hypothesis, shade-intolerant early succession species such as trembling aspen actively recruit into the canopy gaps created by beaver activity (Pastor and Naiman 1992). In this scenario, early succession species undergo competitive release in beaver-created gaps, resulting in stands remaining in an early succession state. This hypothesis is supported by the observation that regeneration of harvested tree species, particularly trembling aspen and willow, is positively correlated with beaver activity (Pastor and Naiman 1992). However, research in northern Ontario has shown that trembling aspen often does not recover well from beaver harvesting activities (Barnes and Mallik 2001). The study, which followed beaver-harvested stands for twelve years, demonstrated an overall increase in conifer abundance and a decline in aspen abundance in support of the "accelerated" succession hypothesis. It appears that repeated harvesting by beaver eventually depletes the resources of aspen roots, reducing the number and vigour of aspen suckers (Gese and Shadle 1943; Barnes and Mallik 2001). However, newly-formed trembling aspen root suckers may produce secondary metabolites that make them unpalatable to beaver (Basey et al. 1988, 1990).

Other investigators have found that recruitment of trembling aspen is inversely proportional to the distance-dependant risk of beaver harvesting damage, while the relationship with conifer recruitment is positive (Donker and Fryxell 1999). This is in direct contrast to the findings of Pastor and Naiman (1992). It may be that both early and late-succession tree species are promoted by the creation of canopy gaps by beaver. In Wisconsin floodplain forest stands affected by beaver activity, succession is not linear at

all: instead, recruitment into gaps is strongly dependent on local environmental conditions (Barnes and Dibble 1988). Clearly more research is needed to determine the underlying mechanisms driving forest succession in beaver-affected stands.

Succession within and surrounding an abandoned beaver impoundment is strongly influenced by both water depth and the frequency/duration of re-flooding (McMaster and McMaster 2001). Re-flooding is determined at least in part by the condition of the abandoned beaver dam: ponds with well-constructed intact dams tend to drain slowly and re-flood more frequently. Plant species composition in recently abandoned impoundments is directly related to water depth. As a dam ages and the impoundment begins to drain, water depth becomes less of a factor and succession follows a linear sequence, from submersed to emergent macrophytes to woody species (Shaw 1993). Eventually the dam deteriorates completely and no longer restricts the stream flow, allowing recruitment from the surrounding riparian forest (McMaster and McMaster 2001). In mountainous regions, the majority of abandoned dams flush their sediments during spring floods and may never reach the meadow stage (Meentemeyer and Butler 1999).

1.2.4 Beaver Disturbance and Wetland Patch Dynamics

A "patch" is a plant community whose species composition and/or structure differs from that of the dominant community on the landscape in which it is embedded (Johnston and Naiman 1990b). Beaver activity creates and perpetuates a complex mosaic of aquatic patches in an otherwise forested landscape (Naiman et al. 1988; Wright et al. 2004).

Emergent macrophyte marshes, bogs and forested wetlands that develop from abandoned beaver impoundments can persist for centuries (Naiman et al. 1988). The influence of beaver activity on wetland community succession and structure is profound. Wetland plant communities originating in abandoned beaver impoundments are in a constant state of flux, since water and soil saturation levels change over time as the beaver dam slowly deteriorates. The vascular plant community found in wetlands created by beaver damming reflects the presence of saturated soil and full sunlight conditions. Saturated soil conditions prevent the invasion of woody species from the surrounding riparian forest community, and likely play a critical role in wetland patch stability over time (Shaw 1993; McMaster and McMaster 2000).

Following abandonment, plant community succession in beaver-created wetland patches may follow a clear linear sequence (Remillard et al. 1987). Four succession stages are characteristic: open water, emergent macrophyte, emergent macrophyte/shrub, and shrub. Succession is often cyclical, since beaver will often re-occupy abandoned dam sites after the depleted food supply has had a chance to regenerate. Beaver dam sites may be continually abandoned and re-occupied over a 10 to 30 year period: re-occupation returns the wetland to an open water community (Remillard et al. 1987).

A multidirectional pathway model for beaver pond succession in boreal forest ecosystems has been proposed (Naiman et al. 1988). It is hypothesized that a specific succession sequence (e.g. to a forested wetland vs. a bog) is dependent on the length of time that the impounded wetland is active. Numerous factors such as hydrology,

topography, and other types of disturbances interact with beaver activity to produce a complex set of succession sequences. For example, a beaver-created wetland patch may follow a circular succession sequence, from an established pond to a wet meadow and eventually a low-order stream that is then re-flooded by beaver. Alternatively, the impoundment may succeed to an emergent wetland, bog or forested wetland. Should this occur, a former impoundment is much more resistant to re-flooding by beaver and it may persist for centuries (Naiman et al. 1988).

The periphery of an old beaver impoundment or meadow typically consists of graminoid or sedge species and conifer saplings, forming a sharp boundary with the surrounding forest (personal observation). Invasion by conifers into the wet meadow community is very slow despite the close proximity of a viable seed source. The anoxic soil conditions created during flooding may play a critical role in limiting tree recruitment (Terwilliger and Pastor 1999). Specifically, over an extended period of time the anoxic soil conditions of a flooded pond completely depletes the fungal community. Conifers, which form essential ectomycorrhizal associations with fungi, may be prevented from colonizing a beaver meadow until the fungal symbionts recolonize the soil (Terwilliger and Pastor 1999).

1.2.5 The Beaver as an Ecosystem Engineer

Ecosystem engineers are "organisms that directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials", while physical ecosystem engineering by organisms involves "the physical

modification, maintenance, or creation of habitats" (Jones et al. 1997). The beaver is an excellent example of an ecosystem engineer. At the landscape level, beavers increase the number and diversity of habitats available to other organisms, which in turn increases regional species richness and diversity (Wright and Flecker 2003; Jones et al. 1997; Rosell et al. 2005). In wetland patches modified by beaver activity in the central Adirondacks of New York, vascular plant species richness increased by 25% compared to undisturbed habitats (Wright et al. 2002). In Alaskan beaver meadows, beaver activity was found to increase bryophyte species richness (Pollock et al. 1998).

Beaver activity greatly affects invertebrate stream communities (Rosell et al. 2005). Benthic and open water macro-invertebrate densities in Ontario and Quebec are two to five times higher in beaver impoundments than in adjacent stream habitats (McDowell and Naiman 1986; France 1997). Mosquito population density decreases overall, and there is a shift in species composition (Baker and Hill 2003). Silt-loving invertebrate species such as dragonfly larvae are favoured over species preferring gravel and sandy substrates (Müller-Schwarze and Sun 2003). In general, stream impoundment by beaver activity results in a shift in invertebrate community composition from shredders and scrapers to collectors and predators (Rosell et al. 2005; Naiman et al. 1988).

Increases in bird and mammal populations can also be attributed directly to the creation of wetland patches by beaver (Brown et al. 1996; Baker and Hill 2003). Beaver ponds are used by birds as stop-over sites on migration flyways: beaver ponds have a large amount of open water, enhanced vegetation cover that affords protection from

predators, and an ample food supply in the form of high invertebrate densities (McCall et al. 1996; Rosell et al. 2005). Many mammal species also benefit from the wetland patches created by beaver. Other semi-aquatic mammals such as muskrat (*Ondatra zibethicus*), otter (*Lutra canadensis*) and mink (*Mustela vison*) will move into an impounded area and remain there long after the beaver colony has departed (Baker and Hill 2003; Rosell et al. 2005). Moose (*Alces alces*) are frequent users of beaver ponds, since the expanded riparian zone around the pond greatly increases the productivity of their preferred food plant species (McMaster and McMaster 2000). While surprisingly few studies have quantified the effect of beaver habitat engineering on plant, insect, bird, and mammal diversity and abundance, the importance of modified stream habitat to many species suggests that beaver play a key role in creating and maintaining a diverse habitat landscape. It is for this reason that many researchers recognize the beaver as a "keystone" species (Rosell et al. 2005).

In boreal forest ecosystems there is little biotic overlap between wetland and forested habitats. Beaver activity increases the diversity and abundance of wetland habitats, which in turn promotes species richness and diversity (Johnston and Naiman 1990a; Wright et al. 2002, 2004). Selective foraging by beaver further increases species richness and diversity in riparian habitats by facilitating the regeneration of both preferred and non-preferred plant species (Donkor and Fryxell 2000; Rosell et al. 2005).

The North American beaver has a considerable impact on its environment by increasing wetland habitat, influencing forest composition and structure, altering forest

succession pathways, and creating a patchy habitat landscape that promotes biodiversity. Beavers significantly modify their habitat by damming small, high-order streams and by flooding large sections of riparian and upland forest. As a central-place forager, beavers remove preferred canopy trees from the local region and thus alter greatly the composition and structure of forest stands. In Riding Mountain National Park, the selective harvesting of trembling aspen by beaver has resulted in the dominance of coniferous tree species in forest stands adjacent to wetlands, lakes, and steams.

Ecosystem engineering by beavers increases landscape heterogeneity and habitat diversity, which in turn promotes species richness and diversity. In the boreal forest of northern Minnesota, it has been shown that beavers play a pivotal ecological role, directly affecting nearly 30% of the landscape though their flooding and harvesting activities. The rapid increase in beaver population density in Riding Mountain National Park since the 1940s is similar to that seen in northern Minnesota, suggesting that the impact of beaver activity on a boreal mixedwood forest ecosystem may be as dramatic as those reported in Minnesota (Naiman et al. 1986, 1988).

1.3 BEAVER MANAGEMENT

1.3.1 Nuisance Beaver

The term "nuisance beaver" is used in reference to beavers whose damming and/or harvesting behaviours result in damage to private or public property. The construction of a beaver dam adjacent to a road has a major impact on road infrastructure, softening the gravel base or even submerging the entire roadway (Müller-Schwarze and Sun 2003). A

major cause of road damage is the repeated damming and blocking of culverts by beaver: a blocked culvert often results in severe road erosion. Beavers are thought to block culverts in response to the environmental cue of water moving down a gradient (Barnes and Mallik 1997).

The flooding that results from beaver damming can also cause considerable damage to farmland, trails, railway lines, golf courses, private yards and other human habitats. The harvesting of mature trees and shrubs by beaver is a major threat to parks and gardens, since aesthetically pleasing trees or shrubs are removed from human settlement areas. Flooding and harvesting by beaver can also have a strong negative impact on forest yields (Baker and Hill 2003). Loss of mature timber to beaver flooding and harvesting can be considerable, particularly in boreal forest regions on rolling terrain. For example, in northern Minnesota almost one-third of the forest habitat is affected by beaver activity (Naiman et al. 1986, 1988).

Perhaps the single greatest threat to humans from nuisance beaver is the potential of catastrophic dam failure. Catastrophic dam failure occurs when an old or weak dam is exposed to a heavy rain event, causing dam collapse and a subsequent downstream flash flood capable of causing considerable damage (Müller-Schwarze and Sun 2003).

Confrontations are inevitable as humans encroach into native beaver habitat in the boreal forest. The threat is of course two-sided: while beaver populations are adversely affected by the movement of humans into their habitat, beaver often cause considerable

economic damage to community infrastructure and managed forest stands. In many regions of rural Canada an aggressive trapping strategy is in place to control or suppress beaver populations near roads and communities. For example, in Manitoba the trapping of beaver is required in order to maintain a registered trap line (Manitoba Conservation 2004). While regular trapping of beaver is a direct and highly effective solution to the problem of nuisance beaver, it is also controversial. Public opinion towards beaver trapping is variable, and many urban dwellers are strongly opposed to anything other than live trapping (Baker and Hill 2003). Alternative methods such as improved culverts, water levelling devices, and wire mesh may provide an alternative to trapping, but each situation must be carefully assessed to determine economic viability. For example, in regions regularly flooded by beaver the hiring of trappers to remove nuisance beaver may be more expensive than installing a Clemson beaver pond leveller (Müller-Schwarze and Sun 2003).

Nuisance Beaver in Riding Mountain National Park

Riding Mountain National Park is almost completely surrounded by agricultural land: it is effectively a forested island in a sea of agriculture. The park is home to a well-established beaver population that is near its ecological carrying capacity (Trottier 1980). Two year old beaver kits disperse from their parent colony in search of a new area to dam and start a new colony (Baker and Hill 2003). It is inevitable that beaver colonies close to the park boundary will produce sub-adults that will move onto private agricultural land downstream in search of new habitat. These become nuisance beaver, causing damage to rural roads, agricultural land and riparian forest stands.

It has been proposed that the only permanent solution to minimizing nuisance beaver damage to private and public land adjacent to RMNP is complete extirpation of beaver from problem areas, followed by an ongoing maintenance program to ensure a beaver-free condition (Trottier 1980). The essential feature of such a management strategy is maintenance of an extirpated state near the park boundary while ensuring a healthy upstream population of beaver within the park itself. Unfortunately, consistent trapping near the park boundary would likely yield such low beaver pelt numbers that it would be uneconomical to the trapper. Furthermore, any lapse in trapping pressure could potentially result in a sudden influx of colonizing beaver as they move into areas where their preferred food, mainly trembling aspen, has been allowed to recover.

In a study in Newfoundland (Bergund and Miller 1977), the removal of fourteen beaver colonies in early spring was unsuccessful: half the areas had been re-colonized by the fall, twelve by the following year, and all fourteen by the second year. Given such results, it is apparent that alternatives to trapping or removal are needed in the Riding Mountain area.

1.3.2 Beaver Management and Conservation Techniques

Beaver have the potential to occupy a wide range of habitats: the species occurs from the northern tree line to riparian zones in hot southern deserts, and from sea level to 3000 m elevation (Hill 1982). The only consistent requirements are an adequate supply of food (woody and/or emergent vegetation), and either standing or slow-moving water.

These conditions are easily met outside of the boundaries of Riding Mountain National Park. As beaver colonize streams adjacent to roads and farmland outside the park, they will begin to exert an economic stress on the surrounding communities. Realistic and economical management solutions must be implemented to curb the potential monetary loss.

Flooding damage can be mitigated by installing appropriately designed culverts and devices to control the flow of water across a dam. Examples of modified culverts include the oversized pipe-arch and the low-profile box culvert. These culverts prevent the beaver from damming the upstream portion of the culvert. An alternative approach is to fence off a culvert to restrict beaver access. Fence size selection is situational, but a highly porous fence is essential to prevent beaver from plugging the fence with sediment (Müller-Schwarze and Sun 2003).

The Clemson beaver pond water leveller is used to reduce the potential for catastrophic dam failure (Baker and Hill 2003). The leveller prevents the dammed water from reaching a certain critical depth, thereby reducing the likelihood of a breach while also minimizing the amount of flooding damage should a breach occur. By controlling the water level of an active dam, such devices minimize the potential for severe flooding while maintaining an aesthetically pleasing beaver pond environment for park patrons (Hammerson 1994). Once installed, pond levellers are unaffected by future generations of beaver moving into the area since the dam remains intact. Beaver dams can also be dynamited, but this is less effective over the long term since beaver will often return to

repair a breached dam (Baker and Hill 2003). Devices such as pond levellers and modified culverts can help reduce the cost of extensive trapping management, as well as the labour intensive process of unplugging unmodified culverts.

Techniques to prevent beaver damage to mature trees are more intensive and usually involve manipulation of individual trees (Baker and Hill 2003). Fencing is commonly practiced, but this can be very expensive and is inappropriate in certain situations. In urban parks and riparian habitats, the lower trunks of mature trees can be wrapped in wire mesh or sprayed with repellent chemicals to deter beaver harvesting (Baker and Hill 2003).

1.4 THESIS OBJECTIVES

I. To summarize historical trends in the beaver population of the riding mountain region.

- Historic data on the beaver population of RMNP are summarized, focusing on the reconstruction of population trends both within the National Park and on adjacent provincial and private lands. How variable is the population size over time?
- Given current beaver population trends, can we predict changes in landscape and hydrological regimes in the RMNP region?

II. To describe the effects beaver have on the structure, composition and succession dynamics of "old growth" boreal mixed wood forest in the upland plateau eco-district and the younger, aspen dominated forests in the knob and kettle eco-district.

- Virtually all shorelines (lakes, ponds, and streams) in Riding Mountain National Park (RMNP) have been affected to a greater or lesser extent by beaver activity. Affected shoreline habitat differs considerably in vegetation composition and structure, ranging from open shrub-dominated stands to very dense stands of white or black spruce. What are the underlying mechanisms producing these differences?
- Beaver selectively harvest mature aspen trees from forest stands immediately adjacent to their ponds. How does this selective removal of canopy aspen affect forest stand dynamics along shorelines? Does canopy aspen removal accelerate

succession by releasing sub-canopy spruce, or does it arrest succession by promoting aspen suckering and so perpetuating aspen dominance? Alternatively, does aspen removal simply reduce stand density without affecting stand dynamics?

III. To determine and describe temporal changes in landscape hydrology and wetland habitat types resulting from increased beaver activity.

- Beaver were reintroduced into RMNP in 1947, and high beaver population densities have been maintained since the 1970s. To what extent have beaver modified the regional landscape, in terms of overall changes in open water, marsh, wet meadow, thicket swamp, conifer swamps/bogs and modified forest habitats?
- To what extent have beaver impoundments and wetlands altered the hydrologic regime of RMNP? How have beaver impoundments modified the landscape over time?
- How important is beaver activity to the maintenance and perpetuation of wetland habitat in RMNP?
- Using the Broschart et al. (1989) predictive model of beaver colony density, can landscape patch analysis be used to supplement or replace current aerial survey techniques for beaver population estimation?

CHAPTER 2

HISTORICAL BEAVER POPULATION TRENDS OF THE RIDING MOUNTIAN AREA

2.1 RIDING MOUNTAIN NATIONAL PARK

Riding Mountain National Park (RMNP) is located in south-western Manitoba, Canada approximately 225 km northwest of Winnipeg. It is a large park, covering an area of 2976 km^2. RMNP is situated within the transition zone between the Saskatchewan Plain to the west and the Manitoba Plain to the east, and is the extreme south-eastern extension of the Mixed wood section of the Boreal Forest Region (Rowe 1972). The park occurs within the humid micro-thermal cool summer climatic zone, which is characterized by long cold winters and short summers (Bailey 1968). RMNP is bordered by the gradually sloping Assiniboine Valley to the west and south, the Wilson and Valley Rivers to the north, and the steep Manitoba Escarpment to the east. These topographic boundary features, combined with the highly modified agricultural land surrounding the park, create an island-like effect for the visitor.

Riding Mountain National Park incorporates four distinct ecological land districts: the Escarpment, the Lowlands, the Knob and Kettle, and the Upland Plateau (Parks Canada 2002). The eastern side of RMNP, which rises sharply over 300 m from the Manitoba Plain, forms part of the Manitoba Escarpment Land District (Bailey 1968). The Manitoba Escarpment, which extends from North Dakota to central Saskatchewan, is

characterized by eroded shale bedrock cut into deep ravines by streams draining the Upland Plateau. The Lowlands Land District is located at the base of the Manitoba Escarpment. Eastern deciduous forests are found within the Lowlands where flooding is common and fire disturbances are rare. Both of these Land Districts occupy a minimal amount of total Park area, and are restricted to the eastern region of RMNP. Swift stream velocity found on and near the escarpment restricts the amount of beaver habitat. The majority of the Park, and the majority of beaver habitat, lies in the Knob and Kettle and Upland Plateau Ecological Land Districts.

The Knob and Kettle Land District occurs in the southern and western reaches of RMNP and is characterized by depressions of water created by melting blocks of ice left by the retreating glaciers. As a result, wetlands drain very slowly and are expansive. Typically, mixed wood boreal forests dominated by white spruce (*Picea glauca*) and trembling aspen (*Populus tremuloides*) are characteristic of this district, interrupted by open prairie habitat and black spruce (*Picea mariana*) bogs. Fires in the early to mid-20th century (Parks Canada 2002) have resulted in large, uninterrupted stands of trembling aspen and balsam poplar (*Populus balsamifera*) throughout the area. A multi-strata shrub community is very prolific in this district, primarily composed of beaked hazelnut (*Corylus cornuta*), cherry (*Prunus* sp.) and mountain maple (*Acer spicatum*). This district maintains a very dense population of beaver (Frey and Avery 2004), as well as other furbearers and ungulates.

Most of RMNP occurs within the Upland Plateau District, a region dominated by boreal mixed wood forest. White spruce and trembling aspen are the major tree species, although balsam poplar, paper birch and black spruce are also prominent. The forest understory is dense and species-rich. The tall shrub beaked hazelnut dominates well-drained sites, while alders are frequent in moist lowlands. The landscape is characterized by rolling hills with an uneven distribution of glacial till, creating many poorly-drained wetlands (Bailey 1968). These wetlands are surrounded by boreal mixed wood forest, which provides ample habitat to support one of the highest density populations of beaver in North America (Parks Canada 2002).

2.2 BEAVER POPULATION TRENDS PRIOR TO PARK ESTABLISHMENT

Riding Mountain was used as a wintering area for both the plains and boreal forest cultures prior to the arrival of Europeans in North America (Parks Canada 2002). The abundance of game animals such as elk (*Cervus elaphus*), moose (*Alces alces*) and deer (*Odocoileus virginianus*) provided ample hunting opportunities to help survive the long winters. Furbearers were also harvested during the winter months: beaver and other species were an important source of warm furs. During the summer months, the plains cultures moved onto the adjacent grasslands to hunt bison (*Bison bison*), while the boreal cultures moved into the lake regions to fish and harvest wild rice. By the mid 1700s the European fur trade was well established in the area, and many indigenous peoples began to obtain their livelihood by trapping beaver and other furbearers (Parks Canada 2002).

Fort Dauphin, established in 1741 by the Hudson Bay Company (HBCA) north of RMNP, was an important trading post in the region and the first permanent European presence in the area (Parker 1978; Parks Canada 2002). The establishment of Fort Dauphin and other trading posts in the Riding Mountain area greatly increased the amount of furs harvested in the region. Their presence was a great convenience to First Nations traders, who before then had to trade much further north (Parker 1978; Anonymous 1985; Parks Canada 2002).

Historic beaver trapping records during the 18th and 19th centuries were obtained from trading post districts in the Riding Mountain region. Unfortunately, many of the post reports and detailed fur return data for the smaller, more isolated trading posts surrounding the current boundary of RMNP have been lost. However, detailed information on fur returns, as well as anecdotal accounts of beaver population trends, are available from surviving post reports from the Shell River District (part of the Northern Department Fur Reports, Manitoba Archives). The Shell River District was large and included portions of eastern Saskatchewan and the Northwest Territories as well as western Manitoba (including the Riding Mountain area).

The beaver population of west-central Canada was high prior to settlement by European farmers. Surviving HBCA Post Journals from Fort Dauphin state that beaver were very abundant during the late 1700s, and that native trappers frequently brought in beaver pelts for trade. For example, in 1795 a typical summer day for Fort Dauphin

residents included a morning fishing trip and a seemingly random encounter with a group of native trappers looking to trade a canoe full of beaver pelts (HBCA 1795).

Trading continued in this manner throughout the late 1700's and early 1800's until the full release of HBCA lands to the crown in 1870. Prior to this release, beaver fur harvest in the Swan River District of HBCA took place at a relatively consistent rate with a mean of 419 pelts harvested each summer by native trappers **(Figure 2.1)**. However, a manageable rate would not last long. Agricultural settlement quickly consumed the landscape south of RMNP in the 1870's (Tabulenas 1983). The problem of uncontrolled trapping was exacerbated by this rapid increase in population. In addition, First Nations trappers were convinced by HBCA officials, with the offer of food, to stay and trap in the region throughout the winter (Tabulenas 1983). The combination resulted in high harvest rates in the area through all seasons.

Within the Swan River District, beaver pelt returns increased sharply from 461 in 1850 to a maximum of 4142 in 1864 **(Figure 2.1)**. At its peak, a mean harvest rate of 2617 pelts per year (± 155 standard error) was sustained for 20 years. This dramatic increase in harvest rate was attributable not to a higher beaver population or a larger harvest area, but to a massive increase in trapping pressure following the influx of European settlers into the area. High demand for beaver pelts in Europe continued to drive up prices and resulted in unsustainable harvest levels. In the late 1800s a large, good-quality beaver pelt commanded a price of four dollars. At this price, a trapper could trade three beaver pelts for a year-old steer (HBCA 1894). Given such a strong

financial incentive, beaver trapping was practiced by both European settlers and native trappers.

By the late 1800s, increased trapping had taken its toll on the beaver population of west-central Canada and populations crashed across the district **(Figure 2.1)**. In spite of the rapid drop in beaver populations in the area, pelt prices actually continued to increase, likely spurring increased harvest effort **(Figure 2.2)**. As the supply of beaver pelts declined and the price of pelts continued to rise, the last few years of the HBCA era in the Riding Mountain area would result in a mean of only 407 pelts per year taken from the area and a low of only 186 in 1890 **(Figure 2.2)**. By 1889, numerous surviving post reports from the Riding Mountain area allude to the declining population of fur-bearing animals (including beaver):

"The furs on hand have mostly been collected direct from Indians :- Beaver, few on hand, but those poor and small" – Post Report, Riding Mountain Outpost 1889

"Owing to settlement fur-bearing animals are dying out in the immediate neighborhood, and in the north there has been a great decrease for the last two years." – Post Report, Shoal Lake Outpost, 1889.

"Only very few furs are brought in here, principally foxes killed by farmers. They amount to only $80 for last outfit and have been sent over to Riding Mountain and included there in the returns." – Post Report, Shoal Lake Outpost, 1889.

These anecdotal accounts, together with the fur-return data from the Swan River District (HBCA 1869, 1885), indicate that the beaver population of the Riding Mountain area was severely depleted by the 1880s. It is possible that the beaver population plummeted even earlier, since populations of fur-bearing species (including beaver, muskrat, marten and fisher) were almost completely extirpated from the Assiniboine Valley by about 1820 (Tabulenas 1983).

2.3 BEAVER POPULATION TRENDS FOLLOWING PARK ESTABLISHMENT

In 1930, when Riding Mountain National Park was established, wolves (*Canis lupus*), lynx (*Lynx canadensis*) and bison (*Bison bison*) had been extirpated from the area, and other game species such as elk and moose were considered scarce (Parks Canada 2002). Fur bearing animals including fisher (*Martes pennanti*), marten (*Martes americana*), muskrat (*Ondatra zibethicus*) and beaver (*Castor canadensis*) were all nearly eliminated from RMNP and the surrounding areas (Bird 1961; Anonymous 1985). Green (1936) estimated that there were approximately 200 active beaver colonies in the RMNP in the later 1800s, an estimate based on the presence of inactive dams and lodges. However, by the mid-1930s the beaver population in the region was estimated at fewer than 50 colonies (and possibly as low as five or six colonies) and concern was expressed that the species could be rendered locally extinct (Green 1936).

The first beaver conservation project in RMNP was initiated by Grey Owl, an early and well known naturalist. Grey Owl arrived at the park in the spring of 1931 and was established by Parks Canada staff at Beaver Lodge Lake, approximately 7 miles northeast of Clear Lake. One of Grey Owl's tamed beaver gave birth to 4 kits and Grey Owl began training them, along with other kits gathered in the area, in an attempt to repopulate the area. However, 1931 was a dry year and Beaver Lodge Lake dropped a full 2 feet in depth, prompting Grey Owl to abandon the project. Grey Owl concluded that once the kits were old enough to colonize the surrounding area they would be unable to do so because of the low water levels and annual snowfall in RMNP. After only 6 months, Grey Owl requested and was moved further west to Prince Albert National Park where he would remain for 7 years.

With the failure of the beaver re-introduction program led by Grey Owl and no follow-up re-introduction initiatives, the beaver population failed to increase following the establishment of Riding Mountain National Park (Green 1936). The population would remain low for the next 16 years before Parks Canada would start a new beaver re-introduction program. In 1947, fourteen animals taken from Prince Albert National Park were introduced into the Upland Plateau District of RMNP to increase the resident population (Rounds 1980). An additional 19 animals were released during 1958 in the Escarpment District in the hope of controlling the flooding of surrounding private lands (Trottier 1980; Rounds 1980). By 1960, beaver were said to be abundant in all areas of Riding Mountain National Park, although no formal survey records exist to confirm this (Rounds 1980).

Since 1973, beaver population census data (based on aerial sample surveys) have been available for Riding Mountain National Park. These data are based on food cache counts in 30 beaver survey blocks (situated randomly within the park), which together account for 23.4% of the total Park area (Frey and Avery 2004). Each food cache corresponds to an individual beaver colony, and the population is estimated using the average Canadian colony size of 5.7 beavers per colony. Total park population is estimated by extrapolating the survey data from the 30 survey blocks. A total of 16 surveys have been undertaken in the Park, the most recent occurring in the fall of 2007 (Frey and Avery 2004).

The first detailed aerial beaver cache survey indicated that by 1973, the population had increased to an estimated 2452 colonies **(Figure 2.3)**. By the time of the 1977 survey, estimates of beaver density in the Upland Plateau eco-district were among the highest recorded in Canada: 3312 colonies in total, or about 1.2 colonies per square kilometre (Trottier 1980). The beaver population in 1977 was considered to be at or near the carrying capacity of the environment (Trottier 1980), a testament to the power of a protected landscape for the recovery of animal populations. During the latter half of the 20th century the population has fluctuated, with a mean density of approximately 3000 colonies. Beaver populations reached a peak of nearly 3900 colonies in 1983 **(Figure 2.3)**.

Between the mid-1990s and the early 21st century, the estimated number of beaver colonies in RMNP showed a substantial decline. The current population estimate (fall 2007) indicates a large decline in the population to 1632 colonies, or about 9300 individuals if the national average of 5.7 beavers per colony is applied (unpublished data, Parks Canada). This is the lowest population estimate since the sample survey program began in 1973 **(Figure 2.3)**. Park-wide beaver survey results support my landscape analysis which predicts a declining beaver population (See chapter 4 results). However, the population decline is not equal across all ecological land districts. For example, the current number of colonies in the Knob & Kettle eco-district remains above the 1973 estimate. Conversely, the population in the Upland Plateau eco-district has declined substantially over the past two decades, and is currently well below the 1973 estimate **(Figure 2.4)**.

Annual precipitation values from the Rossburn (Knob and Kettle eco-district) and Wasagaming (Upland Plateau eco-district) weather stations were plotted against the aerial census data **(Figure 2.5)**. Typically, animal populations will fluctuate with available habitat, and in wetland systems, primary habitat of the Canadian beaver, precipitation plays a critical role in determining water levels. However, annual precipitation amounts do not seem to affect beaver population levels in RMNP **(Figure 2.5)**. A hypothesis for this counter-intuitive result is that beaver behaviour adjusts to low water years. In areas where beaver habitat quality is low and/or the degree of habitat saturation is high, it has been noted that the mean colony size is larger due to the fact that kits will remain with their parents for a third year (Slough and Sadleir 1976). In favourable areas, kits will

typically leave to establish a colony at 1 or 2 years old. It is possible that in low water years, kits will remain with their parents, striking out on their own the year after when the water levels may be more favourable. Further research would be needed to determine if this occurs.

It is difficult to predict the future of beaver populations in Riding Mountain National Park. Current population data suggest that beaver populations are still declining **(Figure 2.3)**. During the 1970's and 1980's, beaver populations may have recovered to levels well beyond the carrying capacity of the park due to the length of their absence and the recovery of streamside aspen after a series of fires in the late 1800's. Strong beaver disturbance levels have shifted streamside forest communities towards spruce or shrub dominance (see chapter 3), reducing available food levels. As aspen populations drop, beaver colonize less preferred stream corridors (Slough and Sadleir 1976; Naiman et al. 1988). Landscape analysis suggests that this is presently occurring in RMNP (see chapter 4). An assessment of available habitat would be needed to estimate carrying capacity and to predict future population levels.

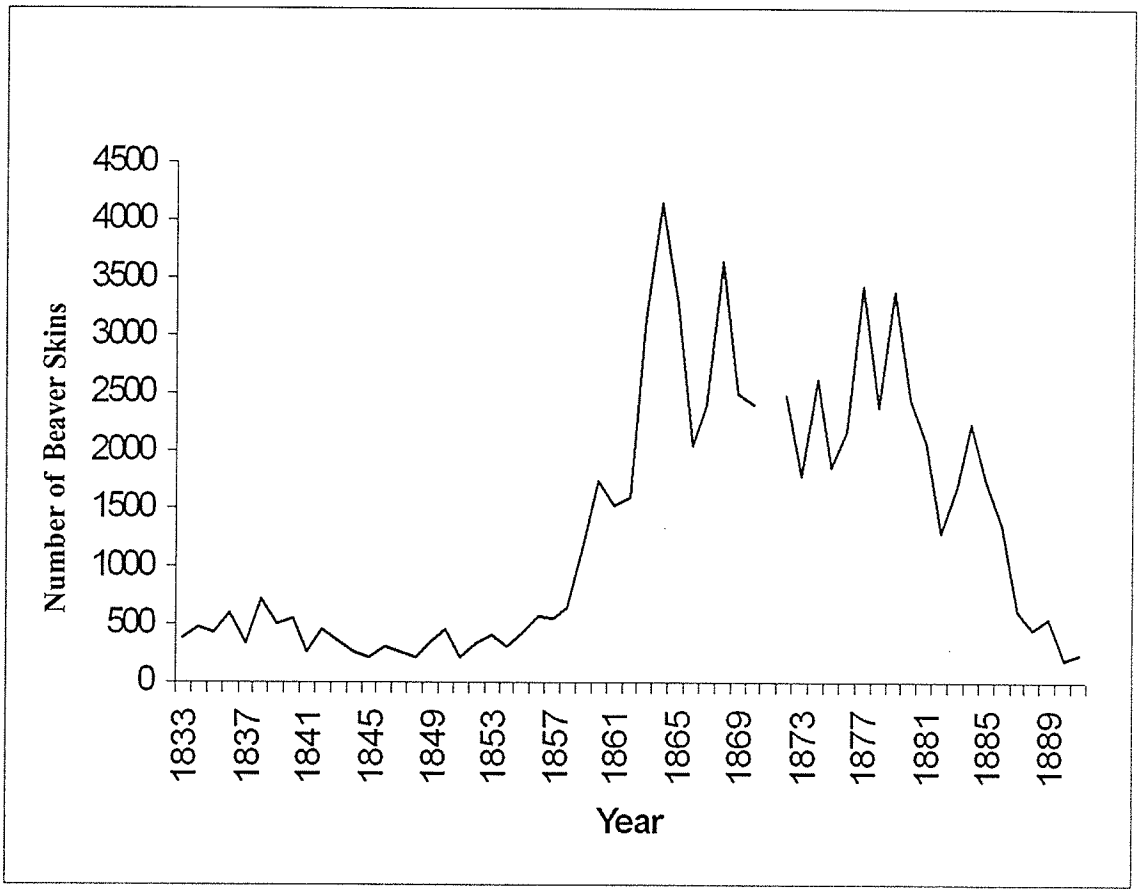

Figure 2.1. Beaver skin returns to the Hudson's Bay Company, Swan River District, 1821-1891.

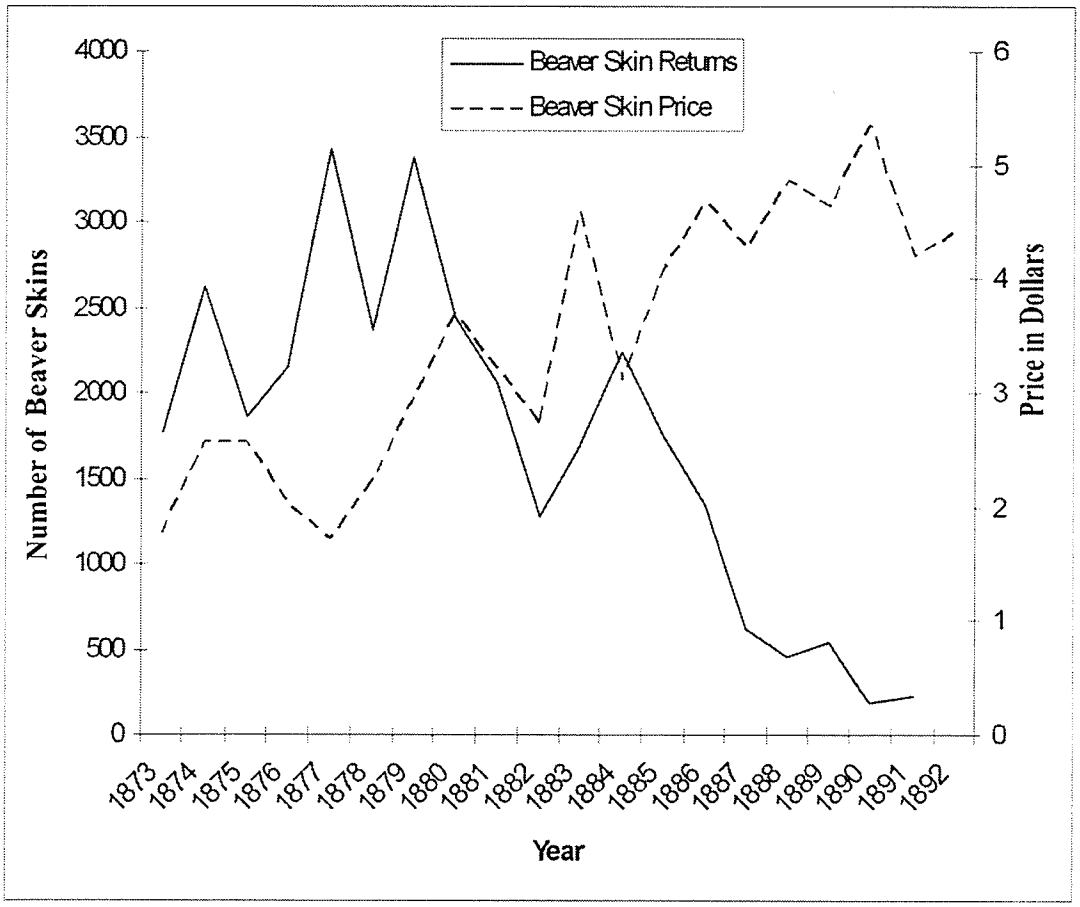

Figure 2.2. Beaver skin returns in comparison with fur tariffs during the years of severe beaver population decline, 1873-1892. Swan River District.

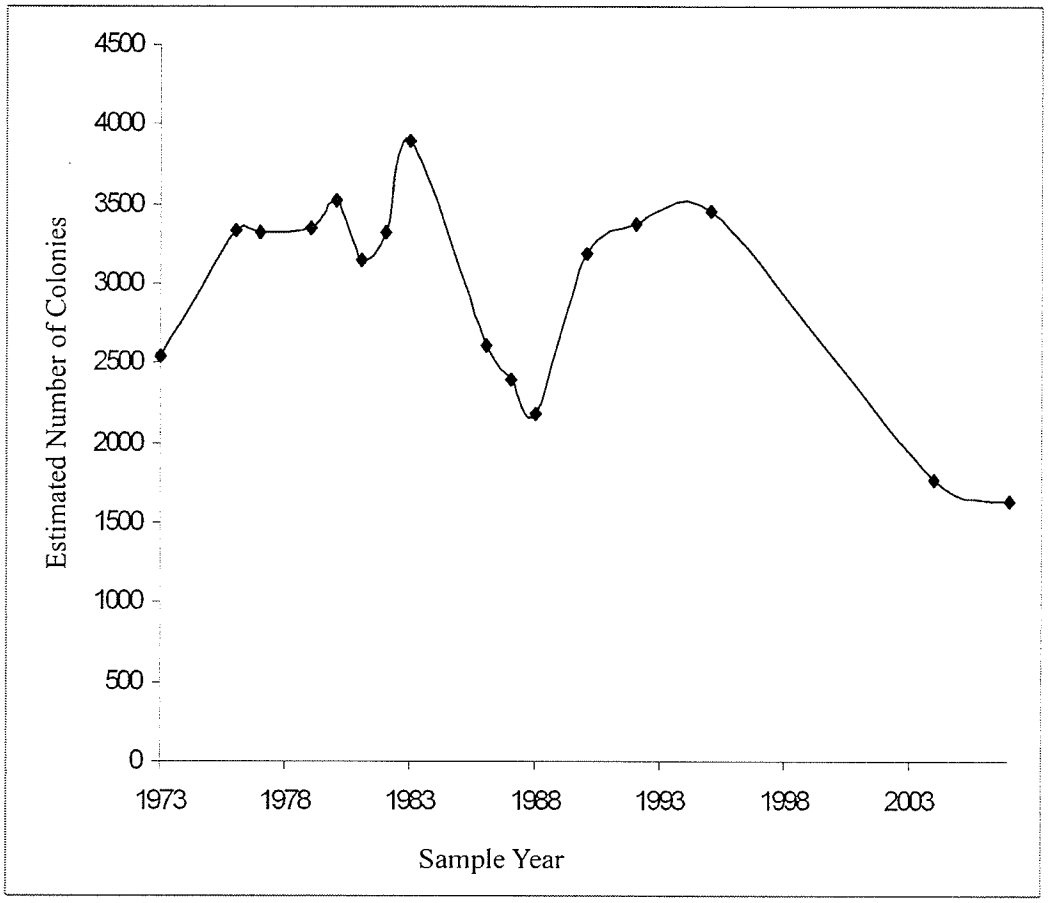

Figure 2.3. Riding Mountain National Park beaver cache estimates from 1973 to 2007.

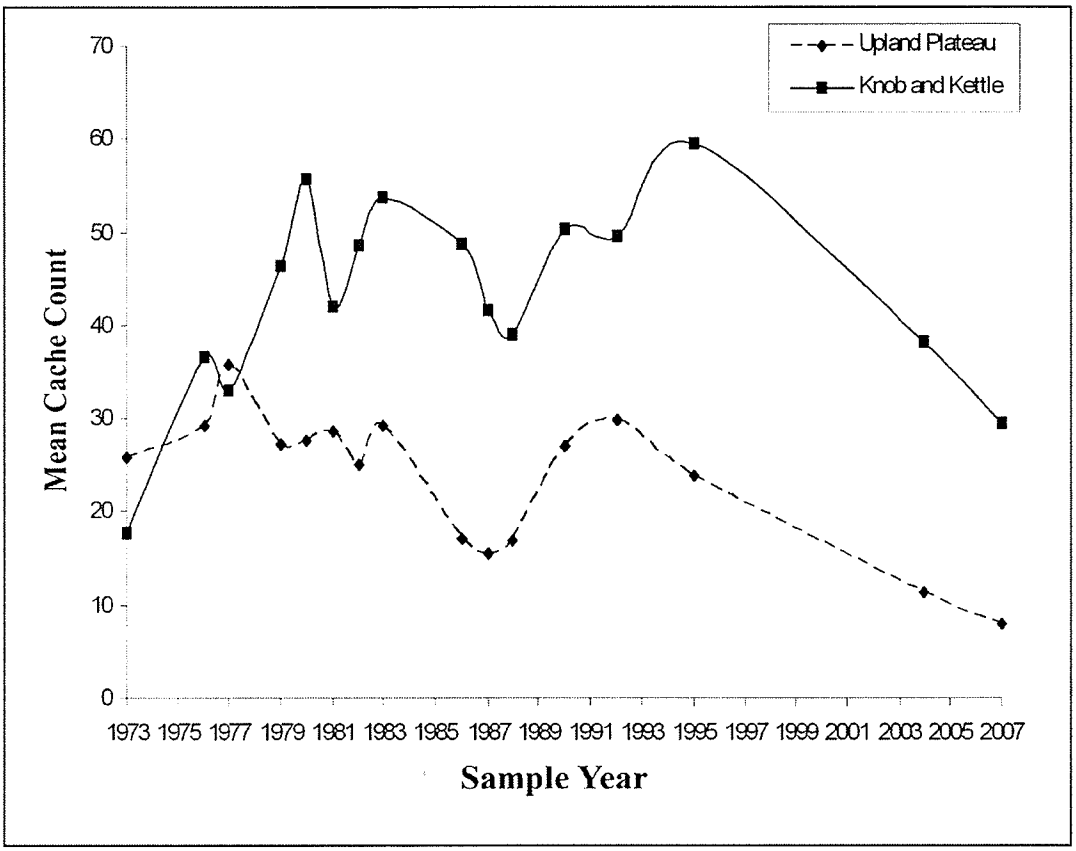

Figure 2.4. Riding Mountain National Park mean cache counts from 1973 to 2007. Mean cache counts are taken from survey blocks lying entirely within the two ecological land districts: The Upland Plateau Eco-district and the Knob and Kettle Eco-district.

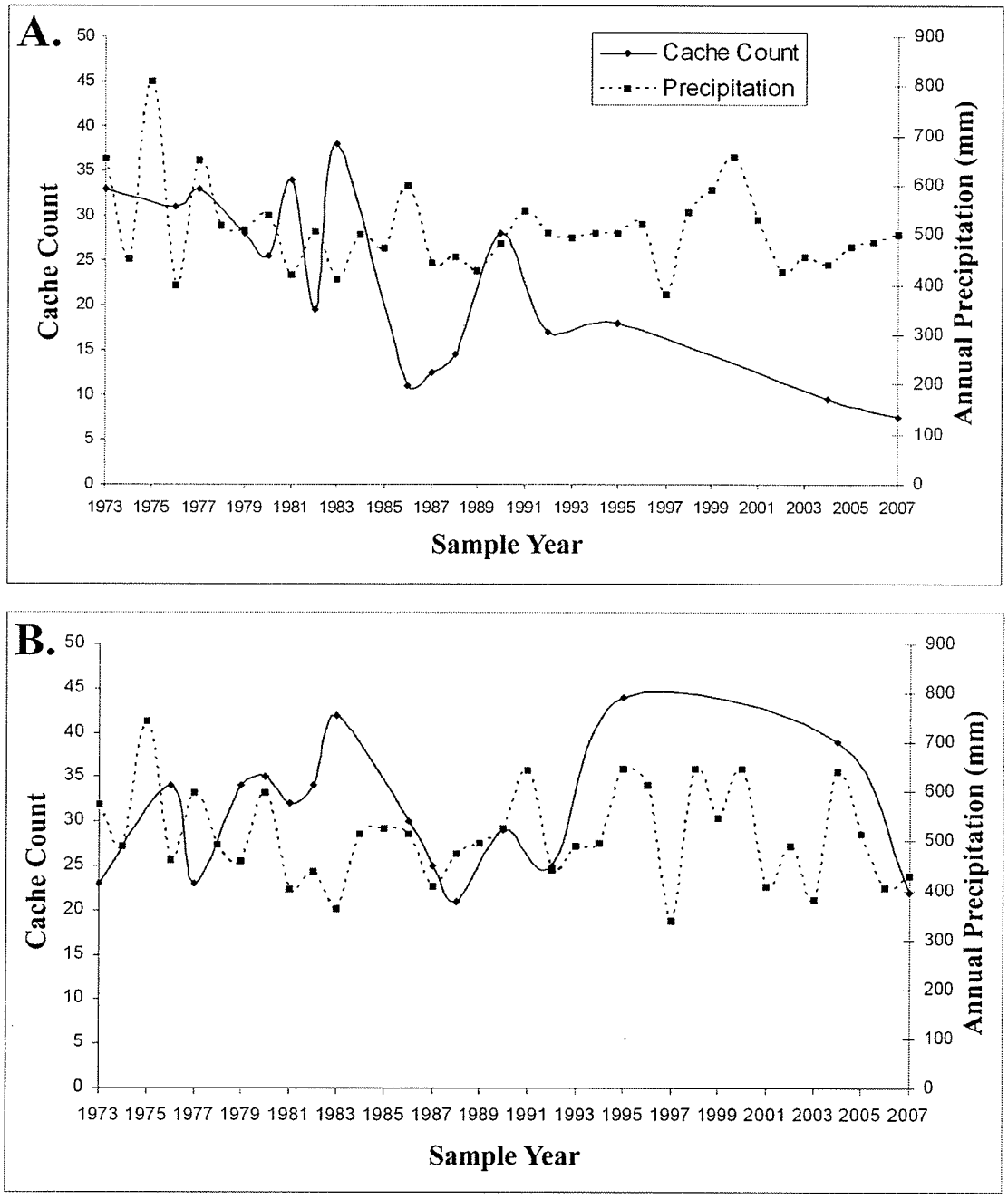

Figure 2.5. Mean beaver cache counts for: (A) Beaver Survey Blocks 96 and 104, plotted with annual precipitation (mm) from the Wasagaming weather station; (B) Beaver Survey Block 72, plotted with annual precipitation (mm) from the Rossburn weather station.

CHAPTER 3

BEAVER DISTURBANCE AND FOREST STAND DYNAMICS

3.1 INRODUCTION

The beaver (*Castor canadensis*) is the largest rodent in North America, weighing up to 30 kg and reaching a head-to-tail length of 120 cm at maturity (Baker and Hill 2003). The beaver is primarily an aquatic species, leaving the water for only brief periods to feed. The beaver uses aquatic habitat for protection, as it has limited mobility on land and is thus highly vulnerable to predators. While beavers have the potential to forage and drag stems up to 200 m away from the water edge, the presence of predators may limit their foraging to within 20-40 m of a shoreline (Barnes and Mallik 2001).

Deciduous woody vegetation constitutes the major dietary component of beaver (Donker and Fryxell 1999). In the boreal forest, important deciduous food trees include trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*) and white birch (*Betula papyrifera*). While beavers show a definite preference for trembling aspen, they will forage on various other trees and woody shrubs, and even herbaceous vegetation, to supplement their diet (Donker and Fryxell 1999). The ability of beavers to fell mature trees and dam moving water is shared only with humans, earning the beaver the epithet "ecosystem engineer" (Naiman et al. 1988). Once established, a pond habitat will continue to be used by the colony until all food resources in the vicinity are depleted: this may take many years or even decades. The use of a long-term home base (in this

case, the beaver pond and lodge) to extract resources from the immediate vicinity, known as "central place foraging", has a strong impact on the boreal forest communities adjacent to low-order streams, ponds and small lakes (Naiman et al. 1988).

The removal of upper canopy trees alters stand composition, since beavers selectively harvest hardwood trees (usually trembling aspen) and generally avoid softwoods. The removal of canopy trees also increases available light to the lower strata in the forest, increasing productivity and ultimately modifying community structure (Johnston and Naiman 1990b). In the boreal forests of the Great Lakes region, beaver affected forests shift towards non-preferred species such as conifers (Donker and Fryxell 1999; Barnes and Mallik 2001) and other, non-preferred hardwoods (Johnston and Naiman 1990a).

Changes in forest composition and structure resulting from beaver disturbance likely depend on sub-canopy composition (Barnes and Dibble 1988). Canopy thinning by beaver may promote the regeneration of shade-tolerant trees (Donkor and Fryxell 1999, Naiman et al. 1986), or release shade-intolerant trees from competition (Pastor and Naiman 1992). Unfortunately, long-term data are not generally available to test the successional models proposed by these researchers. As a result, the long-term effects of beaver disturbance on forest dynamics remain poorly understood.

The objective of this chapter is to describe the effects beaver have on the structure, composition and successional pathways of "old growth" boreal mixed wood forest in the Upland Plateau eco-district of RMNP, and on the younger, aspen dominated forests in the Knob and Kettle eco-district. These data will be used to assess the validity of current beaver-affected succession theories within the forests of Riding Mountain National Park.

3.2 METHODS

Study Area

Riding Mountain National Park (RMNP) is located approximately 225 km northwest of Winnipeg, in south-western Manitoba, Canada. The park covers an area of 2976 km^2. Climate in the region is characterized by long cold winters interrupted by short warm summers, typical of the humid micro-thermal cool summer climatic zone (Bailey 1968). The park lies within the southeastern extension of the Mixedwood section of the Boreal Forest Region (Rowe 1972).

The beaver in Riding Mountain National Park were nearly extirpated following the arrival of European fur companies in the area. The high rate of fur harvest in the region continued until the establishment of Riding Mountain National Park in 1930. By this time the beaver population in the park was estimated at less than 50 families, or perhaps far fewer (Green 1936). Following repeated re-introduction programs in the late 1940s and 1950s, beaver populations have recovered dramatically. The boreal

mixedwood forest, which covers the majority of RMNP, had developed in the absence of beaver disturbance for approximately 100 years prior to the species being reintroduced (see Chapter 2).

Currently, beaver are unevenly distributed in the Park. The lowest population densities are found in the Manitoba Escarpment and Lowland Ecological Land Districts (Frey and Avery 2004); beaver occur at much higher densities in the remainder of the Park. Accordingly, two regions of RMNP with the highest beaver density were chosen for study: (1) Forest Experimental Area (FEA), Upland Plateau eco-district, eastern region of RMNP; (2) Baldy, Bob Hill and Deep Lakes, Knob and Kettle eco-district, western region of RMNP.

Permanent Sample Plots

The Forest Experimental Area (FEA) north of Clear Lake was established during 1946-1948 by the Canadian Forest Service (CFS). The MS-69 rate of growth survey was initiated in 1947. This survey was designed to describe the growth, composition and successional trends of the mixedwood forest within the FEA. The 6.5 x 11.5 km FEA study area consists of a regular grid of 20 x 20 m permanent sampling plots (PSPs) placed approximately 200 m apart. The forest stands were of fire origin, and were about 120 years old when the PSPs were established. Of the 1480 plots established in 1947, approximately half were relocated (GPS coordinates taken) in 2001-2002. These relocated plots were revisited during the 2006 and 2007 field seasons. Those plots showing evidence of beaver activity (eg. cutting of trees, flooding) were carefully

enumerated, as were representative undisturbed upland plots. Detailed data on forest species composition and structure (trunk diameter and tree height), and shrub and understory vegetation composition, were collected in each plot. In addition, all beaver disturbances were recorded, including stump diameter and locations and the relative decomposition of downed trees.

Since very few beaver were active in the area during the initiation of the MS-69 survey, plots were likely unaffected by beaver when they were established in 1947. The release of beaver north of the FEA in the 1950s resulted in a dramatic increase in the beaver population in the park over a relatively short period of time. Today, there are approximately 1500-2000 beaver colonies in Riding Mountain National Park (unpublished data, Parks Canada). Empirical observations indicate that beaver have subsequently flooded and/or cut trees from many of the MS-69 permanent sample plots, particularly those adjacent to aquatic habitat.

Growth Response of White Spruce to Beaver Disturbance

To assess the radial growth response of white spruce (a non-preferred species) to beaver disturbance, five trees were chosen randomly within each of six beaver-affected plots were cored using an increment borer. The six beaver-affected plots were chosen using a stratified-random sample design that was based on their stand structure and composition in 1947: aspen dominated the canopy of three stands, while the other three stands were co-dominated by aspen and white spruce in the canopy. In addition, three "control" trees were cored in areas unaffected by beaver. These control trees were located

in stands very close to the beaver affected area, but showed no sign of beaver disturbance. Each tree was cored twice to minimize errors in ring counting and measurements of ring widths. Cores were glue-mounted and hand-sanded using a fine-grit sandpaper. The mounted cores were scanned at 600 dpi and ring widths measured using Adobe Photoshop CS2 software.

Radial growth for each tree was described as cumulative growth by adding tree rings incrementally ($T_1 + T_2 \ldots\ldots + T_n$, where T = width of one ring, and n = tree age). The mean relative growth rate (RGR) was calculated for all trees after 1975 (estimated time of beaver disturbance) (**Table 3.1**), using the methods outlined in Hunt (1978). Individual trees were assigned to one of three "treatments" according to their spatial location relative to beaver disturbance: (1) edge trees, growing in large canopy openings adjacent to beaver impoundments, no competition for light; (2) core trees, growing in more closed-canopy situations adjacent to beaver impoundments, intraspecific competition for light; (3) control trees, located in closed stands further away from beaver impoundments, high competition for light. A one-way Analysis of Variance (ANOVA) was used to detect any significant differences of the mean radial growth rate of trees between treatments. Analyses were undertaken separately for the two 1947 compositional classes: (a) aspen-dominated canopy; (b) aspen and white spruce co-dominant in canopy.

Sample Transects

Vegetation transects were established at random locations immediately adjacent to beaver-affected wetlands. Transects began at the pond flood line (either open water or

flood-damaged vegetation) and were oriented perpendicular to the shoreline. Transects were 60-80 m in length and 20 m wide, and were enumerated using 20 x 20 m contiguous plots. Transect length was dependant on the foraging distance of the beaver, with the last 20 x 20 m plot showing no evidence of beaver herbivory. Whenever possible, transects were established on both sides of a beaver pond. The data collected were the same as those used in enumerating the permanent sample plots. A total of 31 transects were enumerated, in the following regions: (1) 15 transects in the Forest Experimental Area, Upland Plateau eco-district; (2) 16 transects along the shorelines of Bob Hill, Baldy and Deep Lakes, in the Knob & Kettle eco-district.

3.3 RESULTS AND DISCUSSION

3.3.1 Permanent Sample Plots

A total of 691 of the FEA permanent sample plots were relocated (and GPS coordinates obtained) during the 2004 – 2006 field seasons. Of these, 638 were revisited in the 2006 and 2007 field seasons for evidence of beaver activity (the remaining 53 plots could not be found, or were recently disturbed by human activity). Forty of the 638 plots (6.3%) were flooded beaver wetlands (all trees killed), and another 33 (5.2%) showed evidence of beaver browsing (mainly harvesting of canopy aspen). Based on these findings, approximately 11.5% of the forested region within the FEA has been directly affected by beaver activity since the species was reintroduced in 1947.

The 33 permanent sample plots showing evidence of beaver browsing were carefully examined to determine whether they could be used to quantify the long-term dynamics of beaver-harvested forest stands. The specific requirements were: (1) no flood damage; (2) plot is within the foraging range of beaver (i.e. less than 50m from a shoreline); (3) complete tree data are available for all three Canadian Forest Service sample periods (i.e. 1948, 1958 and 1968). Using these criteria, 17 beaver-affected sample plots proved useable.

All 17 plots contained trembling aspen and/or white spruce as the dominant tree species. Based on the 1948 (pre-beaver disturbance) data, two canopy-structure classes were recognized: (1) aspen-spruce co-dominant in the canopy, $n = 11$; (2) aspen dominant in the canopy, spruce in the lower sub-canopy, $n = 6$. Using the 1948 data, 313 plots unaffected by beaver activity were examined to determine whether they could be "matched" to plots in these two classes. A "match" occurs when the forest structure and composition of a given plot in 1948 is similar to that of any one of the 17 plots. Using this criterion, 77 "matched" plots were found: 54 plots in class 1 (aspen-spruce canopy), and 23 in class 2 (aspen canopy). For each sample year, t-tests were used to detect any significant changes between the affected and unaffected plots.

Comparisons of changes in white spruce and aspen basal area over time, in each of the two classes, is summarized (see **Figure 3.1**):

Class 1 (aspen-spruce canopy): There were no statistically significant differences between the 11 beaver-affected and the 54 "matched" control plots in the both 1947 and 1967, confirming that the plots are well matched. By 2004, trembling aspen basal area was considerably reduced in beaver affected plots compared to control plots, due to beaver felling. Though beaver did not remove a statistically significant amount of aspen ($t_{0.05;59}$ = 1.554, P=0.126), results were confounded due to the presence of several large aspen in one plot that had been girdled, yet were still living. These aspen increased mean aspen basal area for the class and increased variability. White spruce basal area was not significantly different in 2004 ($t_{0.05;59}$ = 0.233, P=0.817). This suggests that beaver have reduced aspen dominance by felling the trees, but that there is no significant compensatory increase in white spruce dominance.

Class 2 (aspen canopy): As with class 1, there were no statistically significant differences between the 6 beaver-affected and the 23 "matched" control plots in both 1947 and 1967. However, by 2004 trembling aspen basal area was significantly reduced relative to control plots ($t_{0.05;31}$ = 3.203, P=0.003), and white spruce basal area dramatically increased ($t_{0.05;31}$ = 3.496, P=0.001). In these stands, the removal of canopy aspen by beaver results in a compensatory increase in white spruce dominance. This suggests competitive release: the removal of canopy trees increases light availability to understory white spruce, resulting in their more rapid growth compared to the control plots.

In all cases the proportion of white spruce increased over time in beaver-affected plots, a result that is universally agreed upon in the literature. However, while some researchers have concluded that beaver harvesting promotes the growth of white spruce and other non-preferred trees (Johnston and Naiman 1990a; Donker and Fryxell 1999), other researchers have hypothesized that beaver merely shift the proportion of softwoods (without promoting their growth) as a result of selective harvesting (Barnes and Dibble 1988; Martell et al. 2006). My long-term data indicate that both scenarios occur, and confirm that competitive release is the underlying mechanism driving the shift in successional trajectory reported by other researchers.

In the permanent sample plots, one of two forest community-types arises following the selective removal of canopy aspen by beaver: (1) an open canopy spruce shrub-land (n=11), or (2) a closed canopy spruce stand (described in more detail below; n=6). My long-term data show that both class 1 stands (aspen-spruce canopy) and class 2 stands (aspen canopy) may develop into open-canopy spruce shrub-lands or closed canopy spruce stands, depending on their initial stand composition.

Following selective harvesting by beaver, closed-canopy spruce stands tend to develop when spruce trees occur in the canopy and sub-canopy strata, and few spruce saplings are present. Maximum seed production in white spruce typically occurs between 45-60 years of age (Rowe 1955). Seed rain into gaps created by beaver through the selective harvesting of mature aspen trees leads to colonization by spruce. Furthermore, colonizing saplings are at a competitive advantage in the low-light, acidic conditions

found beneath a mature spruce canopy. The result is the development of dense, uneven-aged stands of spruce and limited shrub growth **(Figure 3.2)**. Conversely, an open-canopy spruce shrubland tends to develop in stands where most of the spruce are young, healthy saplings. Selective removal of canopy aspen by beaver increases light availability, and the previously suppressed spruce saplings respond by increasing their height growth; these saplings are too young to produce large amounts of seed (Rowe 1955). Increased light also enables tall shrub species such as beaked hazel (*Corylus cornuta*) to proliferate, creating a dense shrub cover that impedes further white spruce establishment. Over time, an open canopy white spruce, shrub-dominated stand develops **(Figure 3.3)**.

Tree core samples confirm the increased growth rate of trees affected by beaver disturbance (**Table 3.1**). Results differed among the treatments. The mean relative growth rate (RGR) of edge trees was significantly higher than both the core and control trees for both the closed canopy aspen class ($F_{2,14}$=7.116, P=0.007) and the aspen-spruce mixed wood class ($F_{2,15}$=8.151, P=0.004). Control trees, typically located within mixed wood stands, had a RGR equal or even higher than that of the trees competing intraspecifically in beaver disturbed areas **(Table 3.1)**. Core trees that were originally in a mixed canopy stand prior to the release event had the lowest RGR of all trees. This low RGR could be due to the higher amount of shading from a neighboring spruce (intraspecific competition) in the beaver affected plots, compared to the relatively low amount of shade produced from neighboring aspen (interspecific competition) in the control area,

especially in early spring or late fall. However, the differences between core and control trees are not statistically significant.

In all six plots, beaver flooding occurred between 1964 and 1978. All ponds adjacent to the plots were full during the 1978 sample period so beaver likely cut trees from the plots sometime between 1975 and 1985. Specific release events were determined by mapping RGR over the lifespan of each tree (**Figure 3.4**). Growth response for edge trees is very pronounced, with a large increase in growth occurring during this decade **(Figure 3.4a)**. This growth increase is not apparent in the adjacent closed-canopy trees in the plot, and in the "control" trees **(Figure 3.4 b,c)**.

3.3.2 Sample Transects

Mean foraging distance for the Forest Experimental Area transects was 23.6 m (maximum 39 m), compared to a mean of 38.4 m (maximum 58 m) for transects along the shores of Baldy, Deep and Bob Hill Lakes. Large differences occur between lakes in the western transects. On Bob Hill Lake, the mean foraging distance was 30.7 m (maximum 58 m), while at Deep Lake the mean foraging distance was 46.9 m (maximum 58 m). These values are comparable to those found in the literature (Johnson and Naiman 1987; Donker and Fryxell 2000; Barnes and Mallik 2001).

Effects of Beaver Harvesting on Forest Stand Composition and Structure

Beaver-affected shorelines in the west end of RMNP (Bob Hill and Deep Lakes) are largely treeless and dominated by dense thickets of beaked hazelnut and other tall shrubs.

By contrast, beaver-affected shorelines in the Forest Experimental Area are typically dominated by white spruce.

Timber harvesting by beaver along the shorelines was high, averaging 20.7 m^2/ha of tree basal area in the Forest Experimental Area and 16.4 m^2/ha of tree basal area along the shores of Baldy, Deep and Bob Hill Lakes (**Figure 3.5**). Only hardwood tree species were harvested by beaver, mainly trembling aspen and balsam poplar with much lesser amounts of paper birch.

The undisturbed forests (i.e. stands beyond the reach of beaver) along the FEA transects contained approximately equal proportions of hardwood (mainly trembling aspen and balsam poplar) and softwood (mainly white spruce) species. By contrast, stands within the foraging range of beaver (within 20 m of the shoreline) along the same transects, while equally dense, are almost completely dominated by white spruce and have only a minor hardwood component (**Figure 3.6 a,b**). This result indicates that beaver play an important role in altering forest stand composition along lakes, watercourses and wetlands, converting mixed hardwood-softwood stands into almost pure white spruce stands. The situation in the western regions of the Park, where softwood tree species are far less abundant, is somewhat different. The extant forests along the Lake transects are dominated by trembling aspen, with much lesser amounts of balsam poplar, white spruce, and paper birch. Along the same transects, stands within reach of beaver are very open and shrub-dominated, with only low abundance of tree species (**Figure 3.6 c,d**). The mean total basal area of undisturbed stands is 26.7 m^2/ha,

but this falls to only 11.3 m^2/ha in beaver-affected stands. In the western regions of the Park, the main effect of beaver is therefore to reduce stand density, converting closed aspen-dominated stands into open stands dominated by tall shrubs and a few large conifers or hardwoods. This likely reflects the low abundance of softwood species in the western portion of RMNP; a limited white spruce seed source, and sporadic white spruce regeneration in most of these stands, limits the ability of white spruce to dominate shoreline areas despite the removal of hardwood competitors by beaver.

Within the FEA, trembling aspen and balsam poplar regeneration (saplings < 1.3 m in height) was similar in beaver-affected and unaffected plots (**Figure 3.7**). Regeneration of white spruce and white birch was slightly greater in beaver-affected plots. Within Beaver Survey Block 72 (Knob & Kettle eco-district), differences in tree recruitment levels between beaver-affected and unaffected plots proved more dramatic. In particular, less common tree species such as bur oak and white birch showed much greater recruitment in beaver-affected plots, averaging seven saplings per plot compared to less than one per plot in unaffected areas **(Figure 3.7)**. This increase in sapling density is mostly attributable to prolific basal sprouting by white birch and bur oak in response to the harvesting of mature stems by beaver (Sinkins, personal observation).

Tall shrub cover was much higher in the western regions of the Park **(Figure 3.8)**. In unaffected stands of the FEA mean shrub cover is just over 50%, while shrub cover approaching 100% is typical of the Knob & Kettle eco-district **(Figure 3.8 a,c)**. Mean shrub cover decreased slightly (to about 40%) in beaver-affected stands within the FEA,

but increased to well over 100% in the Knob & Kettle eco-district **(Figure 3.8 b,d)**. A multi-layered shrub stratum was common in beaver-affected plots in the Knob & Kettle eco-district, resulting in total shrub cover values in excess of 100%.

In the FEA, the higher conifer component restricts shrub growth by shading the understory and acidifying the soil. Since conifer cover often increases as a result of beaver activity, mean shrub cover tends to decline in beaver-affected stands. In the Knob & Kettle eco-district, conifers are far less abundant and shrub cover is therefore much higher. In these stands, the removal of aspen by beaver opens the stands, increasing light availability and thus promoting even higher tall shrub cover.

Shrub community composition also differs between the two eco-districts **(Figure 3.8)**. The Knob & Kettle ecodistrict has a more diverse tall shrub stratum: beaked hazelnut, saskatoon (*Amelanchier alnifolia*), choke cherry (*Prunus virginiana*), pin cherry (*Prunus pennsylvanica*), mountain maple (*Acer spicatum*), and nannyberry (*Viburnum lentago*) all occur in abundance. High diversity results in pronounced stratification of the shrub layer, with very tall species such as mountain maple and the cherries overtopping lower-growing species such as beaked hazelnut and saskatoon.

Beaver selectively feed on tall shrubs such as hazelnut, cherry and mountain maple (Muller-Schwarze and Sun 2003). Beaver exert a strong influence on shrub community structure and composition, since removal of the largest shrub stems by beaver promotes intense basal sprouting and/or clonal root suckering. Vegetative sprouting by tall shrubs

results in thick, dense clonal thickets (personal observation). Clonal proliferation is particularly pronounced in beaked hazelnut; the species also appears to benefit from the removal by beaver of competitors such as mountain maple and the cherries. More research is needed to clarify the profound effect beaver herbivory has on shrub and understory structure and composition.

Forest Stand Types Resulting from Beaver Disturbance

Transect data and field survey results led to the recognition of four major forest stand types that develop following beaver harvesting:

I. Closed Spruce (n=20); Figure 3.2

This stand type is the only one in which the tree canopy is sufficiently closed to prevent prolific shrub growth; canopy and sub-canopy spruce exert a strong shading effect on the understory vegetation. The closed spruce type arises when a reproductively viable cohort of spruce is present during the time of beaver harvesting. Shade provided by the larger trees, combined with establishment of a sapling cohort, results in a dense, closed canopy spruce stand.

II. Open Spruce Shrubland (n=14); Figure 3.3

This stand type consists of a few older softwoods (usually white spruce) overtopping a dense tall shrub thicket. These thickets are often dominated by beaked hazelnut (*Corylus cornuta*). This type occurs when a young white spruce sapling cohort is present during

the time of beaver disturbance. As these saplings grow and become reproductively viable, the shrub stratum is so dense that new saplings cannot become established.

III. Open Hardwood Shrubland (n=10); Figure 3.9

This stand type is similar to the open spruce shrub-land type, but with hardwoods (species palatable to beaver) instead of softwoods. Hardwood species that undergo basal sprouting, such as bur oak (*Quercus macrocarpa*) and white birch (*Betula papyrifera*), are most commonly encountered. This type, which occurs mainly in the Knob & Kettle ecodistrict, develops after large boles are harvested by beaver and basal sprouts (which may also be heavily browsed) develop. Prior to beaver disturbance, these stands are dominated by trembling aspen and/or balsam poplar.

IV. Open Shrubland (n=11); Figure 3.10

Expansive open shrubland communities develop in stands where neither softwoods nor basal-sprouting hardwoods are present prior to beaver disturbance. Since trees are unable to take immediate advantage of the increased light levels following beaver harvesting, tall shrubs are able to proliferate and develop dense, impenetrable thickets that strongly inhibit tree regeneration. Prior to beaver disturbance, these stands are dominated by trembling aspen and/or balsam poplar.

3.3.3 Beaver Foraging Patterns

The large discrepancy in foraging distance between the eastern ponds and western lakes may be attributable to sustained foraging pressure by beaver. The amount of

habitable area on a lake (a much larger body of water) allows multiple beaver colonies to co-exist. Should an entire colony succumb to disease or depredation, another colony on the lake can quickly increase their foraging range to include the newly available habitat. In addition, young from another colony may re-inhabit a recently abandoned lodge (Slough and Sadlier 1976). As evidence supporting this hypothesis, the mean foraging distance on Deep Lake, which had eight lodges, was nearly 50 m. The similar-sized Bob Hill Lake had only two lodges, both abandoned, and an average foraging distance of only 30 m.

By contrast, along streams a single beaver colony creates and maintains a small impoundment (beaver pond). Impounded stream habitats may be more susceptible to population crashes and slower recoveries. When an isolated colony is lost to disease or depredation, there may be no colony in the immediate vicinity to re-establish the abandoned lodge and dam. The wetland will deteriorate after the abandoned dam is breached, and it may be decades before beaver re-colonize the area. Re-colonization is dependant upon a young beaver chancing upon the site. Furthermore, though beaver typically re-occupy abandoned lodges (Slough and Sadlier 1976), they tend not to reconstruct older breached dams, preferring instead to build a new dam further downstream (personal observation). Within the FEA, older abandoned ponds (with breached dams) have a mean foraging distance of only 24 m. It is not uncommon to find large areas of undisturbed, but potentially harvestable, mature aspen stands adjacent to these older ponds. Often, these intact stands occur mainly on the pond edge furthest from the lodge (personal observation). Further research is needed to determine the foraging

behavior of beaver in relation to pond depth, lodge and dam location, and the availability of woody material for construction and food.

3.3.4 Beaver Disturbance and Forest Stand Dynamics

Beaver herbivory exerts a strong influence on forest community dynamics adjacent to wetlands in RMNP. Initially, beaver shift the stand composition towards non-preferred tree species and/or shrubs, an effect that is well documented in the literature (Donker and Fryxell 1999; Barnes and Mallik 2001; Johnson and Naiman 1990a). My data confirm those results for the Riding Mountain area. However, while some researchers have assumed that beaver harvesting promotes conifer growth (Johnston and Naiman 1990a; Donker and Fryxell 1999), others assume that beaver do not increase white spruce growth but merely shift the proportion of conifers as a result of their selective harvesting (Barnes and Dibble 1988; Martell et al. 2006). In contrast, Pastor and Naiman (1992) concluded that in some situations the removal of canopy aspen will actually promote aspen regeneration by suckering.

Some researchers postulate that in addition to the immediate change in stand composition, beaver will "accelerate" succession by increasing the growth of non-browsed trees (Johnston and Naiman 1990a; Donker and Fryxell 1999). I found that this does indeed occur in RMNP. In situations where sub-canopy trees are suppressed below an aspen canopy, spruce will undergo competitive release once the aspen are removed from the canopy by beaver. This competitive release will increase total basal area beyond that of plots unaffected by beaver **(Figure 3.1)**. In situations where aspen and spruce

share canopy dominance at the time of beaver disturbance, no significant increase in basal area was noted over the control plots **(Figure 3.1)**. This in effect is the "shift" towards spruce dominance reported by researchers who do not assume that "acceleration" occurs. Both increased growth and reproduction can influence total stand basal area.

Dendrochronological results show that in both aspen dominated and mixed canopy plots, edge trees have a significantly higher mean relative growth rate (RGR) than the core and control trees after disturbance by beaver **(Table 3.1)**. A sharp increase in RGR is strongly visible as a release event in edge trees, which benefit the most from higher light availability **(Figure 3.4a)**. The highest RGR occurred in spruce trees that were initially suppressed by aspen prior to beaver disturbance (**Table 3.1**). Though assumptions cannot be made concerning total stand basal area when considering the growth rate of individual trees, these results suggest that an important difference in post-disturbance spruce reproduction occurs between the two stand types in addition to growth dynamics.

During the decade immediately following beaver disturbance, conifer tree species can respond with increased reproduction, dependant on the stand structure and composition prior to beaver disturbance. If spruce trees are large enough and at a reproductively viable age at the time of disturbance (not too young or old), seed from white spruce can colonize beaver-created canopy gaps before shrubs can grow and outcompete the saplings for light, adding to the "acceleration" of spruce dominance **(Figure 3.2)**. Conversely, if the

white spruce are unable to produce viable seed, shrubs typically colonize the canopy gaps creating an open stand with a large shrub component (**Figure 3.3**).

In comparison to the aspen-dominated plots, white spruce in mixed-canopy plots are generally much larger and older, decreasing the chance that they will be at a reproductively viable age at the time of disturbance. In contrast, spruce trees suppressed under an aspen canopy are typically younger and have a greater chance of producing viable seed. This hypothesis is supported by the PSP data. Three of the six aspen-dominated plots developed into closed canopy spruce stands after beaver disturbance (50%). In comparison, only three of the eleven mixed wood plots became a closed canopy stand (27%) after beaver disturbance. In these plots, competitive release plays a strong role in increasing white spruce growth and reproduction.

My results indicate that the predictive model of forest response to beaver herbivory proposed by Pastor and Naiman (1992) is not appropriate for RMNP. Their model predicted that the removal of canopy aspen would create gaps that would favor the regeneration of early successional tree species. They also proposed that white spruce regeneration and growth would be suppressed by the maintenance of these early successional forest stands. This model is not valid for the mixed wood stands in RMNP, for two reasons: (1) the model assumes that beaver do not feed on aspen saplings <10 cm in diameter; (2) the model does not take into consideration the competitive advantage that dense clonal shrubs have in the forests of RMNP.

The assumption that beaver do not feed on saplings is supported by numerous studies (Basey et al. 1988, Johnson and Naiman 1990a, Jenkins and Busher 1979). This unusual avoidance of available food has been attributed to the elevated concentrations of phenolic compounds in saplings, deterring beaver herbivory. However, my transect results show that beavers in RMNP appear to feed on aspen saplings repeatedly. This result is unfortunately difficult to quantify, since beaver cut aspen saplings at the base (very close to the root), and the small "stumps" decompose very quickly. However, other current research supports my empirical observations. Barnes and Mallik (2001) did not find any aspen regeneration in their northern Ontario study, even after 12 years of site abandonment by beaver. Current research also demonstrates that beaver will harvest red maple (*Acer rubrum*) and trembling aspen saplings and store them in water for brief periods. Soaking the stems in water leaches out the unpalatable phenolic compounds, rendering the stems palatable to beaver (Muller-Schwarze et al. 2001, Basey et al. 1988). Trembling aspen appear to regenerate in RMNP only when beaver are no longer in the area, and when repeated browsing has not completely destroyed the aspen root system.

In the western areas of RMNP, recruitment of trembling aspen and balsam poplar is strongly inhibited by dense thickets of clonal shrubs (beaked hazelnut in particular). Typically, sapling recruitment in stands with an open shrub-dominated understory only occurs if the shrub stratum is disturbed. Browsing by ungulates may play a disturbance role, but the majority of sapling recruitment takes place in areas disturbed by fallen trees (downed woody debris; personal observation). Beaver can exacerbate this recruitment problem by removing canopy trees, increasing shrub growth in some situations **(Figures**

3.3, 3.8, 3.9, 3.10). Conversely, if the shrub stratum is already dense prior to beaver disturbance, downed aspen can create gaps in the shrub layer, increasing the survival rate of regenerating shade-intolerant tree species (personal observation). This scenario is uncommon in RMNP, and occurs only in areas where beaver are no longer foraging for food. Thus, beaver disturbance will either promote or prevent successful sapling recruitment. This hypothesis would explain my sapling results, which showed no major difference between aspen regeneration in beaver affected and un-affected plots. More research is needed to explain the effect of felled trees and shrub density on sapling recruitment in these stands.

If conifer trees are not in the area, removal of trees by beaver will shift the composition of the stand towards an open canopy shrub community **(Figure 3.10)**. Repeated aspen browsing by beaver and the resultant thick shrub strata will create heavy shade, preventing strong reproduction from the surrounding tree community (personal observation). Basal sprouting trees such as white birch or bur oak, which are not as palatable to beaver, can persist in these communities even when repeatedly browsed by beaver. This creates an open hardwood shrubland **(Figure 3.9)**, a beaver created community type commonly seen in the western region of RMNP.

3.3.5 Beaver Disturbance and Forest Research

The pivotal role beaver play in altering the structure and composition of forest stands adjacent to lakes and ponds must be taken into consideration when discussing forest stand dynamics. This study has shown that beaver disturbance affects forest stand dynamics in

a multitude of ways. At the landscape scale, beaver potentially influence over 25% of the forested landscape of RMNP (see Chapter 4). This study indicates that beaver disturbance is as important as natural disturbance events such as wind-throw or fire. Despite this, few studies of forest dynamics have considered the critical role that beaver disturbance plays in altering stand composition and structure.

Bergeron (1991) used transect data to describe post-fire forest composition in areas with differing fire histories. Data from stands of different age were compared to infer successional trends in a classic chronosequence approach. Many of these transects were located on islands and near the shorelines of lakes. These areas were very likely disturbed by beaver sometime in the past. As noted above, beaver disturbance plays an important role in determining the structure, composition and successional dynamics of these stands. This is especially true of stands along lakeshores, where beaver remove large amounts of woody (mostly hardwood) biomass. Bergeron (1991) found that only 5.8% of the stands sampled along lakeshores and islands (which also happened to be the oldest stands) had a hardwood component over 50%. In RMNP, older upland stands (those not subject to disturbance by beaver) maintain an appreciable hardwood component, whereas older stands near watercourses are often completely dominated by softwoods (mostly white spruce). The confounding of space and time, a common criticism of the chronosequence approach, is immediately apparent. Is the absence of hardwoods in older stands (which also happen to occur near water) attributable to natural successional process (softwoods succeeding hardwoods), or past beaver disturbance?

The point of bringing up the work of Bergeron (1991) is not to insinuate that his methodology is flawed. Instead, I hope that my work, and the work of others, will provide a cautionary note to researchers working in and around wetland and lake systems where beaver are (or were) present. Beaver disturbance has a powerful effect on these forests. In RMNP, even large aspen stumps decompose completely within 50 years, and thus stands that once contained aspen may be completely unrecognizable as beaver disturbed. A 60 year-old stand adjacent to a water-body may show no signs of beaver disturbance, but it was likely affected by beaver in the past and had its composition and structure (and successional pathways) forever altered. I recommend that future forest succession research take place at least 50 m (more if possible) from lakes and wetlands, unless the researcher can conclusively say that beaver have not been in the area.

Table 3.1. Mean relative growth rate (RGR) of trees cored within two beaver affected stand types (± 1 standard error (SE)) in the Forest Experimental Area, Riding Mountain National Park. Trees are separated into 3 groups, based on their location in or around the affected stand. Relative growth rate is reported in mm * mm^{-1} * $year^{-1}$.

	Edge Trees			Core Trees			Control Trees		
Stand Type (1947)	**RGR**	**SE**	**n**	**RGR**	**SE**	**n**	**RGR**	**SE**	**n**
Closed Canopy Aspen	0.080	0.005	4	0.040	0.002	5	0.038	0.002	8
Aspen-Spruce Mixedwood	0.041	0.005	5	0.024	0.001	4	0.029	0.001	9

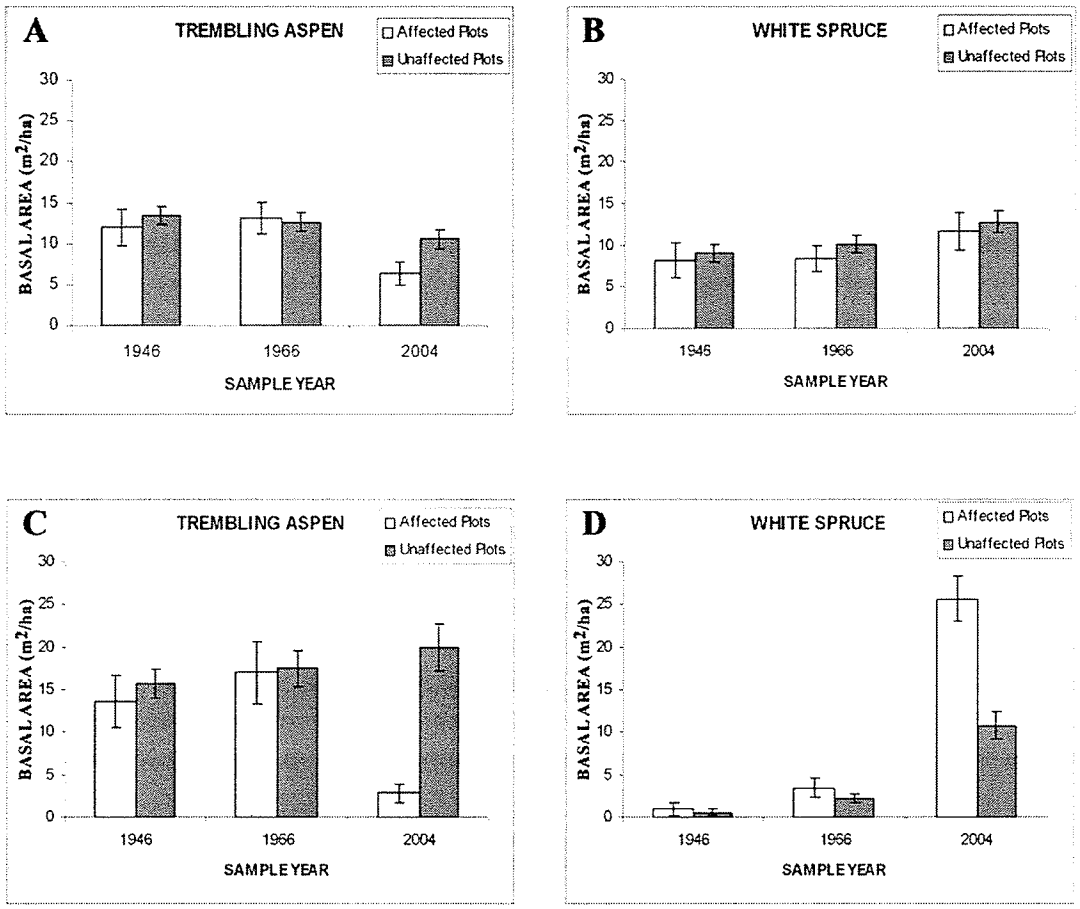

Figure 3.1. Mean tree basal area (m^2/ha, ± 1 standard error) over three sampling years from permanent sample plots in the Forest Experimental Area of Riding Mountain National Park, comparing temporal trends in trembling aspen and white spruce abundance between beaver-affected plots and control (unaffected) plots. **A,B**: stands co-dominated by trembling aspen and white spruce in 1946 (11 affected plots, 54 control plots). **C,D**: stands dominated by trembling aspen in 1946 (6 affected plots, 23 control plots).

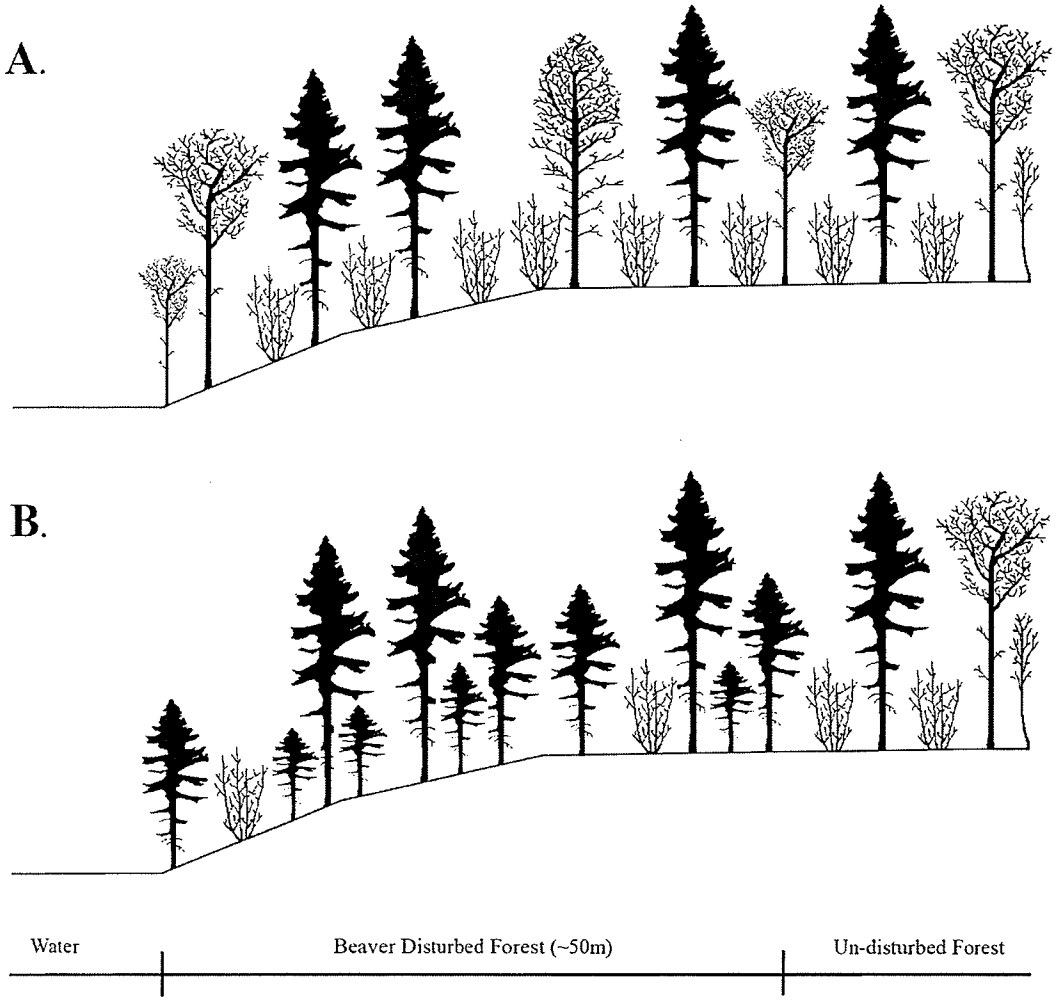

Figure 3.2. Successional trajectory leading to a closed canopy white spruce stand after removal of trembling aspen and balsam poplar by beaver. A= pre-beaver disturbance; B=post-beaver disturbance. See Appendix 3 for vegetation symbol descriptions.

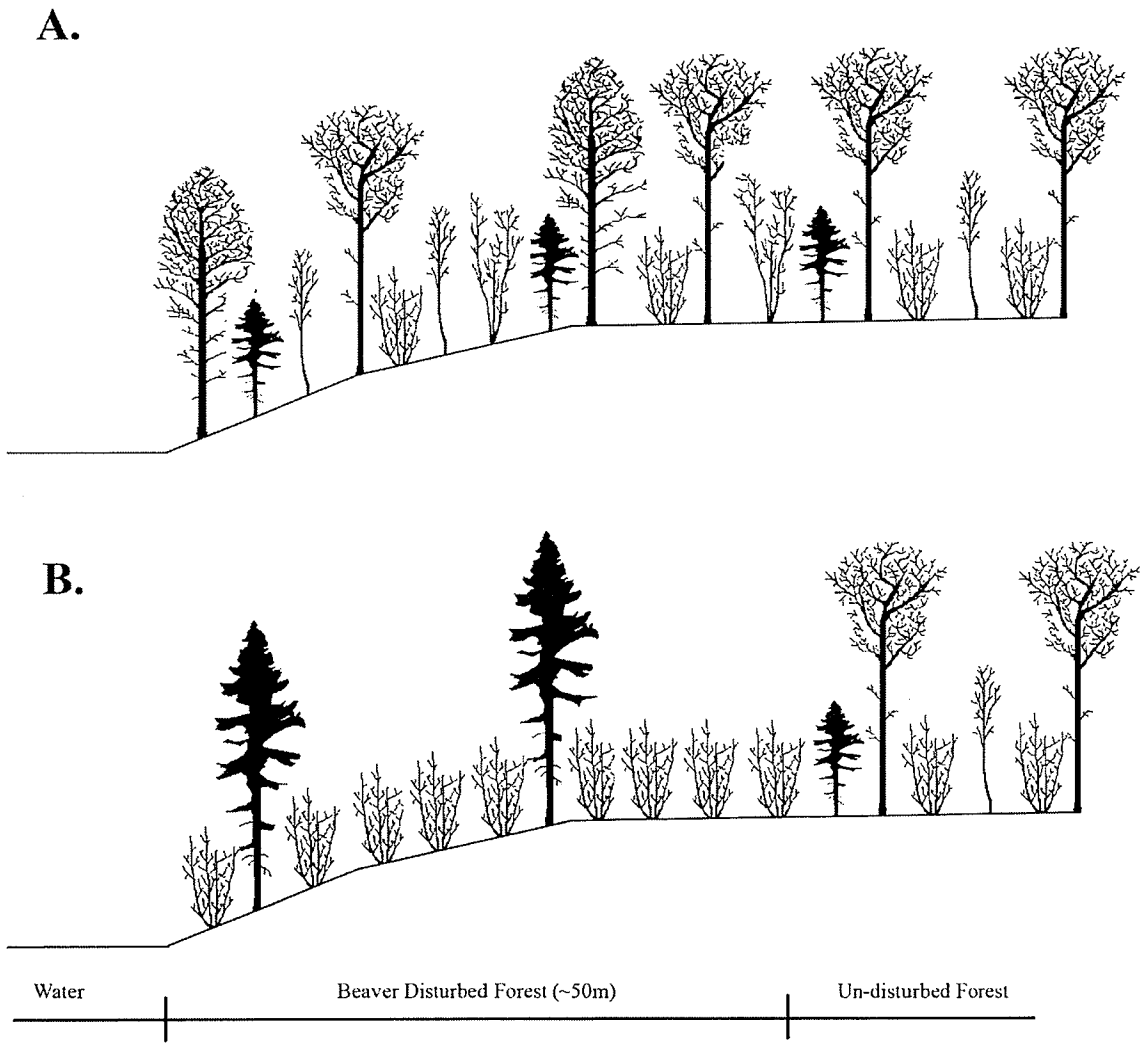

Figure 3.3. Successional trajectory leading to an open canopy white spruce shrubland after removal of trembling aspen and balsam poplar by beaver. A = pre-beaver disturbance; B = post-beaver disturbance. See Appendix 3 for vegetation symbol descriptions.

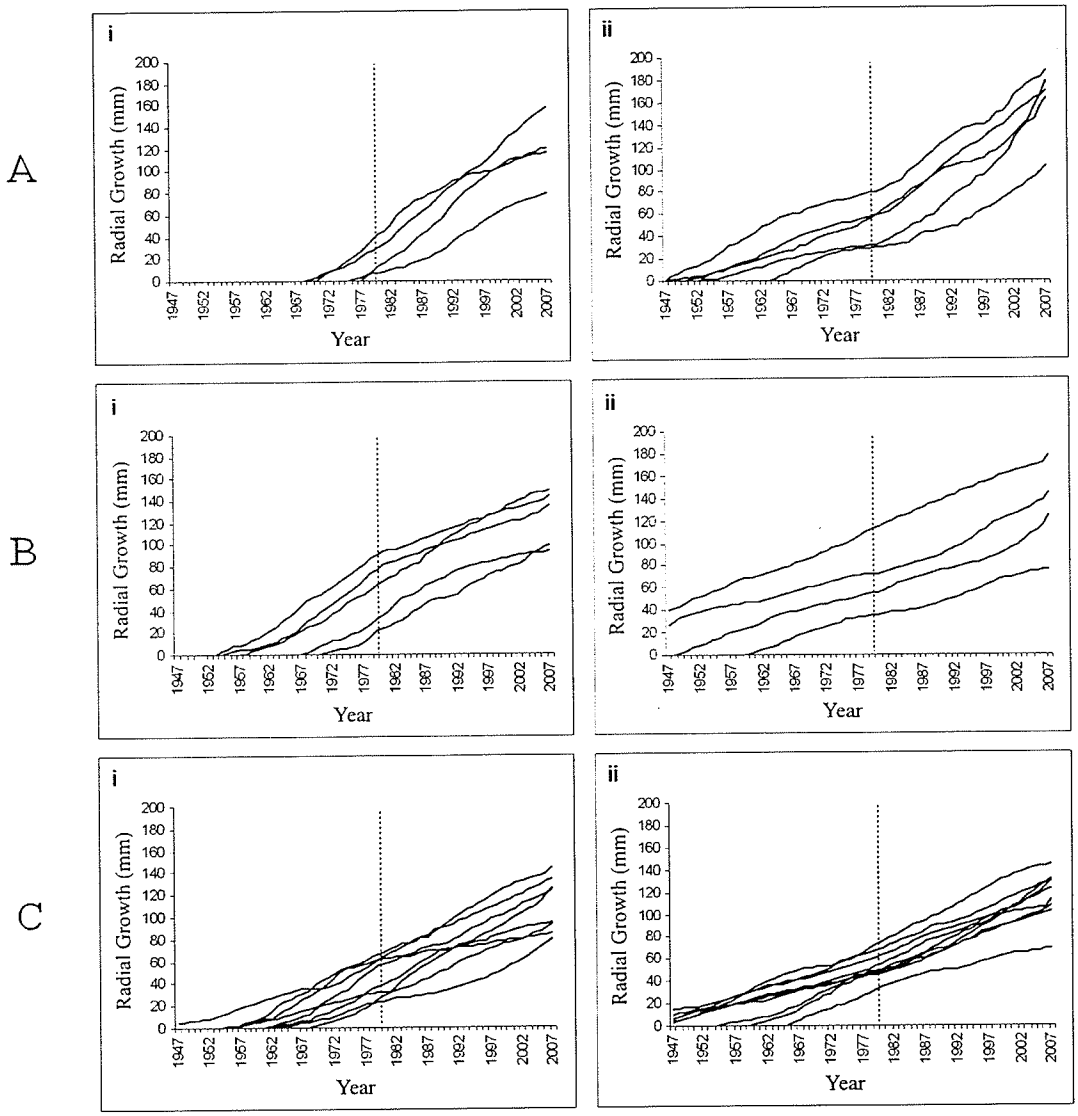

Figure 3.4. Cumulative radial growth of white spruce trees over a 60-year period. Graphs in row A = edge trees; B = core trees; C = control trees. Graphs in colum i = dominated by aspen in 1947; ii = mixed canopy of aspen and spruce. Dashed line indicates the estimated time of beaver disturbance.

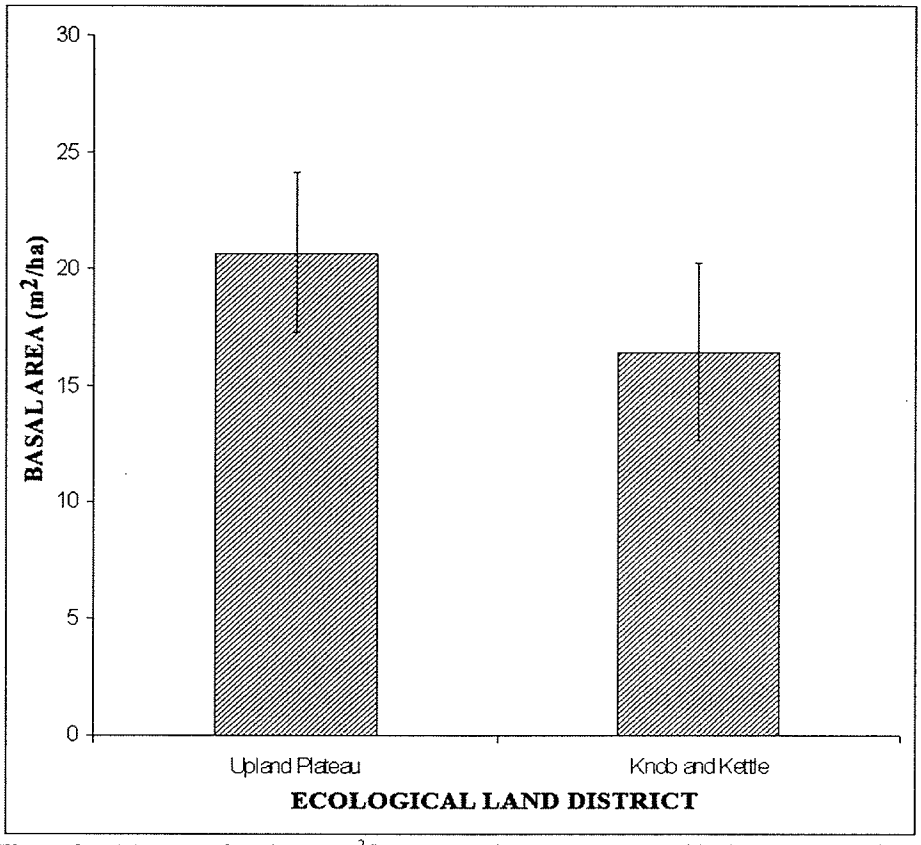

Figure 3.5. Mean tree basal area (m^2/ha, ± 1 standard error) removed by beaver within foraging distance of shorelines in Riding Mountain National Park, obtained by measuring the stumps of beaver-harvested trees. The vast majority of harvested trees are trembling aspen and balsam poplar. Sample sizes (number of transects) are 15 in the Upland Plateau ecodistrict, and 16 in the Knob and Kettle ecodistrict.

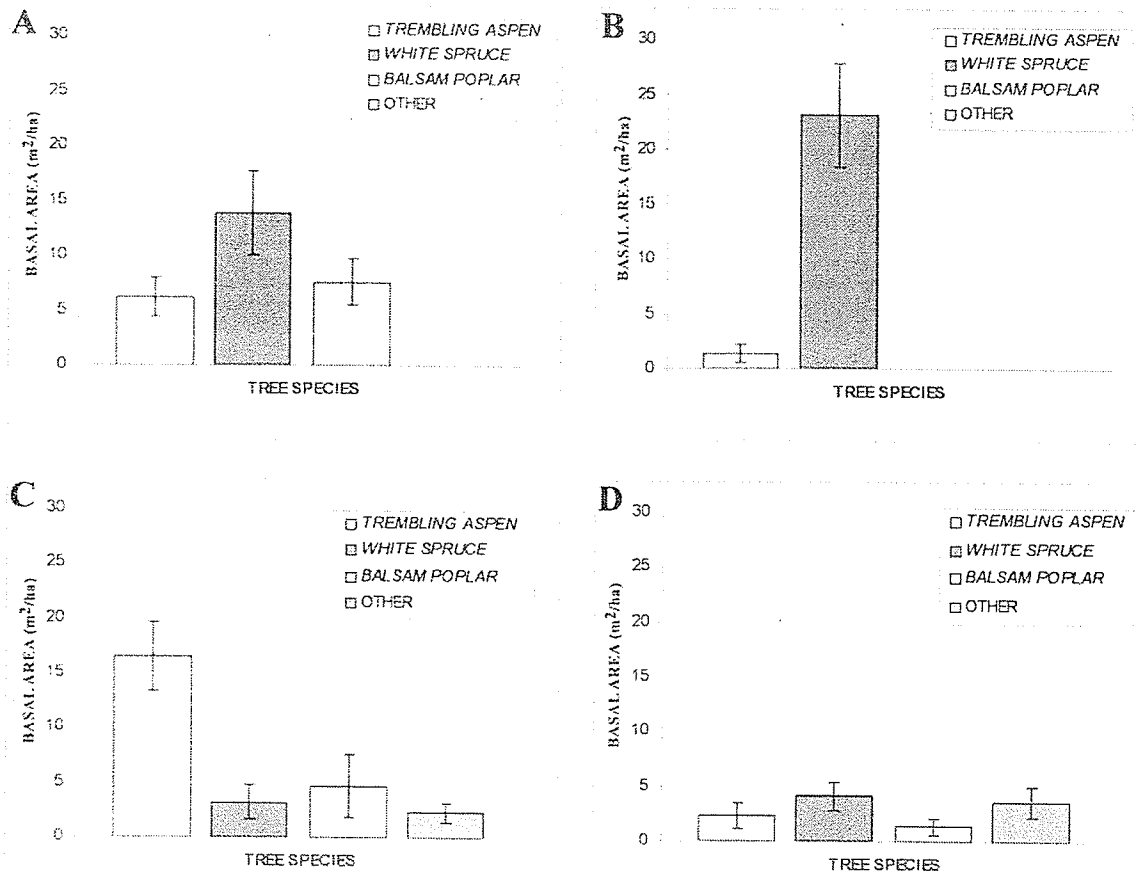

Figure 3.6. Mean tree basal area (m^2/ha, +/- 1 standard error) comparing species abundance patterns between beaver-affected (harvested areas near shorelines) and unaffected (non-harvested areas) along transects in Riding Mountain National Park. A,B: Upland Plateau Ecodistrict (n = 15 transects), A = unaffected stands, B = beaver-affected stands. C,D: Knob and Kettle Ecodistrict (n = 16 transects), C = unaffected stands, D = beaver-affected stands. The "other" category includes white birch (*Betula papyrifera*) and lesser amounts of bur oak (*Quercus macrocarpa*).

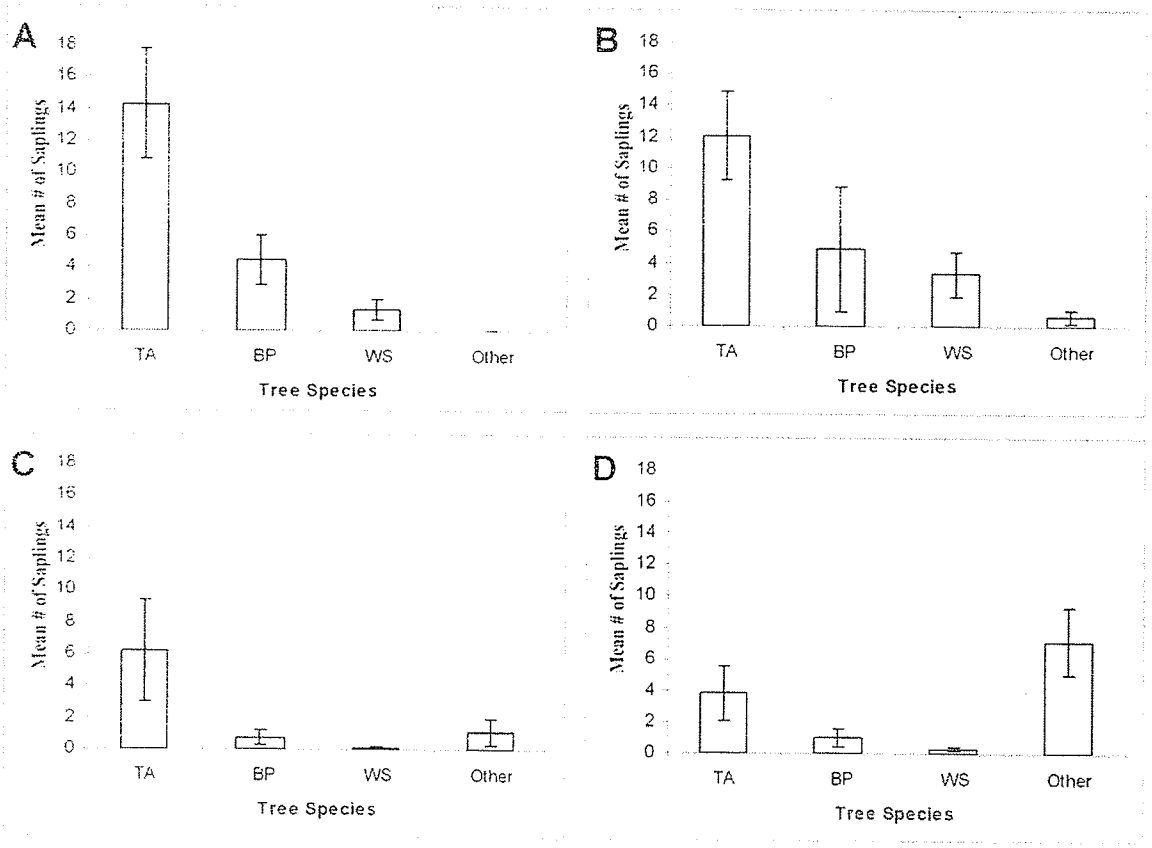

Figure 3.7. Mean sapling count (+/- 1 standard error) comparison of tree species in beaver-affected (harvested areas near shorelines) and unaffected (non-harvested areas) along transects in Riding Mountain National Park. A,B: Upland Plateau Ecodistrict (n = 15 transects), A = unaffected stands (n = 16 plots), B = beaver-affected stands (n = 10 plots). C,D: Knob and Kettle Ecodistrict (n = 16 transects), C = unaffected stands (n = 14 plots), D = beaver-affected stands (n = 24 plots). The "other" category includes white birch (*Betula papyrifera*) and lesser amounts of bur oak (*Quercus macrocarpa*) and balsam fir (*Abies balsamea*).

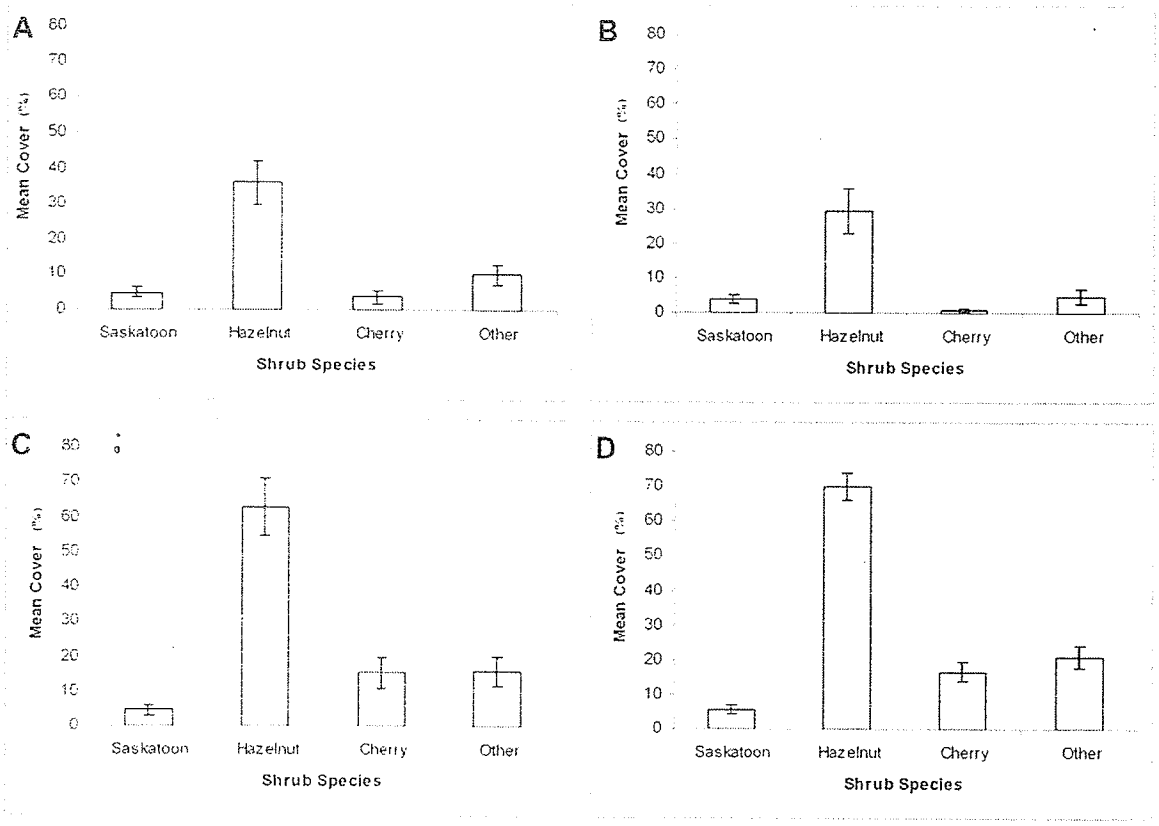

Figure 3.8. Mean percent cover (+/- 1 standard error) comparison of shrub species composition in beaver-affected (harvested areas near shorelines) and unaffected (non-harvested areas) stands along transects in Riding Mountain National Park. A,B: Upland Plateau Ecodistrict (n = 15 transects), A = unaffected stands (n = 16 plots), B = beaver-affected stands (n = 10 plots). C,D: Knob and Kettle Ecodistrict (n = 16 transects), C = unaffected stands (n = 14 plots), D = beaver-affected stands (n = 24 plots). The "other" category includes, among others, mountain maple (*Acer spicatum*), nannyberry (*Viburnum lentago*) and red-osier dogwood (*Cornus stolonifera*).

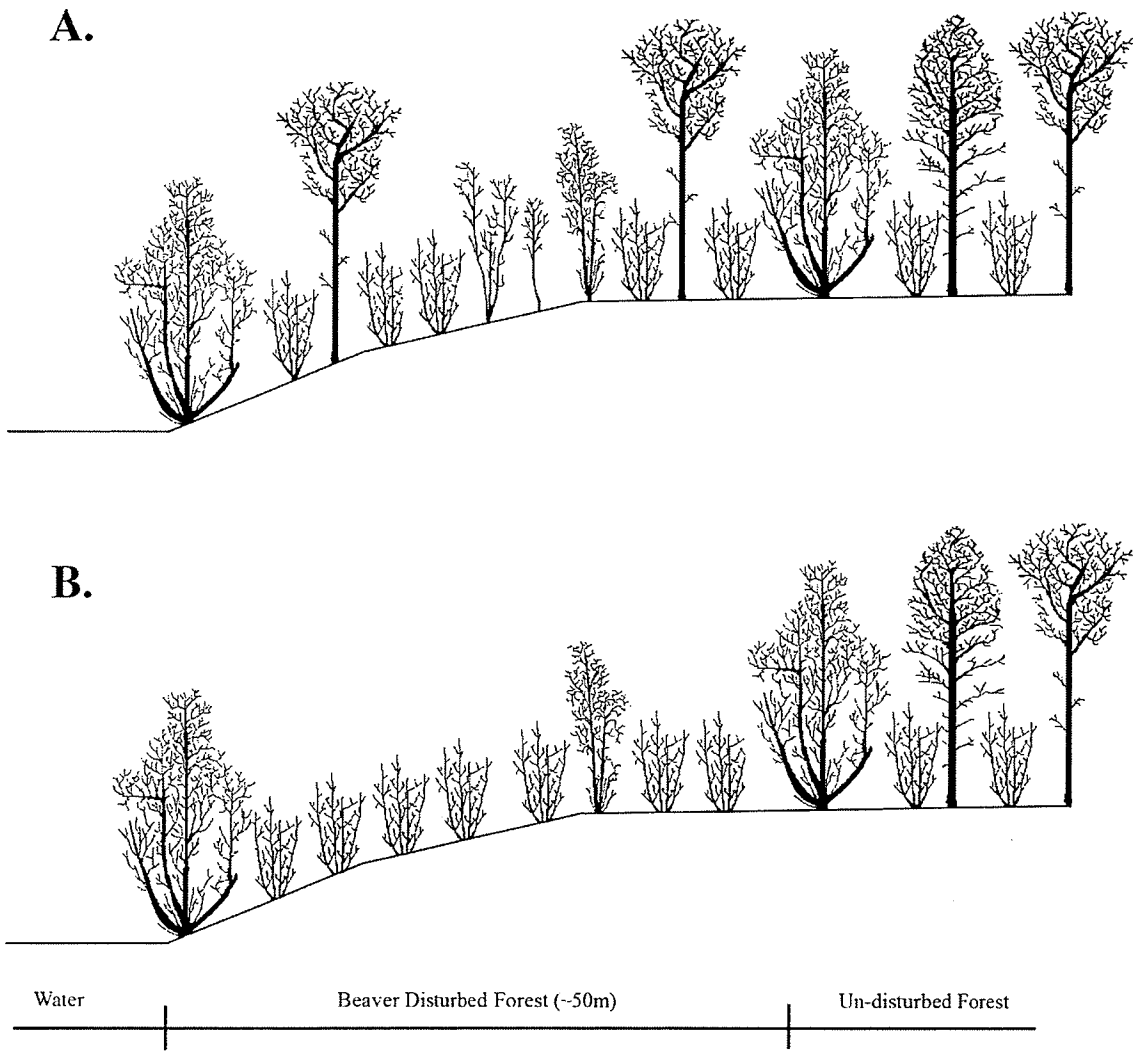

Figure 3.9. Successional trajectory leading to an open hardwood shrubland after removal of trembling aspen and balsam poplar by beaver. A = pre-beaver disturbance; B = post-beaver disturbance. See Appendix 3 for vegetation symbol descriptions.

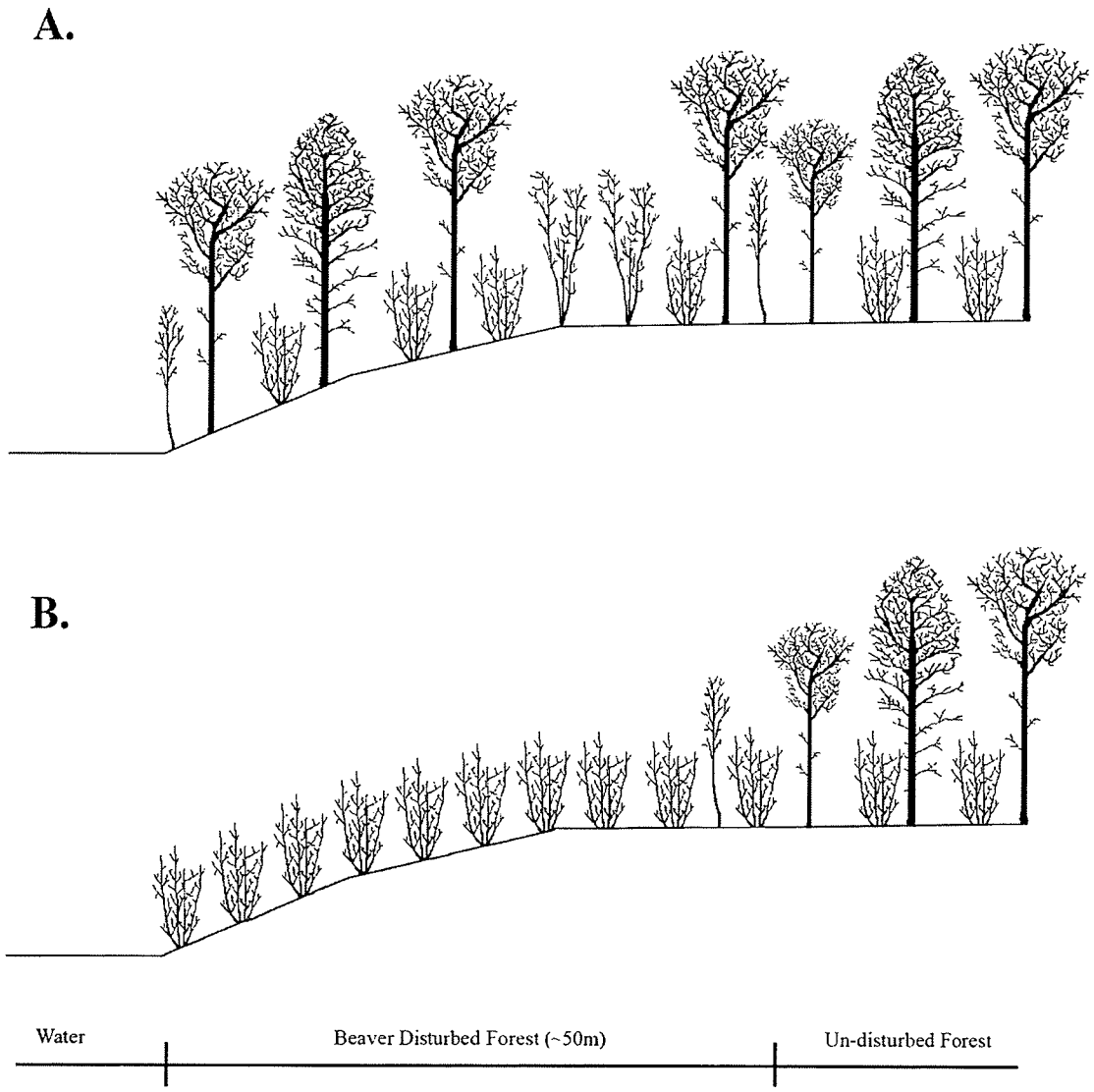

Figure 3.10. Successional trajectory leading to an open shrubland after the removal of trembling aspen and balsam poplar by beaver. A = pre-beaver disturbance; B = post-beaver disturbance. See Appendix 3 for vegetation symbol descriptions.

CHAPTER 4

BEAVER DISTURBANCE AND LANDSCAPE HYDROLOGY

4.1 INTRODUCTION

To increase food availability and offer protection from predators, beavers (*Castor canadensis*) have evolved highly specialized behaviors that allow them to convert forest into aquatic habitat by damming slow-moving creeks and streams. Beavers diligently maintain the dam(s) – repairing leaks and breaches – for as long as the pond is occupied (Naiman et al. 1988). The pond habitat can persist for years or even decades, maintained by a specific beaver colony and its progeny. Once all food resources in the vicinity (mainly upland woody plants and some herbaceous plants) are depleted by the colony, the dam is abandoned.

Beaver dams reduce low-order stream flow and create wetland habitat. Damming also increases the shoreline perimeter, which in turn increases the potential food supply of the beaver colony (Ray et al. 2001). A den or lodge is generally constructed near the centre of the pond, using the same methods and materials used to construct the dam. The lodge is the primary residence of the colony, protecting it from inclement weather and from predators such as timber wolves (*Canis lupis*), coyotes (*Canis latrans*), and bears (*Ursus spp.*) (Baker and Hill 2003). Returning to a central lodge and foraging outward allows the beaver colony to maintain the dam. Central place foraging also concentrates the herbivory of the colony to the area in and around the pond, disturbing vegetation

structure, composition and succession patterns in both wetland and adjacent upland habitats.

Over time, beaver disturbance affects large stretches of the stream corridor in various ways. Beaver often build multiple dams along small-order streams, creating a stair-step flow regime that slows water flow and produces large marsh and open-water areas. Successions of beaver dams were noted to increase average stream width from 10.5m to 33.9m in Wyoming (McKinstry et al. 2001). In northern Minnesota, comparable increases resulted in the replacement of wet meadow with more diverse marsh habitat (Broschart et al. 1989). Beaver impoundments become nutrient sinks for both carbon and nitrogen. This effect is largely attributable to decreased stream velocity, which results in the accumulation of sediment and organic debris over time (Naiman et al. 1986; Naiman et al. 1988). Nutrient accumulation greatly increases the productivity of aquatic habitats created by beaver impoundments. Ponds are typically shallow, providing a large littoral region for the development of aquatic communities.

Beaver-mediated wetland patches provide habitat for an assortment of other animals. Ponds reduce stream flow, stabilize fluctuating water levels and create a physical barrier in the stream. This change increases the density and biomass of aquatic invertebrates, shifting the distribution of feeding groups (McDowell and Naiman 1986). Similarly, dam environments may be either beneficial or detrimental to fish species, depending on their preferred habitat (Murphy et al. 1989; Cunjack 1996; France 1997) and their ability to negotiate dams (Gard 1961).

The complex habitat structure in beaver impoundments is important to many birds and animals. Beaver-created ponds and lodges, associated vegetation changes such as increased marsh and tall shrubs, and beaver-felled trees all provide critical habitat. Adult waterfowl prefer beaver created ponds (>0.4ha) over natural wetlands of the same size (Peterson and Lowe 1977). The importance of beaver ponds to waterfowl is substantial and well documented, but beaver ponds may be even more important to some other bird species (Reese and Hair 1976). For example, piscivores such as great blue heron (*Ardea herodias*) and belted kingfisher (*Ceryle alcyon*) occur more frequently in beaver-created wetlands than in areas with no beaver activity (Grover and Baldassarre 1995). Ponds create important habitat for semi-aquatic mammals such as muskrat (*Ondatra zibethicus*), mink (*Mustela vison*) and otter (*Lontra canadensis*) (Rutherford 1955; Green 1932). Beaver ponds also have high reptile richness and diversity (Metts et al. 2001). In South Carolina, some species of amphibians were found only at beaver impoundments (Russel et al. 1999). Moose (*Alces alces*) and elk (*Cervus elaphus*) frequent beaver impoundments because of the high amount of available food such as aquatic plants (in the beaver pond) (Muller-Schwarze 1992), shrubs (in beaver disturbed forest) and tree saplings found at the base of beaver-cut stumps (personal observation).

Beaver also fell trees and flood upland forest, which in turn provides food and habitat for other animals. Downed trees provide food for terrestrial invertebrates (Spieth 1979; Saarenmaa 1978) and white-tailed deer (*Odocoileus virginianus*) (personal observation). Tree snags in beaver ponds provide nesting habitat for woodpeckers and perching sites

for hunting raptors such as osprey (*Pandion haliaetus*) (Grover and Baldassarre 1995). Abandoned beaver lodges can provide denning sites for bobcat (*Lynx rufus*) and marten (*Martes martes*) (Lovallo et al. 1993; Rosell and Hovde 1998). Each of these animals interacts with the food web in its own way, increasing the effect of beaver activity over the ecosystem. Their powerful influence on ecosystems has earned the beaver the appropriate descriptor "ecosystem engineer" (Jones et al. 1994); the beaver is truly a keystone species (Naiman et al. 1986).

Landscape studies illustrate the impact that beaver can have on ecosystems. In Voyageurs National Park (northern Minnesota, USA), the reintroduction of beaver in 1940 increased the proportion of wetland habitat on the landscape from 1% to 13% by 1986 (Naiman et al. 1988). By creating a 100m buffer around these impoundments, Naiman et al. (1988) estimated that beaver potentially affect an additional 12-15% of total landscape area through the harvesting of woody stems from forested uplands adjacent to impoundments. Thus, a total of 25 to 28% of the landscape was estimated to be currently or potentially affected by beaver disturbance in Voyageurs National Park by the late 1980s (Naiman et al. 1988).

In northern Minnesota, dam frequency was found to be as high as 2.0 - 3.9 dams per kilometer of stream (Naiman et al. 1988). A similar study in boreal Quebec (a region of optimal beaver habitat) found frequencies of 8.6 - 16 dams/km (Naiman et al. 1986). I found beaver dam densities as high as 28 dams/km along watercourses in the Upland Plateau forests north of Clear Lake in Riding Mountain National Park. This value –

while above the average for the region – is testament to the role of beaver in creating aquatic habitat patches. Such patches are sharply divided from the background matrix of forest habitat. With the relatively high proportion of aspen trees in RMNP and the large, dense beaver population (Frey and Avery 2004), beaver activity in the area could have an important role in landscape patch dynamics and wetland habitat. Currently, no research has investigated the effect of beaver in the boreal mixed woods and knob and kettle/aspen parklands of central Canada.

In Riding Mountain National Park, managers conduct aerial surveys of beaver food caches to estimate beaver colony density within a given area. This technique is problematic with inaccuracies such as observer bias, snow cover, vegetation cover, etc. confounding the results. In an attempt to reduce these errors, Broschart et al. (1989) developed a model to predict beaver colony density based on wetland attributes on the landscape. In their study area, Broschart et al. (1989) found that their model was very effective at predicting beaver colony density and had the dual function of assessing total landscape change as a result of beaver activity. If its predictions are accurate, the model could prove to be very useful to wildlife and vegetation managers in the Riding Mountain area when developing monitoring and management protocols for beaver and the various species which depend on beaver pond habitat for survival.

The primary objective of this chapter is to determine and describe temporal changes in landscape hydrology and wetland habitat types resulting from increased

beaver activity. Additionally, two objectives associated with the relationship between beaver and wetland habitat patches on the landscape will be explored:

1. Compare the differences in beaver-mediated wetland dynamics between ecological land districts in Riding Mountain National Park.
2. Test the assumptions of the Broschart et al. (1989) predictive model of beaver colony density for the landscape in the Riding Mountain area.

4.2 METHODS

Study Area

Riding Mountain National Park (RMNP) is located in southern Manitoba, 225 km northwest of Winnipeg. The eastern area of the park forms part of the Manitoba Escarpment, which rises 300 m above the Manitoba Plain to the east. To the west stretches the Saskatchewan Plain. RMNP lies within the Mixedwood section of the Boreal Forest Region (Rowe 1972), which extends westward through central Saskatchewan and east-central Alberta. The Riding Mountain area lies within the humid micro-thermal cool summer climatic zone, where the winters are long and cold and the summers are short and warm (Bailey 1968).

Beaver populations are unevenly distributed throughout the park. Beaver populations are lowest in the escarpment and lowland ecological land districts (Frey and Avery 2004) and very dense in the remainder of the Park. Accordingly, two regions of RMNP were

chosen for study: (1) Forest Experimental Area (FEA), Upland Plateau eco-district, eastern region of RMNP; (2) Aerial Beaver Survey Block 72 (Block 72), Knob and Kettle eco-district, western region of RMNP.

Located in the western and southern regions of RMNP, The Knob and Kettle Ecological Land District is characterized by shallow depressions of water created by melting blocks of ice left as the glaciers retreated from the area during the end of the last ice age, creating many poorly-drained wetlands (Bailey 1968). In part due to a recent fire history, expansive trembling aspen (*Populus tremuloides*) forests mixed with small stands of white spruce (*Picea glauca*) are characteristic of this district, interrupted by open prairie habitat and black spruce (*Picea mariana*) bogs (Parks Canada 2002).

Most of RMNP occurs within the Upland Plateau Ecological Land District, a region dominated by boreal mixed wood forest. White spruce and trembling aspen are the dominant upland tree species, although balsam poplar (*Populus balsamifera*), paper birch (*Betula papyrifera*) and black spruce are also prominent in some situations. The landscape is characterized by large rolling stretches of glacial till with numerous wetlands. Both the Upland Plateau and the Knob and Kettle eco-districts have wetlands that are surrounded by boreal mixedwood and aspen forests, which provides ample habitat to support one of the highest density population of beaver in North America (Parks Canada 2002).

Sampling Protocol

Initially, an extensive ground survey was undertaken to aid in the interpretation of aerial photographs. In total, 150 beaver-affected wetlands (110 in the FEA, 40 in Block 72) were located and enumerated. Each site was photographed, GPS coordinates were taken, and general notes on physiographic features and vegetation composition and structure were made. An additional 101 wetlands (58 in the FEA, and 43 in Block 72) were enumerated in greater detail. These wetlands served as detailed "ground-truth" locations, and were selected from the 2004 digital orthophotos to represent all of the major texture-patterns present on the images. Since the impounded water, conifer bog, dry meadow and human disturbance classes were easily distinguished on all digital photos, they were not targeted for extensive ground surveillance. A representative 10 x 10 m plot was randomly located within each wetland. Percent cover of major plant species were recorded, GPS location was taken, and general notes on qualitative observations including beaver activity and water depth were made.

A temporal sequence of composite aerial photographs (1964 or 1969, 1978 and 2004) was examined to assess changes in flooding activity by beaver. Individual aerial photographs were scanned at a resolution of 600 dpi, and then merged to form composite photo-mosaics using Adobe Photoshop CS3 software. The photo-mosaics were then geo-rectified using ESRI ArcMap 9.2 image analysis software. The Patch Analyst file extension v.3 (a spatial pattern analysis tool based on ESRI ArcGIS 3.2) was used to create polygons outlining each wetland class and calculate area. The classification was done manually, using visual differences in texture, pattern and colour/shade (see **Figure**

4.1). Stereoscopic interpretation of the photographs, as well as extensive "ground-truth" data (vegetation and landform descriptions at various GPS-locations), were used to aid in the visual classification. In addition to landscape classification, the location of beaver dams (classified as abandoned (fully breached) or extant (filled with water, or only partially breached)) were recorded on the images.

A large number of wetland vegetation types were identified during the field survey. However, not all of these could be confidently distinguished using standard aerial photography analysis. A broader classification scheme was therefore employed for landscape analysis, recognizing eight landscape classes: (1) impounded water; (2) marsh; (3) wet meadow; (4) thicket swamp; (5) conifer swamp or bog; (6) upland forest; (7) grassland; and (8) human disturbance (roads/trails, gravel pits, tenting/day-use areas).

The "core-area function" of Patch Analyst was used to determine the potential amount of forest habitat affected by beaver activity. To accomplish this, all class types unaffected by beaver were merged into a single class. The classes of impounded water, marsh and wet meadow – those known to be associated with beaver activity – were retained for analysis. Forest habitat within a specified threshold distance of wetland shorelines are assumed to be potentially subject to tree removal by beaver. Naiman et al. (1988) used a threshold of 100 m. Although beaver have been shown in some studies to fell trees and haul woody stems as far as 200 m from the shoreline of their pond (Baker and Hill 2003), my transect results indicate typical foraging distances of only 40-50 m in RMNP (Sinkins, unpublished data). I therefore used a more conservative threshold

distance of 50 m. A 50 m buffer-strip of forest was added to the FEA boundary to accommodate limitations of the core area software. The software was then used to determine the amount of forest habitat within 50 m of the beaver-affected classes. The total core area was then subtracted from the total area of all unaffected classes giving the area potentially affected by beaver herbivory.

Data Analysis

Analytical and interpretive methodologies were based on those used by previous researchers (Broschart et al. 1989; Hammerson 1994; Johnson & Naiman 1990a,b,c; Meentemeyer & Butler 1996; Reese-Hansen 2004). Specifically, each wetland class was determined as a percentage of the total landscape area, and the results tabulated. Over the temporal series of aerial photographs, these percentages are expected to shift as beaver populations expand or decline.

4.3 RESULTS AND DISCUSSION

4.3.1 Ground Truthing and Wetland Classification

Analysis of the 101 vegetation plots, and their interpretation as texture-pattern signatures on the aerial photographs, led to the recognition of three readily identifiable wetland classes (**Table 4.1**):

I. Marsh Class ($n = 33$)

The marsh class is typically permanently flooded, and contains a combination of open water and emergent vegetation. This class has a unique textural signature that is readily identifiable on aerial photographs (**Figure 4.1**). These sites were typically productive and nutrient-rich, with a combination of floating and submergent vegetation in open water intermixed with emergent and upland vegetation. In some cases mono-dominant marsh communities occur, consisting of cattail (*Typha* spp.), water horsetail (*Equisetum fluvitale*) and/or bulrush (*Scirpus* spp.). Additionally, in areas near freshly breached beaver dams or in seasonally-flooded regions, a diverse community of weedy species may occur on exposed mudflats.

II. Wet Meadow Class ($n = 45$)

The wet meadow class is typically dense and dominated by graminoids. The textural signature of this class on aerial photographs is generally smooth, with few or no shrubs or no open water (**Figure 4.1**). These communities grade from drier sites dominated by bluejoint grass (*Calamogrostis canadensis*) and awned sedge (*Carex atherodes*), to wetter sites dominated by lake sedge (*Carex lacustris*) and water sedge (*Carex aquatilis*). Herbaceous species are limited to those able to survive beneath a dense graminoid canopy, such as bedstraw (*Galium trifidum*), and those found in openings created by disturbances such as mint (*Mentha arvensis*) and Canada thistle (*Cirsium arvense*).

III. Thicket Swamp Class ($n = 23$)

In the thicket swamp class shrub cover exceeds 25%, and is often much higher. The textural signature is finer than that of upland forest (**Figure 4.1**). However, in areas near a pond wetland shrub communities can be confused with upland shrub thickets; these were distinguished using a stereoscope. Typically, upland shrub communities (dominated by beaked hazelnut, *Corylus cornuta*) have a lower profile and a finer texture, and they often occur on slopes. Two main thicket swamp community types were identified: those dominated by river alder (*Alnus rugosa*), and those dominated by willows (*Salix* spp.). Although these species were found in both study areas, wetland shrub thickets in the FEA are usually dominated by river alder, whereas willows were more common in Beaver Survey Block 72. In both cases, sites with high shrub cover contained more herbaceous species, whereas the more open-canopy sites tended to contain graminoids. Upland plants may occur on the raised hummocks at the base of the shrubs, increasing local biodiversity.

4.3.2 Landscape Classification

<u>Landscape Classification – Forest Experimental Area</u>

Comparison of the 1964, 1978 and 2004 landscape classifications of the Forest Experimental Area (FEA) indicate a large increase in wetland cover over time (**Figure 4.2 a,b,c**). A more detailed view of one portion of the study area (**Figure 4.3**) highlights the nature of these changes. In 1964 beaver abundance was low, and wetlands (impounded water, marsh, wet meadow, and thicket swamp classes) accounted for only 4.84% of the landscape. Beaver had just begun to move into the area following the 1947

release at Elk Lake (east of the FEA). By 1964 they had constructed 12 dams, mostly in the eastern section of the FEA close to the release site (**Figure 4.4a**). In 1964 all of these dams were holding water and in good condition, indicating that they contained active colonies.

By 1978 (fourteen years later), a total of 258 beaver dams were found within the FEA (**Figure 4.4b**). Only 6 of these dams were fully breached, indicating a total of 252 active dams. This is confirmed by the landscape classification, which shows an increase in impounded water habitat from only 0.02% in 1964 to 0.54% by 1978 (**Table 4.2**). The amount of marsh habitat also increased during this time interval, from 0.47% to 1.92% of the landscape. These increases confirm the dramatic effects of beaver on stream and wetland hydrology in the region.

In the 2004 composite image, 324 beaver dams were found within the FEA (**Figure 4.4c**). The majority of these dams were still holding water (n = 207), but a large number had been fully breached (n = 117). Currently, most new damming activity is taking place in the western edge of the FEA, the furthest distance away from the 1947 release point. Overall, the large increase in beaver activity over the 1964-2004 period resulted in more than a doubling of wetland habitat within the FEA, to 10.12% of the landscape. The largest increases occurred in the impounded water class (increasing from 0.02% to 0.57%), and the wet meadow class (increasing from 2.78% to 6.86%). These changes are summarized in **Table 4.2**. When beaver move into the area and build dams, the water table is raised and forested habitat is converted to wetland. The area of conifer bog

habitat declined from 2.21% to 1.77% over the period, while upland forest habitat declined from 92.95% to 88.12%.

The amount of upland forest habitat potentially affected by beaver activity (i.e. tree felling) increased from 18.20% to 21.34% between 1964 and 2002. Combined with wetland habitat, this result indicates that nearly one-third of the FEA study area (21.34% + 10.12% = 31.46%) is potentially affected by beaver activity.

Landscape Classification – Beaver Survey Block 72

As in the Forest Experimental Area, an expanding beaver population within Beaver Survey Block 72 resulted in an increase in total wetland area on the landscape (**Figure 4.5a,b,c**). However, there were some differences that appear to be attributable to topographic variation. The FEA is characterized by a myriad of slow-moving streams with steep-sided slopes, whereas the undulating knob-and-kettle topography in Block 72 results in long, gradual slopes, extensive wetlands, and little moving water. A shallow water table results in expansive thicket swamps, which in the 1960s accounted for 10.15% of the landscape compared to only 1.57% of the FEA (**Table 4.2**). In general, the proportion of wetland and other non-forested habitat is much higher in the Knob & Kettle eco-district.

Analysis of the 1969 aerial photographs indicated that this region had a very high proportion of wetlands prior to beaver disturbance, totaling 17.6% of the landscape (**Figure 4.5a**). Impounded open water, which accounts for only 0.3% of the landscape in

1969, is attributable to the presence of 4 active beaver ponds **(Figure 4.6a, Table 4.2)**. By 1978 the beaver population had increased substantially; there were 33 active dams in the region, and 2 additional breached dams **(Figure 4.6b)**. Impounded water increased to 3.4% of the landscape, and marsh habitat nearly doubled between 1969 and 1978, from 2.8% to 4.66% **(Figure 4.5b)**. By contrast, wet meadow habitat decreased from 4.36% to 2.55% **(Table 4.2)**, indicating that beaver activity often results in the flooding of wet meadow habitat.

The 2004 aerial photographs indicate that a large number of dam sites were abandoned between 1978 and 2004. In 2004 there were 26 active beaver dams, plus an additional 23 abandoned (fully breached) dams **(Figure 4.6c).** The amount of impounded water habitat remained above 3%, but large changes in the proportions of marsh and wet meadow habitat occurred between 1978 and 2004 (**Table 4.2**). The amount of wet meadow habitat increased considerably, from 2.75% to 7.35% of the area. Conversely, marsh habitat declined from 4.66% to only 2.29%. This shift in wetland habitat is attributable to the increase in abandoned, breached dams; wet meadows tend to develop on exposed mudflats following dam site abandonment. Thicket swamps, which are sensitive to increases in the water table, decline from 10.15% to 8.53% by 1978, and to only 6.96% in 2004. In 1969 there was nearly twice as much thicket swamp as wet meadow habitat, but by 2004 wet meadows were more common than thicket swamps.

Unlike the FEA, the amount of forested habitat potentially affected by beaver activity did not change between 1969 and 2004, remaining at about 26-27% of the landscape.

This is likely attributable to the very gentle sloping, knob-and-kettle topography of Block 72. Although beaver population density in the region is high, beaver-mediated disturbances are largely confined to poorly drained lowlands. Beaver disturbance increased total wetland area by only 1.81% (from 17.96% to 19.77% of the landscape), compared to a near doubling of wetland habitat in the FEA (albeit to a more modest 5.82% of the landscape). Whereas beaver often flood upland forest in the FEA, in Block 72 beaver activity tends to flood existing thicket swamps and other wetlands, often killing tall shrubs.

Beaver activity in the Knob & Kettle eco-district results in only a modest increase in total wetland area. It does, however, substantially alter wetland composition. Combined with overall wetland habitat, my results indicate that nearly half of Beaver Survey Block 72 (26.85% + 19.77% = 46.62%) is currently – or potentially – affected by beaver activity. As in the FEA, this number may be somewhat inflated by the inclusion of small wetlands that are unlikely to be exploited by beaver. Such wetlands are more common in the Knob & Kettle eco-district than the FEA. Despite this caveat, it is apparent that beaver activity has the potential to directly modify a substantial proportion of landscape in this eco-district.

4.3.3 Predictive Model of Beaver Colony Density

Beaver Population Modeling in RMNP

In northern Minnesota, Broschart et al. (1989) developed a model to predict beaver colony density based on a landscape classification of wetlands. The model was developed to address problems of observer bias and other inaccuracies associated with aerial surveys of beaver food caches. Their predictive model, which was designed for use in conjunction with aerial surveys, was developed to provide insight into beaver carrying capacity and wetland dynamics. Their study took place at Voyageurs National Park, Minnesota, on the Canadian Shield. Like the Riding Mountain region, Voyageurs National Park has seen a large increase in the beaver population since the species was re-introduced in the 1940s.

The Broschart model uses two habitat variables (both expressed as proportions of total landscape area) to predict beaver colony density: the proportion of marsh habitat and the proportion wet meadow habitat. Their model is based on the following empirical observations:

1) Marsh habitat is positively correlated with an increasing beaver population. As beaver impound low-lying areas, the water table rises and creates a complex marsh community.

2) Wet meadow habitat is negatively correlated with an increasing beaver population, since wet meadows are associated with dam abandonment. When a beaver dam is breached (either partially or fully), a seasonally flooded wet meadow develops that may persist for decades (Shaw 1993).

Based on this relationship between marsh and wet meadow habitat (both independent variables), Broschart et al. (1989) were able to accurately estimate colony density in their study area. The model was derived using a stepwise multiple regression analysis where: X = the proportion of wet meadow habitat, W = the proportion of shallow marsh, Y = the number of beaver colonies per km of survey route. The model uses two separate equations to estimate colony density. The first model (model I) uses a simple linear analysis with only one habitat variable (marsh) and is fairly precise ($R^2 = 0.93$). The second model (model II) uses a polynomial approach, taking into account both habitat variables (marsh and wet meadow). This resulted in a modest increase in model accuracy ($R^2 = 0.98$).

$$Y = 0.09 + 61.86(W) \qquad \text{[Model I]}$$

$$Y = 0.26 + 94.14(W) - 45.33(X) \qquad \text{[Model II]}$$

The Broschart models may also be applicable to the Riding Mountain area. If so, it could be a useful tool for assessing current and past beaver population trends, and for providing insight into habitat changes and the carrying capacity of the beaver population. However, it should be noted that the Minnesota study was undertaken when the beaver

population was increasing, whereas the RMNP population is currently in decline (see chapter 2).

In the Knob and Kettle eco-district of RMNP, expansive wetlands render the Broschart model inaccurate for population estimations. Sample years with large amounts of marsh produced grossly inflated population estimates using both the one-variable and two-variable methods (**Table 4.3**). In 2004, following the rapid drop in marsh habitat and the resultant wet meadow increase, the two-variable model actually predicted a negative beaver population of -54 colonies (**Table 4.3**). With large wetlands throughout the eco-district, more dramatic shifts in wetland types can occur in comparison with the rocky, steep-sided streams on the Canadian Shield. Though the model assumptions may still hold true to some extent, a recalculation of the stepwise multiple regression analysis would need to be undertaken for each landscape type for these predictive regression models to be useful or accurate.

Examining Model Assumptions for RMNP

During the period of population increase (1969 to 1978), data collected in Beaver Survey Block 72 were consistent with the Broschart model assumptions. In 1969, few beaver had colonized the area; only 4 active dams were present, although a few more colonies may have been present on non-impounded water bodies. The year 1969 thus serves as an example of a landscape largely unaffected by beaver disturbance. By 1978, the beaver population had increased substantially. Between 1969 and 1978 beaver had created 29 new impoundments, for a total of 33 active dams (**Figure 4.5 a,b**). As

predicted by the Broschart model, marsh habitat increased from 2.8% to 4.66% of the study area, while wet meadow habitat decreased from 4.69% to 2.75% (**Table 4.2**). Aerial survey data for Survey Block 72, which began in 1973, shows that the number of beaver food caches increased from 20 in 1973 to 34 by 1979. This confirms that the beaver population was increasing during the 1970s (**Table 4.3**).

By 2004, a total of 23 beaver dam sites were abandoned (breached dams), although the number of active dams (26) remained high. Most of these 26 active dams (a total of 19) remained from 1978; only 7 small dams were new to the area. It is plausible that the population is declining and that some of the 26 "active" dams were recently abandoned but are still holding water. If this is correct; the Broschart model correctly predicts a population decline; by 2004 marsh habitat had declined to 2.29%, while wet meadow habitat increased to 7.35% (**Table 4.2**). This conclusion is not supported by the aerial survey data, however. The beaver population of Survey Block 72 has fluctuated considerably, increasing during the 1970s and early 1980s, declining during the late 1980s and early 1990s, increasing to high values in both 1995 and 2004, and declining to mid-1980s levels in the 2007 survey (**Table 4.3**). The model fails to predict the population increase from the early 1990s and 2004 (from 25 to about 40 beaver caches). The failure of the model likely reflects the stable (though fluctuating) beaver population in the study region. The Broschart model was developed in a region where the beaver population was increasing; the positive and negative correlations of marsh and wet meadow habitat hold true in such a situation. However, a relatively stable population (fluctuating around a mean), greatly complicates the relationship between beaver

numbers and wetland habitat change. In Survey Block 72 relatively few new dams are being established, and extant or newly abandoned dam sites hold vast amounts of water.

The long-term persistence of beaver ponds in Survey Block 72 also confounds the rather simplistic predictions of the Broschart model. Wet meadow habitat in the Riding Mountain region is characterized by mono-dominant stands of clonal graminoids, such as bluejoint grass (*Calamagrostis canadensis*) and awned sedge (*Carex atherodes*) (**Table 4.1**). Over time these species out-compete disturbance-driven marsh communities, resulting in more wet meadow habitat (Shaw 1993). Clonal graminoid species will also colonize open water. The presence of long-lasting beaver ponds (such as those that occur throughout Survey Block 72) will therefore result in an increase in wet meadow habitat over time. This succession trend mitigates the correlation between wetland habitat change and beaver population trends.

Although beaver census surveys were not undertaken within the FEA, Survey Blocks 96 and 104 are immediately adjacent to the FEA study site. Beaver cache counts for these two blocks indicate that the beaver population increased from the early 1970s to 1978, but declined considerably by 2004. Aerial photograph interpretation indicates that few beaver were present in 1964, but that by 1978 the population was high. This is in agreement with the aerial survey census data. The Broschart model predicts that marsh habitat should increase, and that wet meadow habitat should decline, during this period. My results are not fully consistent with these predictions; while marsh habitat does indeed increase between 1964 and 1978, wet meadow habitat does so as well (**Table 4.2**).

For the 1978 to 2004 period, during which the beaver population declined, the Broschart model predicts a decrease in marsh habitat and an increase in wet meadow habitat. These trends did in fact occur (**Table 4.2**).

4.3.4 Beaver Disturbance on the Landscape

Total landscape changes resulting from beaver activity in RMNP are less dramatic than those found in northern Minnesota (Voyageurs National Park) by Johnson and Naiman (1990c). Both areas had similar population increases over a similar time period, the main difference between them is topographic; variable and rocky on the Canadian Shield of Minnesota, versus the rolling glacial till of RMNP. On the Canadian Shield, herbaceous wetland patches are almost entirely the result of beaver disturbance. All wetland community types (as a percentage of total landscape) increased over the course of the Minnesota study in the 45 years following beaver reintroduction (Johnson and Naiman 1990c): Thicket Swamp (0.2% to 1.2%), Wet Meadow (0.4% to 3.1%), Marsh (0.1% to 5.4%), and Impounded Water (0 to 1.9%). In contrast, thicket swamp and wet meadow (Block 72 only) wetland classes in RMNP decreased, while the marsh and open water classes increased, over a similar time period (**Table 4.2**).

A major reason for the discrepancy in results is the long-term persistence of wetland patches in RMNP even in the absence of beaver. Prior to beaver disturbance, wetlands constituted only 1% of the landscape in Minnesota. Without beaver disturbance, herbaceous wetland communities are rare in their study area (Johnson and Naiman

1990c). In contrast, wetlands communities in RMNP constituted 7% of the FEA and 18.5% of Block 72 prior to beaver disturbance. As beaver colonize small, stream-based wetland systems in Minnesota, flood disturbance inundates large tracts of upland forest. Forested upland habitat declined from 96.2% of the study area in 1940 to 84.5% in 1986, a result directly attributable to beaver flooding (Johnson and Naiman 1990c). In RMNP, beavers often flood previously existing wetland types, shifting the composition of wetland community types and creating new wetland patches. In some situations dam building is unnecessary in RMNP, since beaver are able to build a lodge in the center of an existing pothole wetland (personal observation).

Even though these two study areas are very close in terms of vegetation type and location, major differences occur in the effect beaver disturbance has on wetland communities. On the Canadian Shield, beaver are the driving force in the creation of all wetland patch types on the landscape. Though this is also true to some extent in RMNP, beaver disturbance also modifies the composition of existing wetland patches.

Research in the Kitimat Valley of northern British Columbia showed a total wetland area of only 0.1% in 1947, prior to beaver disturbance. By 1993, beaver had moved into the valley and increased wetland area to 1.3% of the landscape (Reese-Hansen 2004). This increase is much more modest than those reported in both my study and by Johnson and Naiman (1990c). This difference is likely attributable to limited habitat availability in the mountainous regions of British Columbia. Beaver are unable flood fast-moving streams, and many lower valleys are developed by humans. Furthermore, unlike RMNP

and Voyageurs National Park, the Kitimat Valley is not a protected area and therefore is subject to trapping pressure and a higher amount of land use by humans, including road construction and various forestry practices (Reese-Hansen 2004).

Johnson and Naiman (1990c) also calculated the amount of forested habitat that could potentially be affected by beaver herbivory. To do this, they mapped a 100m buffer zone around all beaver impoundments on the landscape and calculated the total area. They concluded that beaver potentially affect a further 12-15% of the forested upland, over and above the area disturbed by flooding. Following this methodology, but using a more conservative distance of 50m (based on my transect data), I found that beaver harvesting can potentially affect a further 21% of the landscape of the FEA, and 26% of Block 72. It is unclear why my values are much higher than reported from Minnesota, but differences in sampling protocols might contribute to the discrepancy. Johnson and Naiman (1990c) based their distance calculations almost entirely from beaver impoundments since the vast majority of wetlands are beaver-created. By contrast, my analysis included both natural wetlands (small lakes and pothole wetlands) and beaver impoundments.

When the beaver population crashes (as it did in RMNP in the late-1800s), it appears that beaver-created wetlands succeed to wet meadow, thicket swamp or upland forest habitat, as evidenced in the 1964-1969 photo series **(Figure 4.2a, 4.5a)**. Prior to reinvasion by beaver, permanent watercourses were typically dominated by thicket swamp, while areas with semi-permanent water were typically wet meadows. Colonization by trees may occur in areas where a drop in the water table creates a drier

meadow. Reinvasion of woody species may be a very slow process, however. During a 70-year period in Minnesota, no woody plants were observed to have invaded beaver meadows (Johnston and Naiman 1990c). Terwilliger and Pastor (1999) found that the invasion of spruce and fir trees into a beaver meadow is slowed by the destruction of the ectomycorrhizal fungal community during the anaerobic flood years. Contrary to these findings, I found that tree invasion of beaver-made meadows in RMNP can begin within 20-30 years, primarily by white spruce. Further research is needed to elucidate the differences and investigate the effect of a crashing beaver population on the ecosystem.

4.3.5 Wetland Modeling for the Wildlife Manager

My research demonstrates that the assumptions of the Broschart et al. (1989) model are appropriate for RMNP. Unfortunately, my results also indicate that while the Broschart model may be useful, it must be used with caution; the model is too simplistic, and needs to be recalibrated. Furthermore, the methodology used to produce a wetland classification (to produce the necessary variables for the model) is very time consuming: wetland classification of a single sample year for each my study sites took approximately 50 hours. However, the analysis of wetland dynamics, while time consuming, is very useful for detailed investigations of the role of beaver in the creation and perpetuation of critical wildlife habitat.

In the future, a supervised classification approach could conceivably be developed, and this would greatly reduce the time required to produce a wetland classification.

Monitoring programs could then be developed for critical habitat of various organisms. However, my experience indicates that the development of a supervised classification of wetlands would be very difficult to develop to a point that it would be sufficiently accurate for detailed habitat analysis. Overlapping optical signatures of different wetland classes, and problems associated with shadowing effects and woody vegetation structure, preclude the development of sophisticated supervised classification.

According to Slough and Sadlier (1976), two major factors must be considered when developing a beaver management plan: (1) protection of beaver habitat from destructive land use practices; (2) food supply management. Habitat is adequately protected in RMNP, but the unregulated beaver population is producing a park-wide shift of beaver-affected forests from aspen towards spruce or shrub dominance (see Chapter 3). The food supply is best managed through a strongly regulated trapping program, or through fire (Slough and Sadlier 1976). Fire is currently used as a management tool in RMNP for grassland communities, where deliberately set fires are easily controlled (Parks Canada 2002). Using similar techniques based on historic fire cycles, park managers may be able to promote aspen regeneration around wetland systems in order to stabilize and maintain a healthy beaver population. Fire management of forest stands is a very difficult and challenging undertaking, however. Research is needed to explore the plausibility of such an intensive strategy and its possible effects on wetland communities.

In both of the RMNP eco-districts that I studied, beaver have a substantial impact on wetland habitat composition and structure. To the wildlife manager, knowledge of the

role of beaver in creating and modifying wetland habitat can be critical. For example, a reduction of wood duck (*Aix sponsa*) abundance may be attributed to a reduction in beaver impoundments, since the species uses cavities in snags around beaver wetlands as nesting sites (Carr 1940). Managers could place artificial structures in remaining wetlands to mimic these cavities, mitigating the loss of beaver in the area. Although such approaches are useful, the maintenance of a healthy beaver population is essential to the management of the various species that depend on wetland habitat.

My landscape analyses clearly demonstrate that various wetland habitat changes are largely attributable to beaver activity and a fluctuating beaver population. In the future, supervised wetland classification in combination with aerial beaver surveys will provide managers with the tools necessary to understanding shifting habitat variables associated with fluctuating animal populations.

Table 4.1. Wetland class types used in the patch analysis. Each class type* encompasses a range of community types indistinguishable by aerial photography analysis. A small description accompanies the class types quantified. Typical plant species are grouped in growth form types and ranked in order from most to least frequent.

Wetland Class Type	Description	Typical Plant Species
Marsh (n=33)	Standing or slow moving water with emergent plant cover greater than 25%; permanently flooded with a diverse plant community. In some cases the community is dominated by *Typha* sp., *Equisetum fluvitale* or *Scirpus* sp. Diverse flood disturbed communities on exposed mud flats occur occasionally.	**Woody:** *Salix* sp. **Herb:** *Galium trifidum, Scutellaria galericulata, Cicuta bulbifera, Sium suave, Bidens cernua, Mentha arvensis, Polygonum* sp., *Lycopus uniflorus, Impatiens capensis, Rorippa islandica, Cirsium arvense* **Graminoid:** *Carex lucustris, Carex aquatilis, Calamagrostis canadensis, Carex utriculata, Eleocharis palustris, Carex atherodes, Glyceria grandis, Carex viridula* **Aquatic:** *Typha latifolia, Lemna minor, Ranunculus gmelinii, Polygonum amphibium, Sagittaria cuneata, Hippuris vulgaris, Potamogeton* sp., *Sparganium emersum*
Wet Meadow (n=45)	Permanently or semi-permanently flooded communities dominated by thick patches of graminoids. Drier sites dominated by *Calamagrostis canadensis* and *Carex atherodes*. Wet sites dominated by *Carex lacustris* and *Carex aquatilis.*	**Woody:** *Salix* sp. **Herb:** *Galium trifidum, Scutellaria galericulata, Mentha arvensis, Polygonum* sp., *Cirsium arvense, Sium suave, Urtica dioica, Geum aleppicum, Aster puniceus, Impatiens capensis, Bidens cernua, Cicuta bulbifera, Solidago canadensis* **Graminoid:** *Carex atherodes, Calamagrostis canadensis, Carex lacustris, Carex viridula, Poa palustris, Carex utriculata, Carex aquatilis* **Aquatic:** *Lemna minor*
Thicket Swamp (n=23)	Tall shrubs dominant with cover greater that 25%. Rich herb communities in closed canopy sites. Open canopy sites generally result in high graminoid cover. Raised hummocks at the base of the shrubs results in incursions of upland herb species.	**Woody:** *Salix* sp., *Ribes hudsonianum, Alnus rugosa, Rosa acicularis, Picea glauca, Rubus ideaus* **Herb:** *Galium trifidum, Scutellaria galericulata. Mentha arvensis, Urtica dioica, Cirsium arvensis, Polygonum* sp., *Geum aleppicum, Potentilla norvegica, Caltha palustris, Impatiens capensis, Aster puniceus, Geum rivale, Rubus pubesens* **Graminoid:** *Carex lacustris, Calamagrostis canadensis, Carex atherodes, Carex aquatilis, Poa palustris*

*Note: The Open water, Bog, Dry Meadow and Human Disturbance class types were not extensively sampled

Table 4.2. Landscape level wetland change in the Forest Experimental Area (FEA) and Beaver Survey Block 72, Riding Mountain National Park. Excluding human disturbance and permanent lakes (Ministik, Grayling, Baldy, unnamed).

	FEA (%)			Block 72 (%)		
Patch Type	1964	1978	2004	1969	1978	2004
Upland Forest	92.95	91.51	88.12	78.52	77.71	78.50
Conifer Bog	2.21	1.78	1.77	0.55	0.51	0.31
Grassland	0.00	0.00	0.00	2.97	2.44	1.41
Thicket Swamp	1.57	1.38	1.84	10.15	8.53	6.96
Wet Meadow	2.78	2.86	6.86	4.69	2.75	7.35
Marsh	0.47	1.92	1.15	2.80	4.66	2.29
Impounded Water	0.02	0.54	0.27	0.32	3.40	3.17

Table 4.3. Population counts and estimates for beaver Survey Block 72, Knob and Kettle eco-district, Riding Mountain National Park.

	Wetland Proportion		Number of Colonies per km			Predicted Colony Count, Block 72		
Year	Wet Meadow	Marsh	One Variable*	Two Variables*	Aerial Survey	One Variable*	Two Variables*	Aerial Survey
1969	0.047	0.028	1.820	0.549	**0.389	107.5	32.4	**23.0
1978	0.028	0.047	2.973	3.166	***0.482	175.6	187.0	***28.5
2004	0.074	0.023	1.506	-0.916	0.660	89.0	-54.1	39.0

* Calculated using the predictive model provided by Broschart et al. (1989).

** 1973 value, earliest available, beaver population was likely lower in 1969.

*** Average taken from the 1977 and 1979 aerial census values.

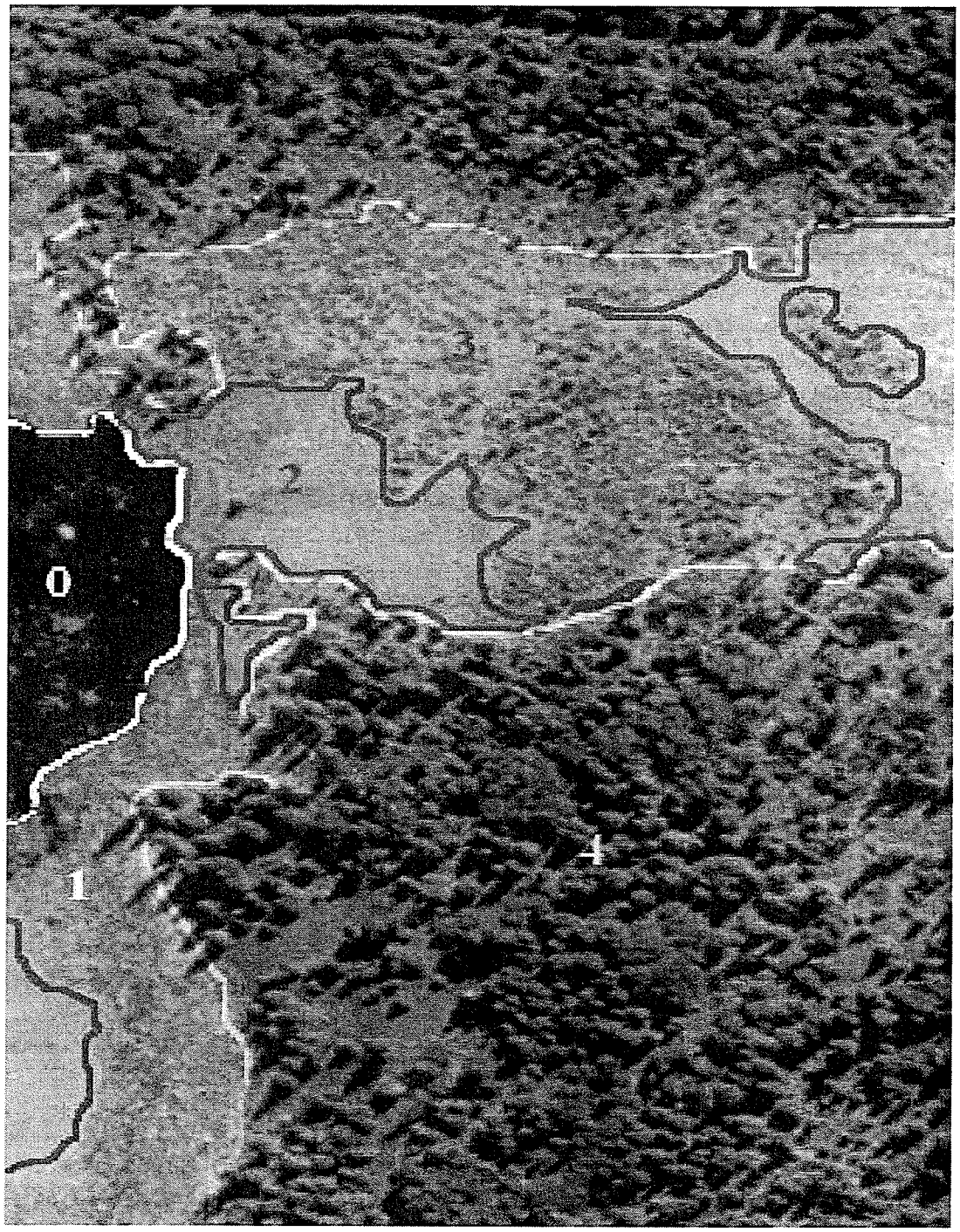

Figure 4.1. Example of the visual differentiation of wetland habitat types using a combination of aerial photographs and digital images. 0 = Open Water; 1 = Marsh; 2 = Wet Meadow; 3 = Thicket Swamp; 4 = Upland Forest.

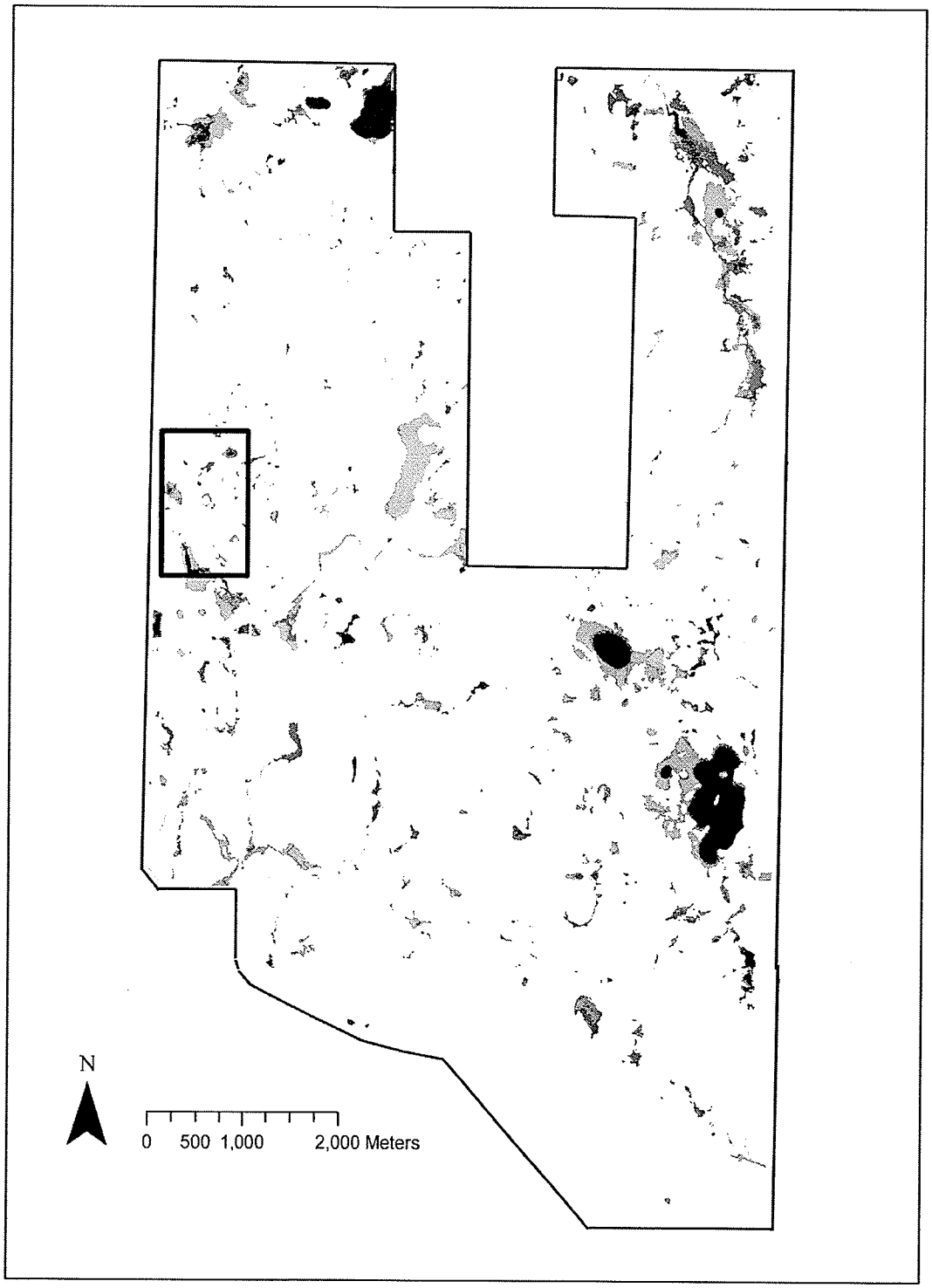

Figure 4.2(a). Wetland patches within the Forest Experimental Area in 1964. ■ = Open and Impounded Water; ■ = Marsh; ■ = Wet Meadow; ■ = Thicket Swamp; ■ = Bog/Conifer Swamp; □ = Upland Forest. Boxed section indicates area highlighted in figure 4.3.

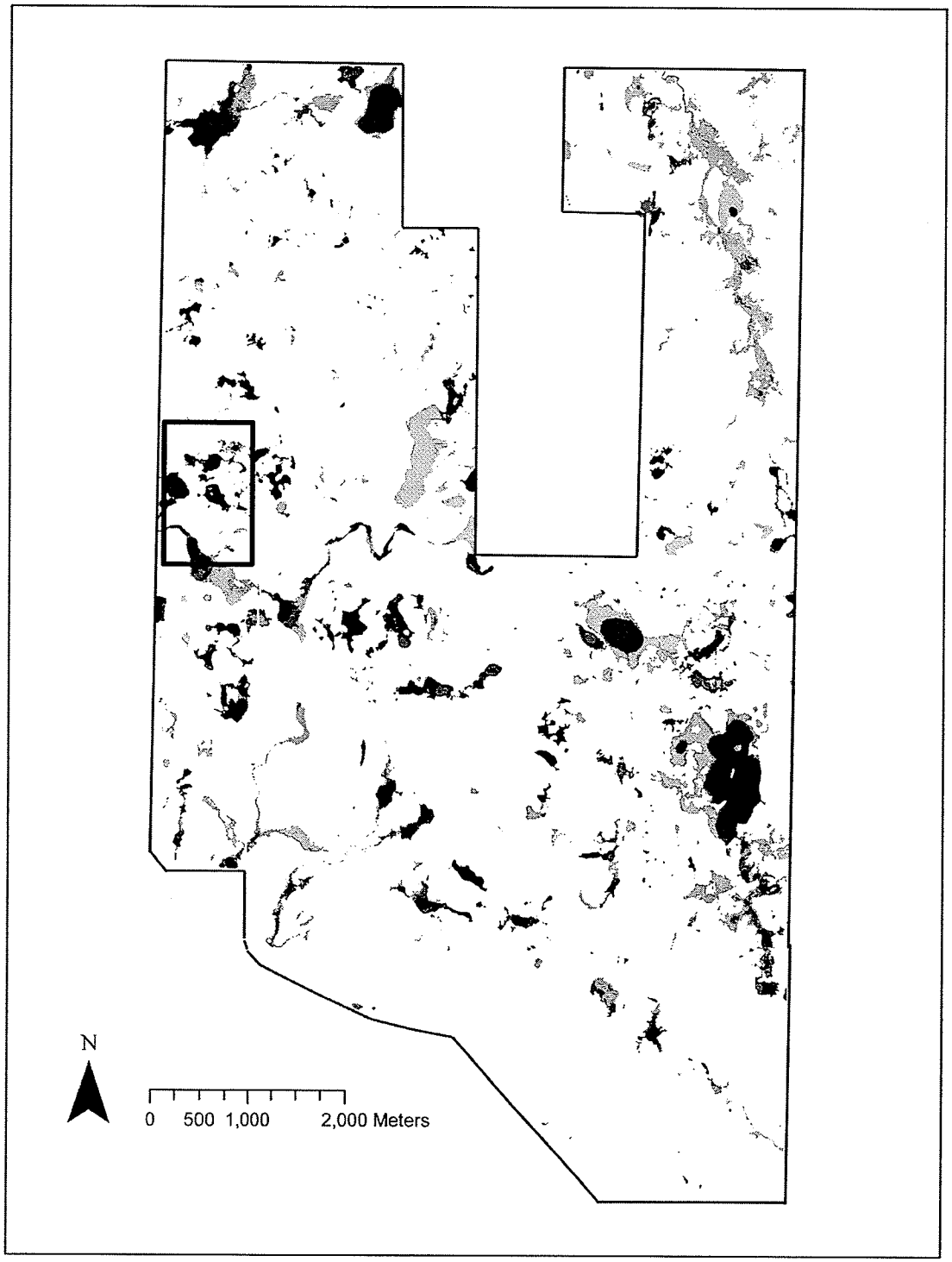

Figure 4.2(b). Wetland patches within the Forest Experimental Area in 1978. ■ = Open and Impounded Water; ■ = Marsh; ■ = Wet Meadow; ■ = Thicket Swamp; = Bog/Conifer Swamp; □ = Upland Forest. Boxed section indicates area highlighted in figure 4.3.

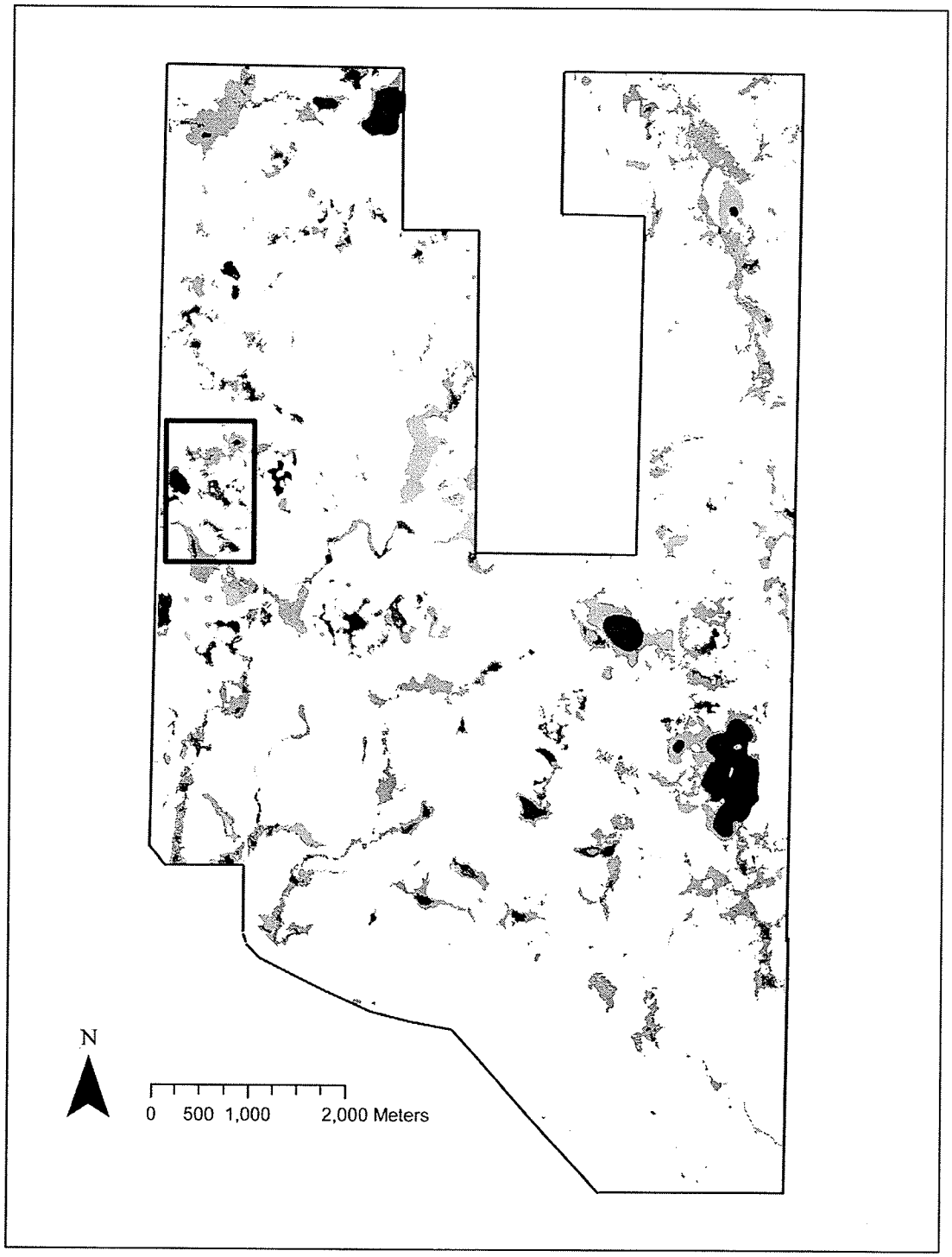

Figure 4.2(c). Wetland patches within the Forest Experimental Area in 2004. ■ = Open and Impounded Water; ■ = Marsh; ■ = Wet Meadow; ■ = Thicket Swamp; ■ = Bog/Conifer Swamp; □ = Upland Forest. Boxed section indicates area highlighted in figure 4.3.

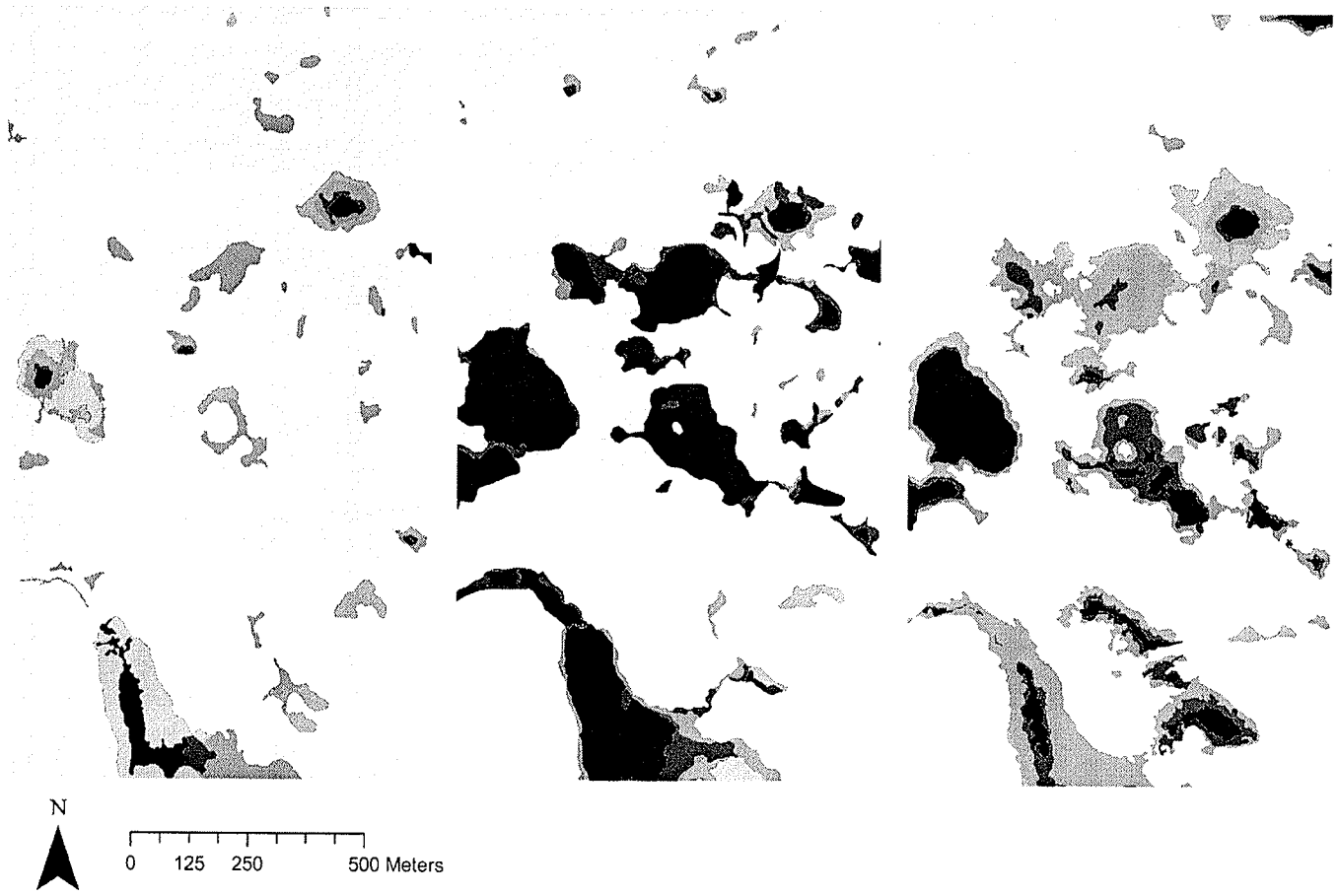

Figure 4.3. Example area showing the change in wetland patch dynamics from 1964 (left), 1978 (middle) to 2004 (right). ■ = Open and Impounded Water; ■ = Marsh; ■ = Wet Meadow; ■ = Thicket Swamp; = Bog/Conifer Swamp; □ = Upland Forest.

Figure 4.4(a). Dam locations (n=12) within the Forest Experimental Area (FEA), Riding Mountain National Park in 1964. Circles denote dams holding water. The FEA is bordered in a thin line, roads are represented with a thick line and trails are represented with a dashed line.

Figure 4.4(b). Dam locations (n=258) within the Forest Experimental Area (FEA), Riding Mountain National Park in 1978. Circles denote dams holding water (n=252) while triangles denote dams that have been fully breached (n=6). The FEA is bordered in a thin line, roads are represented with a thick line and trails are represented with a dashed line.

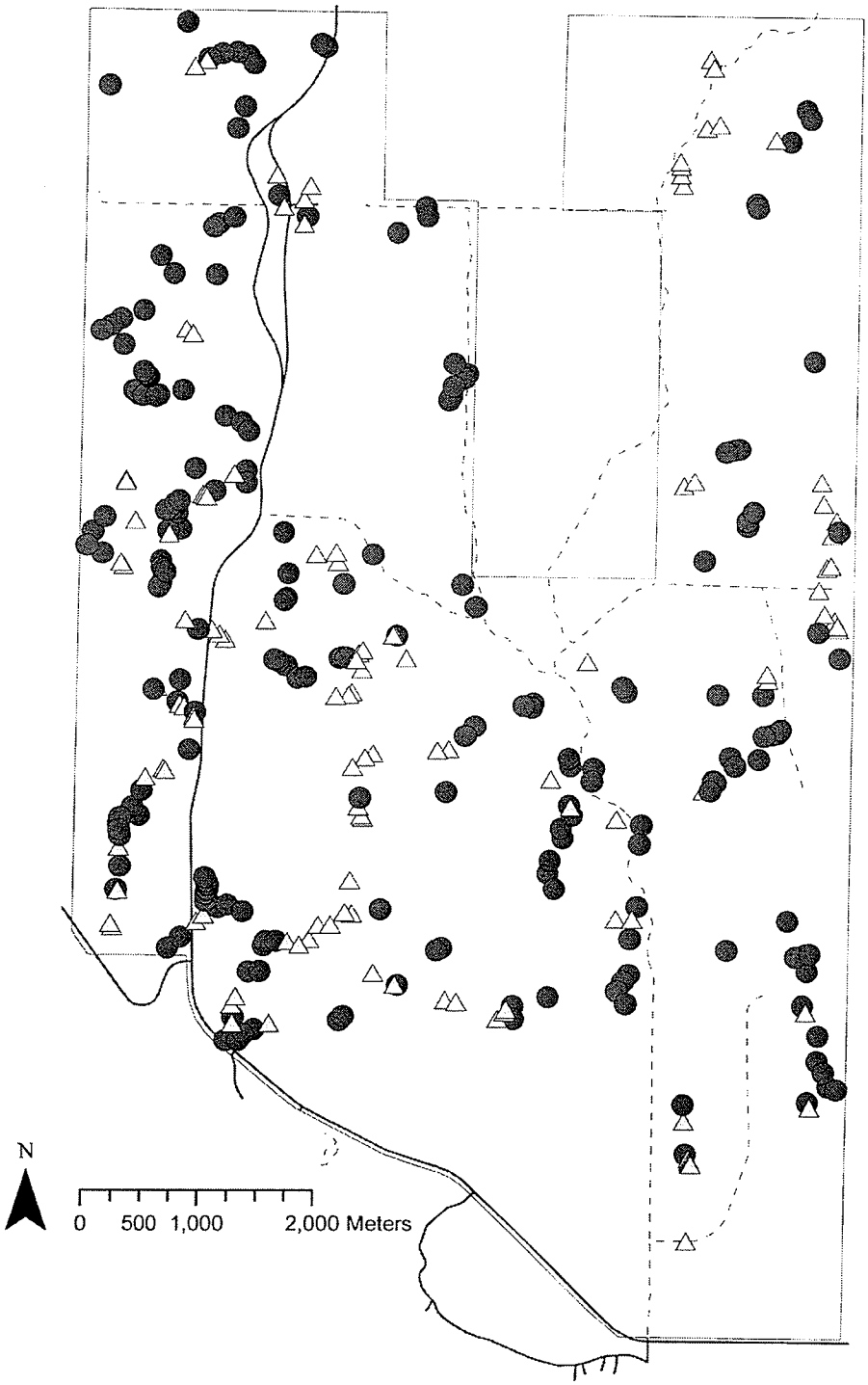

Figure 4.4(c). Dam locations (n=324) within the Forest Experimental Area (FEA), Riding Mountain National Park in 2004. Circles denote dams holding water (n=207) while triangles denote dams that have been fully breached (n=117). The FEA is bordered in a thin line, roads are represented with a thick line and trails are represented with a dashed line.

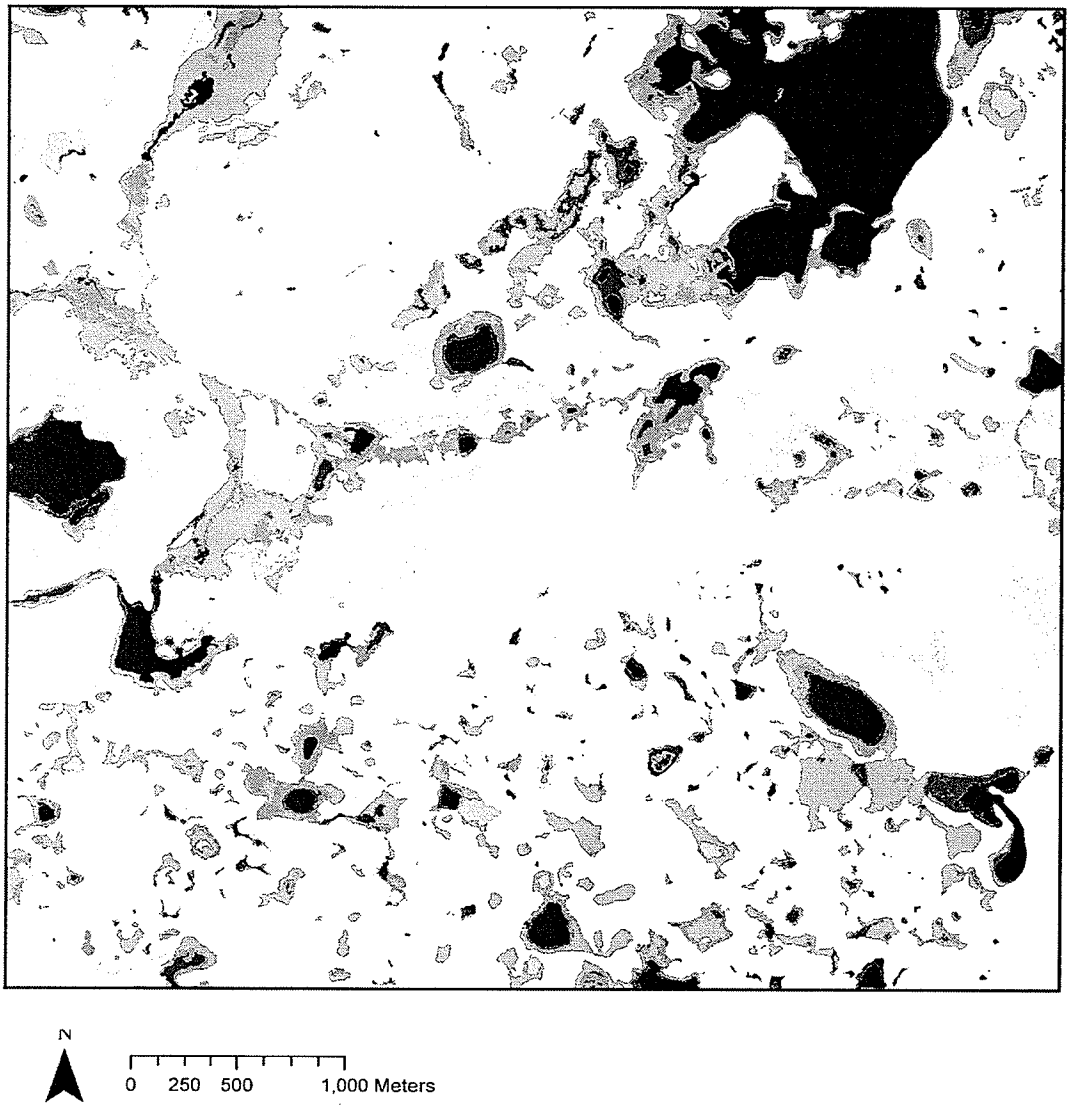

Figure 4.5(a). Wetland patches within Beaver Survey Block 72 in 1969. ■ = Open and Impounded Water; ■ = Marsh; ■ = Wet Meadow; ■ = Thicket Swamp; ■ = Bog/Conifer Swamp; □ = Upland Forest. Grasslands are outlined within the forest.

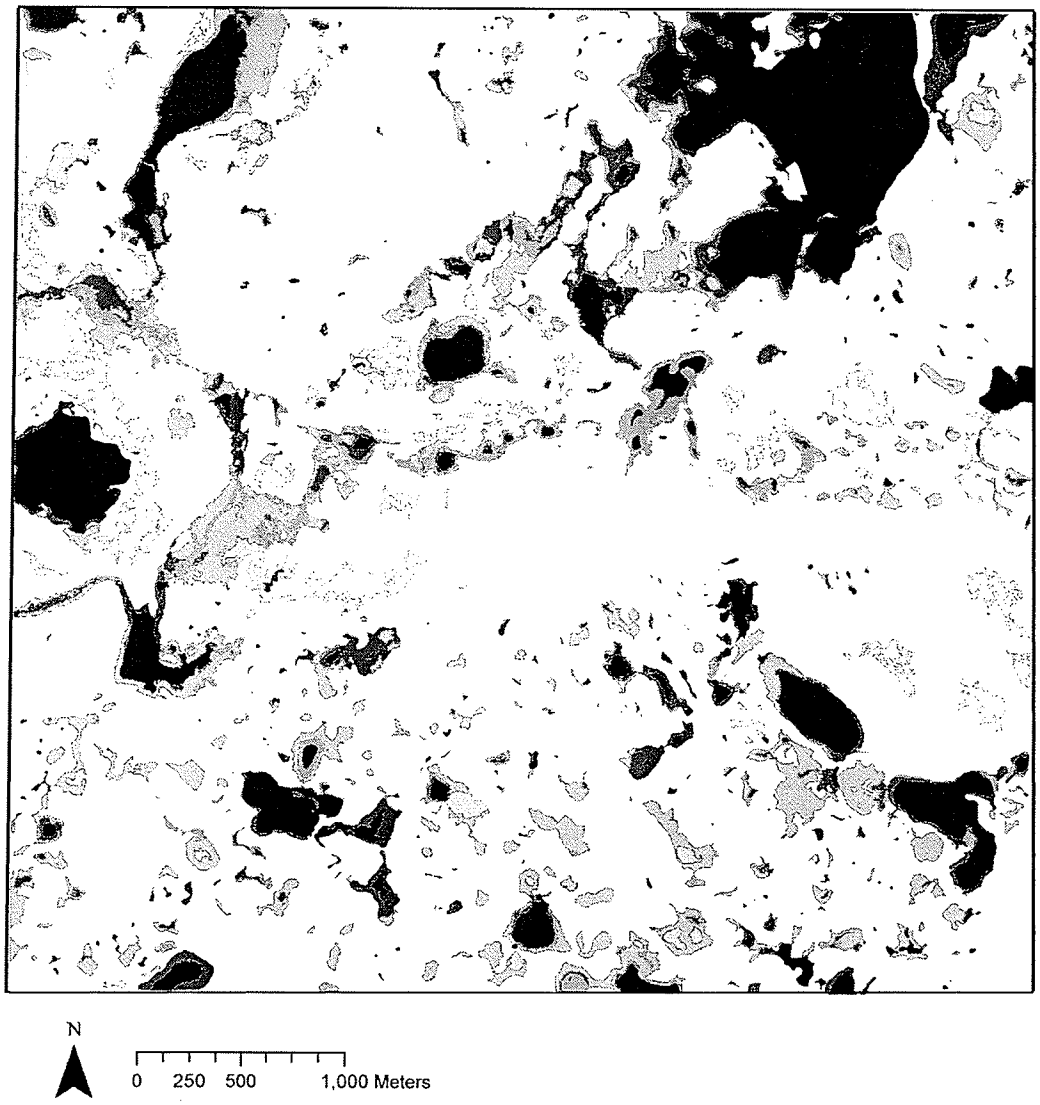

Figure 4.5(b). Wetland patches within Beaver Survey Block 72 in 1978. ■ = Open and Impounded Water; ■ = Marsh; ■ = Wet Meadow; ■ = Thicket Swamp; ■ = Bog/Conifer Swamp; □ = Upland Forest. Grasslands are outlined within the forest.

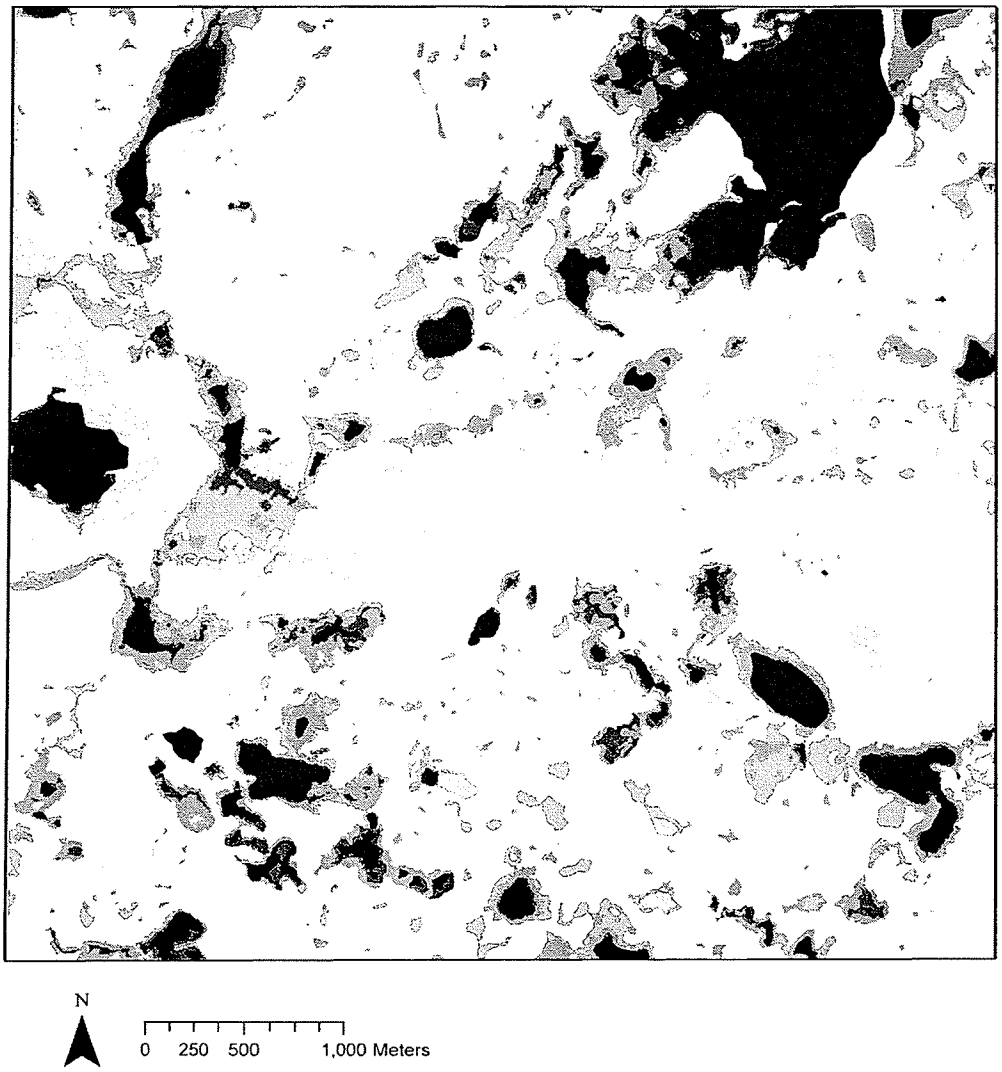

Figure 4.5(c). Wetland patches within Beaver Survey Block 72 in 2004. ■ = Open and Impounded Water; ■ = Marsh; ■ = Wet Meadow; ■ = Thicket Swamp; ■ = Bog/Conifer Swamp; □ = Upland Forest. Grasslands are outlined within the forest.

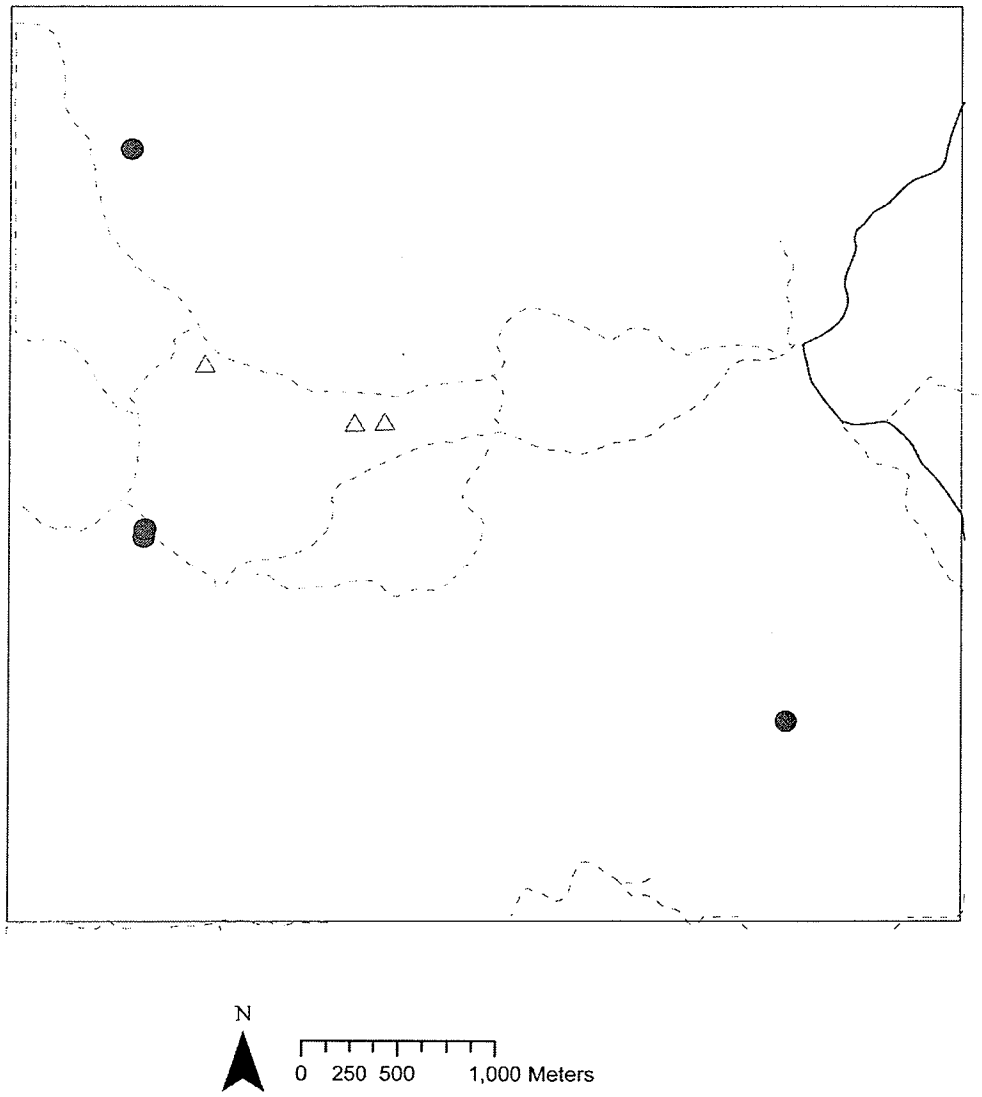

Figure 4.6(a). Dam locations (n=7) within Beaver Survey Block 72, Riding Mountain National Park in 1969. Circles denote dams holding water (n=4) while triangles denote dams that have been fully breached (n=3). Block 72 is bordered in a thin line, main trails are represented with a thick line and secondary trails are represented with a dashed line.

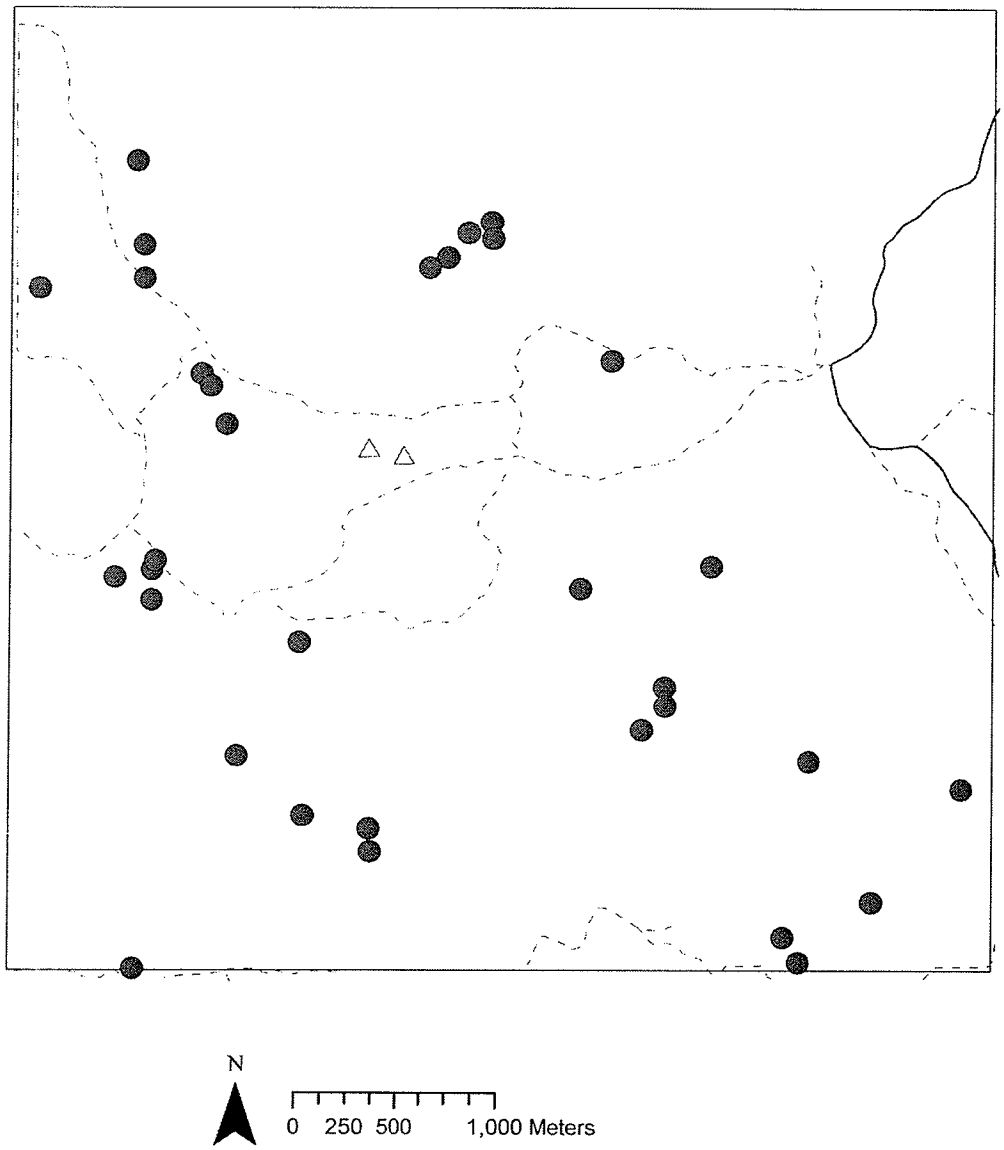

Figure 4.6(b). Dam locations (n=35) within Beaver Survey Block 72, Riding Mountain National Park in 1978. Circles denote dams holding water (n=33) while triangles denote dams that have been fully breached (n=2). Block 72 is bordered in a thin line, main trails are represented with a thick line and secondary trails are represented with a dashed line.

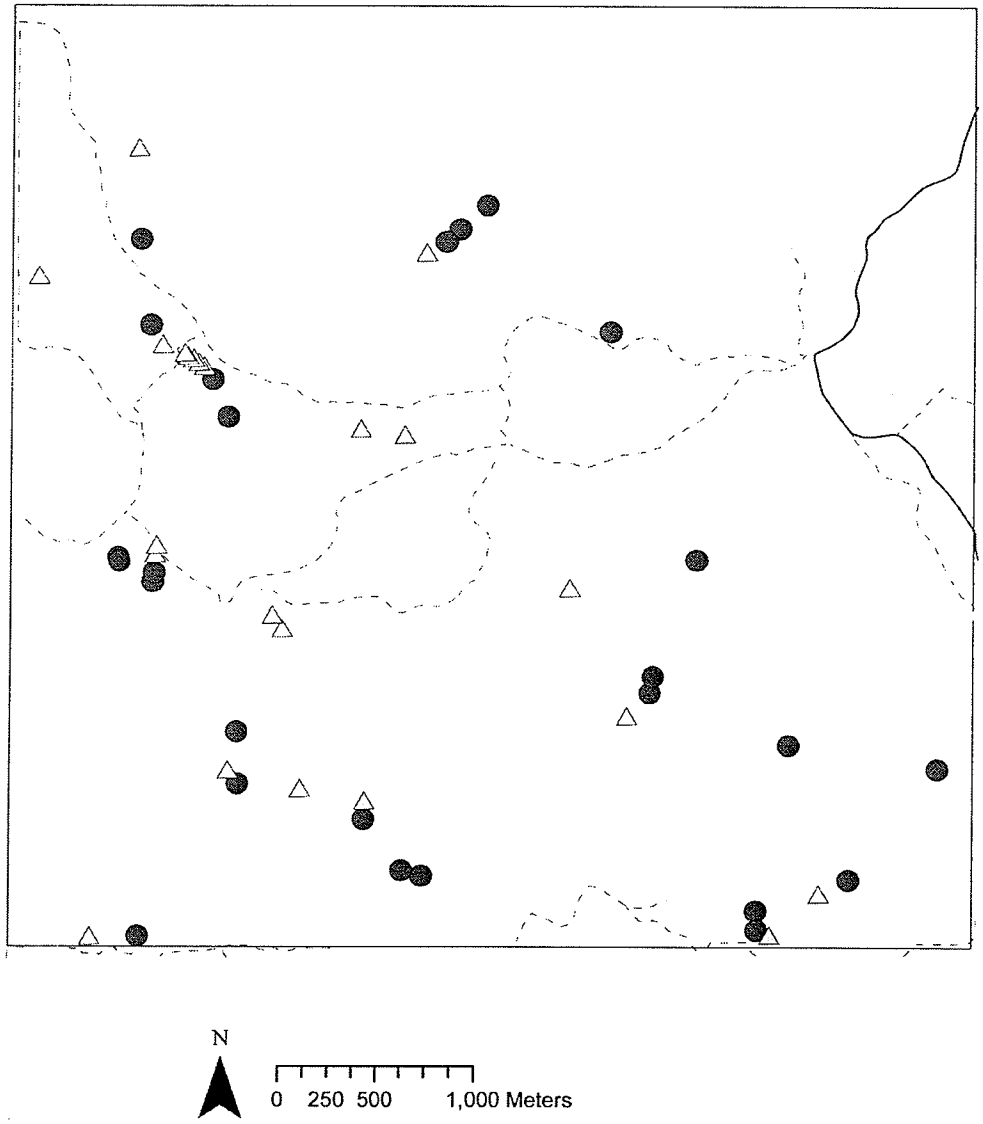

Figure 4.6(c). Dam locations (n=49) within Beaver Survey Block 72, Riding Mountain National Park in 2004. Circles denote dams holding water (n=26) while triangles denote dams that have been fully breached (n=23). Block 72 is bordered in a thin line, main trails are represented with a thick line and secondary trails are represented with a dashed line.

CHAPTER 5

SUMMARY AND CONCLUSIONS

Hudson Bay Company Records (Swan River District) indicate that beaver were abundant in the Riding Mountain region prior to European settlement. Large numbers of beaver pelts were harvested from the region during the 1700s and much of the 1800s. However, by the 1880s over-trapping led to a precipitous drop in the beaver population and near-extirpation of the species in many areas. The combination of time, fire disturbances and protection within Park boundaries allowed forests to recover and grow relatively beaver free for approximately 100 years or more.

The near-extirpation of beaver from Riding Mountain National Park (RMNP) led to re-introduction programs in the late 1940s and early 1950s. By the early 1970s the species had recovered, and today beaver are found throughout the Park. Aerial beaver surveys were undertaken by Parks Canada since 1973 and suggest that the rapidly expanding beaver population was likely above carrying capacity by 1985. The population fluctuated after the mid-1980's and is currently at its lowest levels since the survey began. Today, beaver populations are distributed unevenly throughout the park. The Upland Plateau and the Knob and Kettle eco-districts have the highest beaver population densities in the Park and were chosen as the focus of this investigation

The first major objective of this study was to describe the effects beaver have on the structure, composition and succession dynamics of "old growth" boreal mixed wood forest in the upland plateau eco-district and on the younger, aspen dominated forests in

the Knob and Kettle eco-district. To accomplish this, a combination of permanent sample plots and vegetation transects were quantified.

A large number of permanent sample plots were established in the Forest Experimental Area (FEA) of RMNP in the late 1940s, prior to the re-introduction of beaver. 638 of these plots were relocated in 2006 and 2007 to look for evidence of beaver activity. Forty (6.3%) of the forested plots were flooded by beaver, and another 33 (5.2%) showed evidence of harvesting of canopy aspen. Seventeen of these harvested plots were examined to determine changes in forest composition and structure attributable to beaver activity. Harvesting of aspen from mixed forest stands (aspen and spruce in the canopy) reduced aspen dominance, but there was no significant compensatory increase in white spruce dominance. By contrast, harvesting of aspen-dominated stands (i.e. aspen in the canopy) reduced aspen dominance but also resulted in a compensatory increase in white spruce dominance. Tree cores confirm the above results and demonstrate a large increase in relative growth rate after the removal of canopy aspen.

The beaver is primarily an aquatic species, but much of its foraging activity occurs in upland aspen stands. Mean foraging distance (distance from water's edge) is 23.6 m in the FEA, and 38.3 m along lakeshores in western regions of RMNP. Beaver-affected shorelines in the west are largely treeless and dominated by dense thickets of beaked hazelnut and other tall shrubs. By contrast, beaver-affected forest stands in the FEA are typically dominated by white spruce. Timber harvesting by beaver is high, averaging 20.7 m^2/ha (tree basal area) in the FEA and 16.4 m^2/ha along the shores of the western lakes. Only hardwoods were harvested. Trembling aspen was by far the preferred

species, although some balsam poplar and paper birch were also felled. In the western region, tall shrubs were sometimes harvested as well.

In RMNP, four stand types develop following beaver harvesting. Harvested stands containing spruce, and with a sufficiently closed canopy, develop into closed spruce stands; this stand type is common in the FEA. Open spruce shrublands, consisting of mature spruce overtopping a dense thicket of tall shrubs, develop from stands containing hardwoods in the canopy and white spruce saplings. Open hardwood shrublands consist of a few mature hardwoods (usually bur oak and/or white birch) overtopping a dense tall shrub thicket. These stands develop in areas lacking softwoods, and where hardwoods undergo basal resprouting following beaver harvesting. Open shrublands develop in areas where softwoods are absent and beaver browse intensity is high. This type is characterized by dense, impenetrable thickets of tall shrub species (particularly beaked hazelnut). The latter two stand types are most commonly encountered in the western regions of RMNP, where white spruce and other softwoods are less abundant.

My results show that beaver have a large impact in the forests adjacent to their wetlands. By removing selective tree and shrub species, they dramatically alter forest structure and composition, and in some situations growth and reproduction. Researchers working in these areas must recognize the impact beaver herbivory has on forests and treat them as communities that have been subjected to a unique disturbance type.

The second major objective of this study was to determine and describe temporal changes in landscape hydrology and wetland habitat types resulting from increased beaver activity. To accomplish this, aerial survey results, aerial photography analysis and

wetland classification was undertaken over a 40-year period for the Upland Plateau and Knob and Kettle eco-districts.

Historical aerial photograph interpretation led to the recognition of three identifiable, beaver-affected wetland classes in RMNP. The marsh class consists of permanently flooded wetlands with a combination of open water and emergent vegetation. Dominant plants include cattail (*Typha* spp.), water horsetail (*Equisetum fluvitale*) and bulrushes (*Scirpus* spp.). The wet meadow class consists of dense stands of graminoids; there is no open water and few shrubs. Drier meadows are dominated by bluejoint grass (*Calamogrostis canadensis*) and awned sedge (*Carex atherodes*), while wetter ones are dominated by sedges (*Carex lacustris, C. aquatilis*). The thicket swamp class consists of a mix of tall shrubs (exceeding 25% cover), graminoids, and herbs. There are two thicket swamp types: those dominated by river alder (*Alnus rugosa*), and those dominated by willows (*Salix* spp.).

A temporal landscape classification series (1964, 1978, and 2004) of the FEA was produced from digitized aerial photographs. The classification indicates a large increase in the amount of wetland over time, corresponding to an increasing beaver population. In 1964 only 12 beaver dams were present, and wetlands (impounded water, marsh, wet meadow, and thicket swamp) accounted for only 4.84% of the landscape. By 1978 there were a total of 258 beaver dams, only 6 of which were abandoned (breached). Between 1964 and 1978, impounded water increased from 0.02% to 0.54%, and marsh habitat from 0.47% to 1.92%. In 2004 there were 324 beaver dams; 207 were active, and 117 breached (abandoned). Between 1964 and 2004, beaver activity more than doubled FEA wetland habitat, to 10.12% of the landscape. Large increases occurred in impounded

water (from 0.02% to 0.54%) and wet meadow (from 2.78% to 6.86%). Increases in wetland habitat occurred at the expense of forested habitat: conifer bog decreased from 2.21% to 1.77%, and upland forest from 92.95% to 88.12%. The amount of forest habitat potentially affected by beaver activity increased from 18.20% to 21.34%. Including wetland habitat, nearly one-third of the FEA (21.34% + 10.12% = 31.46%) is potentially affected by beaver activity.

A temporal landscape classification series (1969, 1978, and 2004) was also undertaken for Beaver Survey Block 72 in the western region of RMNP. Wetlands are more common here; in 1969 wetlands comprised 17.6% of the area, but only 4 active beaver dams were present. By 1978 there were 33 active and 2 breached dams. Impounded water increased from 0.3% to 3.4% of the landscape, and marsh habitat from 2.8% to 4.66%. By contrast, wet meadow habitat decreased from 4.36% to 2.55%, indicating that beaver activity often floods wet meadows. In 2004 there were 26 active and 23 breached dams. Large changes in wetland composition occurred between 1978 and 2004. Wet meadow increased from 2.75% to 7.35%, whereas marsh habitat declined from 4.66% to 2.29%. This shift reflects the development of wet meadows on exposed mudflats following dam site abandonment. Thicket swamps, which are sensitive to rising water tables, declined over time from 10.15% in 1969 to 6.96% in 2004. Unlike the FEA, the proportion of forested habitat potentially affected by beaver did not change over time, remaining at about 27%. Including wetland habitat, nearly half of Survey Block 72 (26.85% + 19.77% = 46.62%) is potentially affected by beaver activity.

The Broschart model, developed in Minnesota to predict beaver colony density using landscape wetland classification, was tested for use in RMNP. The model hypothesizes

that marsh habitat increases, and wet meadow decreases, during periods of beaver population increase. Our results suggest that the Broschart model is too simplistic for use in RMNP. The model is only suited to situations in which the beaver population is increasing, and it fails to consider natural vegetation dynamics (exclusive of those attributable to beaver activity). However, landscape classification is very useful to understanding how beaver activity affects the creation, perpetuation and dynamics of critical wetland habitat.

Beaver flood disturbance plays a large role in the proportion and perpetuation of wetlands on the landscape in RMNP. Wildlife managers must pay particular attention to the beaver population in their area when establishing any management protocols for animals that depend on wetland habitat.

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Appendix 1

Photographs of beaver affected forest stand types and wetland classes used in the landscape analysis.

Figure 1. Closed canopy spruce stand.

Figure 2. Open canopy spruce shrubland.

Figure 3. Open canopy hardwood shrubland.

Figure 4. Shrubland.

Figure 5. An example of the open water class, Forest Experimental Area.

Figure 6. An example of the marsh class, Forest Experimental Area.

Figure 7. An example of the wet meadow class, Forest Experimental Area.

Figure 8. An example of the thicket swamp class, beaver survey block 72.

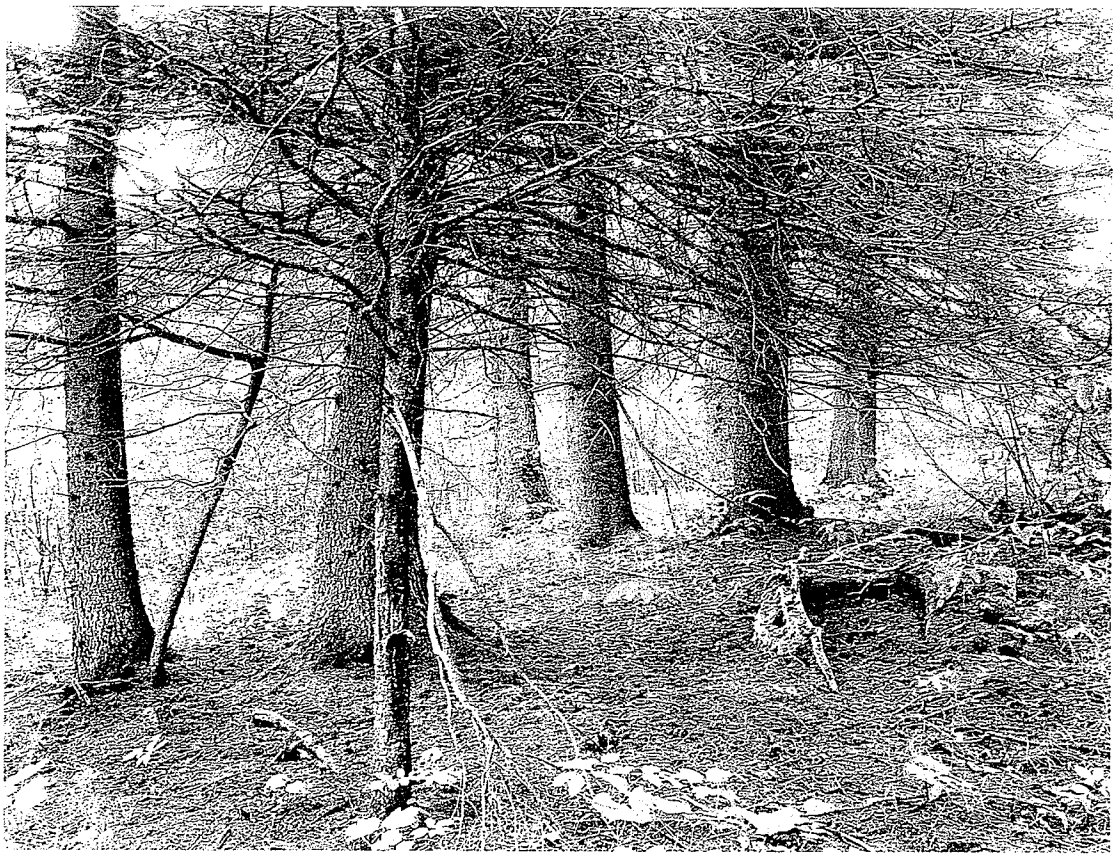
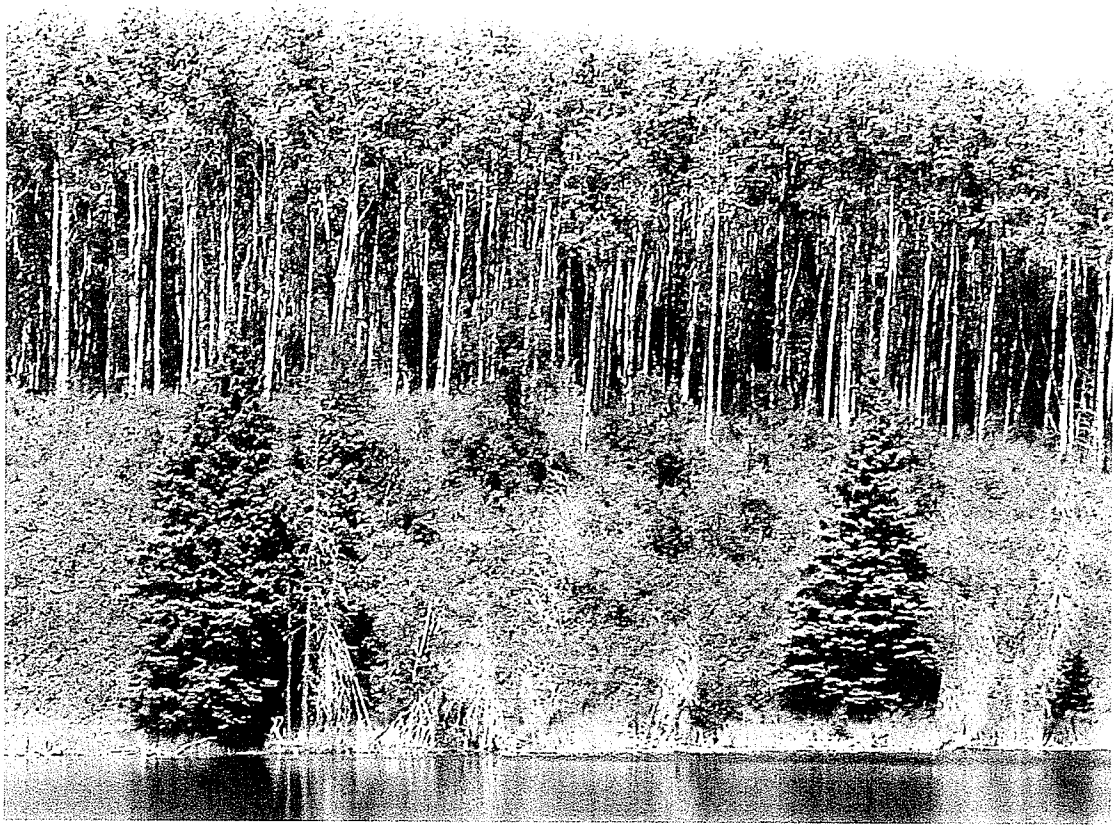


Figure 1. (Top) Closed canopy spruce stand.
Figure 2. (Bottom) Open canopy spruce shrubland.



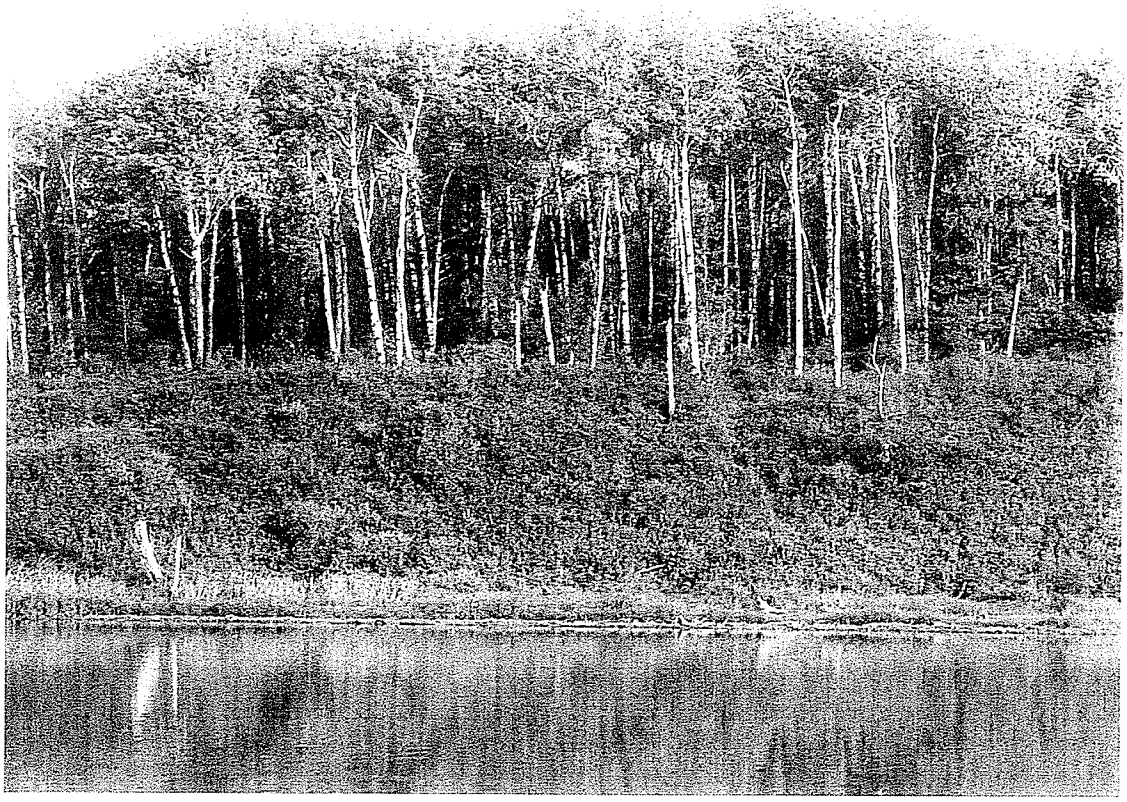


Figure 3. (Top) Open hardwood shrubland.
Figure 4. (Bottom) Open shrubland.

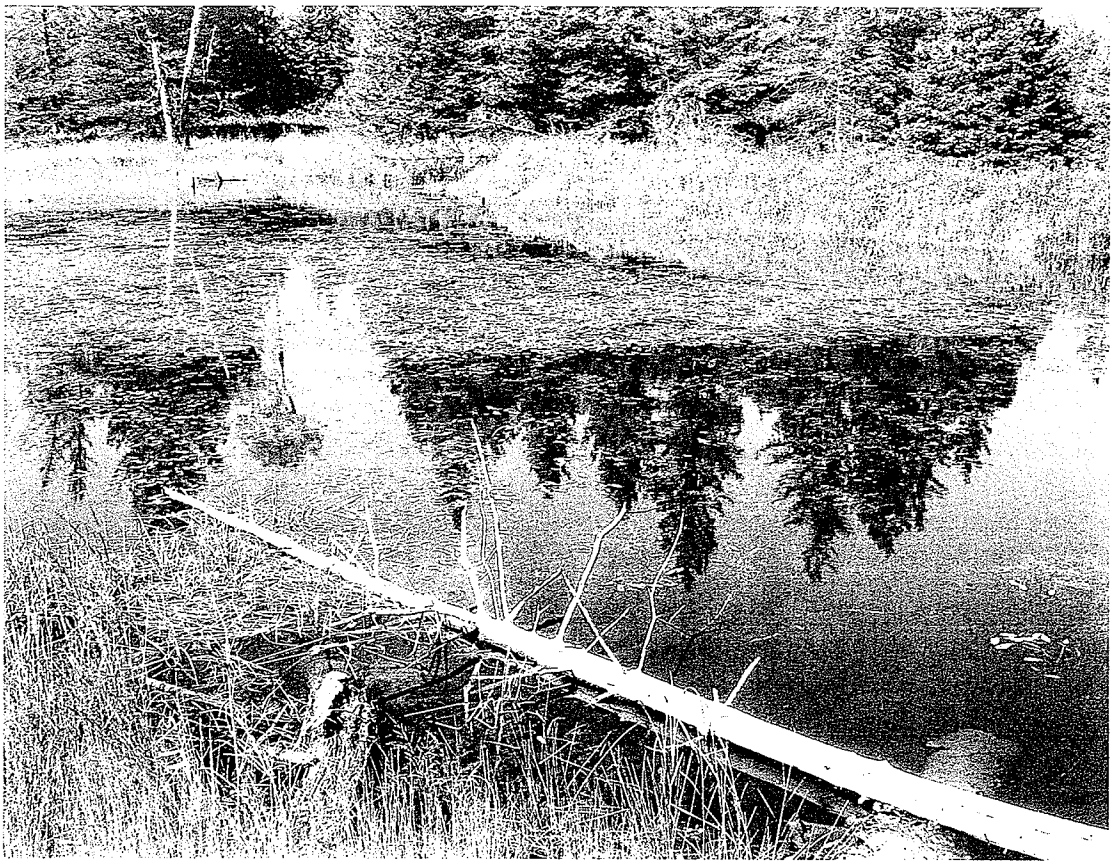


Figure 5. (Top) An example of the open water class, Forest Experimental Area.
Figure 6. (Bottom) An example of the marsh class, Forest Experimental Area.

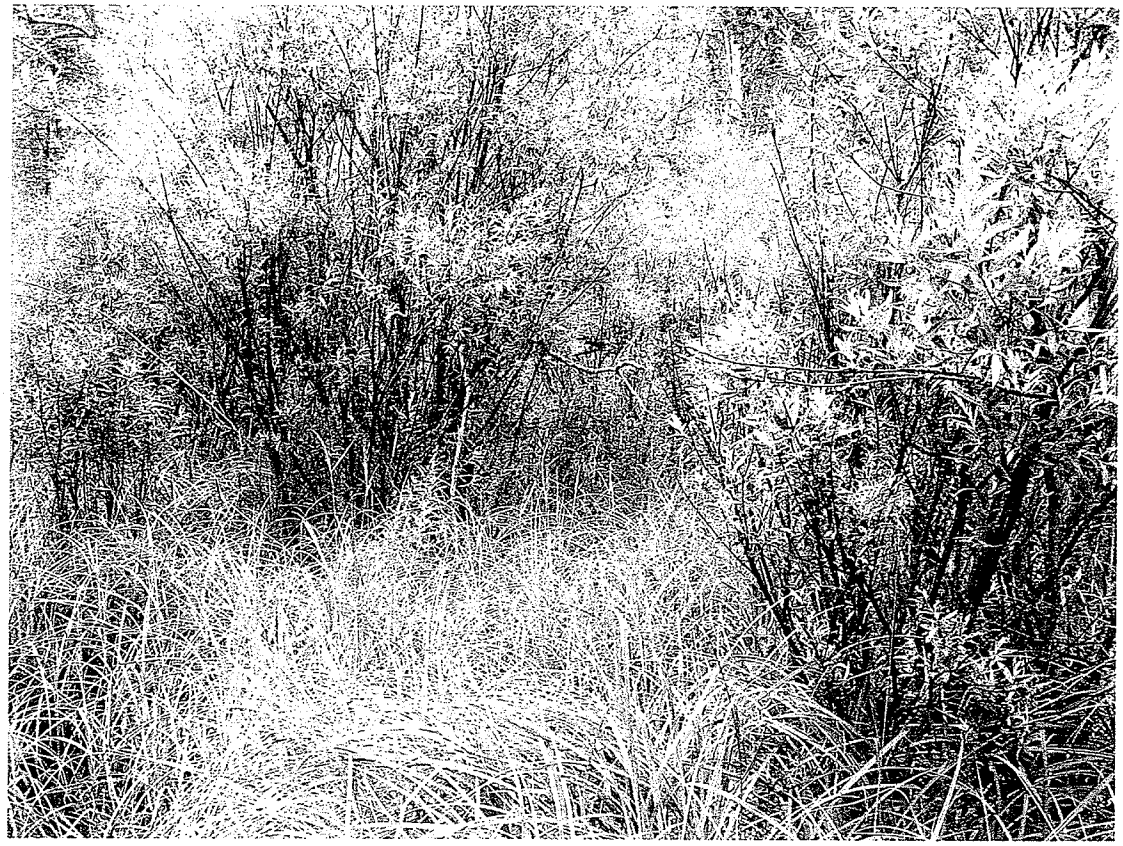


Figure 7. (Top) An example of the wet meadow class, Forest Experimental Area.
Figure 8. (Bottom) An example of the thicket swamp class, beaver survey block 72.

Appendix 2. A list of plant species encountered in RMNP, Forest Experimental Area and beaver Survey Block 72.

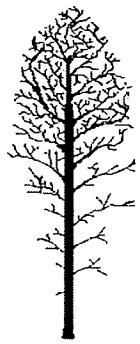
Plant Form	*Genus*	*Species*	Common Name
Trees	*Abies*	*balsamea*	Balsam fir
	Betula	*papyrifera*	White birch
	Fraxinus	*pennsylvanica*	Green ash
	Larix	*laricina*	Tamarack
	Picea	*glauca*	white spruce
	Picea	*mariana*	Black spruce
	Populus	*balsamifera*	Balsam poplar
	Populus	*tremuloides*	trembling aspen
	Quercus	*macrocarpa*	Bur oak
Shrubs	*Acer*	*spicatum*	Mountain maple
	Alnus	*crispa*	Green alder
	Alnus	*rugosa*	River alder
	Amelanchier	*alnifolia*	Saskatoon
	Arctostaphylos	*uva-ursi*	Common bear-berry
	Betula	*gladulosa*	Bog birch
	Cornus	*stolonifera*	Red-osier dogwood
	Crataegus	*chrysocarpa*	Hawthorn
	Diervilla	*lonicera*	Bush honeysuckle
	Ledum	*groenlandicum*	Labrador tea
	Lonicera	*dioica*	Twining honeysuckle
	Prunus	*pensylvanica*	Pin cherry
	Prunus	*virginiana*	Choke cherry
	Ribes	*glandulosum*	Shunk currant
	Ribes	*hudsonianum*	Northern black currant
	Ribes	*lacustre*	Black currant
	Ribes	*oxyacanthoides*	Wild gooseberry
	Ribes	*triste*	Red currant
	Rosa	*acicularis*	Prickly rose
	Rhamnus	*alnifolia*	Alder-leaved buckthorn
	Rubus	*ideaus*	Wild raspberry
	Salix	*sp.*	Willow shrubs - various
	Shepherdia	*canadensis*	Buffaloberry
	Sorbus	*decora*	Western mountain ash
	Spiraea	*alba*	Narrow-leaved meadowsweet
	Symphoricarpos	*albus*	Common snowberry
	Symphoricarpos	*occidentalis*	Western snowberry
	Viburnum	*edule*	Lowbush cranberry
	Viburnum	*lentago*	Nannyberry
	Viburnum	*trilobum*	Highbush cranberry
Herbs	*Achillea*	*millefolium*	Common yarrow
	Actaea	*rubra*	Baneberry
	Agastache	*foeniculum*	Giant hyssop
	Agrimonia	*striata*	Agrimony
	Alisma	*plantago-aquatica*	Broad-leaved water-plantain
	Anemone	*canadensis*	Canada anemone
	Anemone	*quinquefolia*	Wood anemone
	Apocynum	*androsaemifolium*	Spreading dogbane
	Aquilegia	*canadensis*	Wild columbine

	Aralia	*nudicaulis*	Wild sasparilla
	Arenaria	*lateriflora*	Blunt-leaved sandwort
	Aster	*borealis*	Marsh aster
	Aster	*puniceus*	Purplestemmed aster
	Bidens	*cernua*	Nodding beggar's ticks
	Calla	*palustris*	Water Arum
	Callitriche	*verna*	Vernal water-starwort
	Caltha	*palustris*	Yellow marsh-marigold
	Campanula	*aparinoides*	Marsh bell flower
	Cicuta	*bulbifera*	Bulb-bearing water-hemlock
	Cicuta	*maculata*	Water-hemlock
	Circaea	*alpina*	Small enchanters-nightshade
	Cirsium	*arvense*	Canada thistle
	Coptis	*trifolia*	Goldthread
	Cornus	*canadensis*	Bunchberry
	Disporum	*trachycarpum*	Fairybells
	Eleocharis	*palustris*	Creeping spike-rush
	Epilobium	*angustifolium*	Fireweed
	Epilobium	*glandulosum*	Purple-leaved willowherb
	Epilobium	*palustre*	Marsh willowherb
	Erigeron	*philadelphicus*	Philadelphia fleabane
	Erysimum	*cheiranthoides*	Wormseed mustard
	Eupatorium	*purpureum*	Spotted joe-pye weed
	Fragaria	*virginiana*	Common strawberry
	Galeopsis	*tetrahit*	Hemp-nettle
	Galium	*boreale*	Northern bedstraw
	Galium	*trifidum*	Small bedstraw
	Galium	*triflorum*	Sweet-scented bedstraw
	Geum	*aleppicum*	Yellow avens
	Geum	*rivale*	Purple avens
	Goodyera	*repens*	Lesser rattlesnake plantain
	Habenaria	*hyperborea*	Northern green bog orchid
	Habenaria	*obtusata*	Blunt-leaved bog orchid
	Heracleum	*lanatum*	Cow-parsnip
	Hieracium	*umbellatum*	Narrow-leaved hawkweed
	Hippuris	*vulgaris*	Common mare's tail
	Impatiens	*capensis*	Spotted touch-me-not
	Lactuca	*tatarica*	Common blue lettuce
	Lathyrus	*ochroleucus*	Creamy peavine
	Lathyrus	*venosus*	Purple peavine
	Lemna minor	*Lemnmin*	Common duckweed
	Linnaea	*borealis*	Twinflower
	Lycopus	*uniflorus*	Northern bugleweed
	Lysimachia	*ciliata*	Fringed loosestrife
	Lysimachia	*thyrsiflora*	Tufted loosestrife
	Maianthemum	*canadense*	Wild lily of the valley
	Maianthemum	*trifolium*	Three-leaved soloman's seal
	Mentha	*arvensis*	Wild mint
	Menyanthes	*trifoliata*	Buckbean
	Mertensia	*paniculata*	Tall lungwort
	Metteuccia	*struthiopteris*	Ostrich fern
	Mitella	*nuda*	Bishops cap
	Monenses	*uniflora*	One-flowered wintergreen
	Monotropa	*uniflora*	Indian pipe
	Myriophyllum	*spicatum*	Spiked water-milfoil

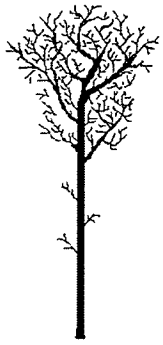
	Myriophyllum	*sp.*	Water-milfoil
	Orchis	*rotundifolia*	Round-leaved orchid
	Parnassia	*palustris*	Marsh grass of parnassus
	Petasites	*palmatus*	palmate-leaved coltsfoot
	Petasites	*saggitatus*	Arrow-leaved coltsfoot
	Polygonum	*sp.*	Smartweed
	Polygonum	*amphibium*	Water smartweed
	Potamogeton	*sp.*	
	Potentilla	*anserina*	Silverweed
	Potentilla	*norvegica*	Rough cinquefoil
	Potentilla	*palustris*	Marsh cinquefoil
	Pyrola	*asarifolia*	Pink wintergreen
	Pyrola	*secunda*	One-sided wintergreen
	Ranunculus	*gmelinii*	Yellow water-crowfoot
	Rorippa	*islandica*	Marsh yellow cress
	Rubus	*acaulis*	Dwarf raspberry
	Rubus	*pubescens*	Dewberry
	Rumex	*maritimus*	Golden dock
	Sagittaria	*cuneata*	Arum-leaved arrowhead
	Sagittaria	*latifolia*	Broad-leaved arrowhead
	Sanicula	*marilandica*	Snakeroot
	Scutellaria	*galericulata*	Marsh skullcap
	Sium	*suave*	Water-parsnip
	Smilacina	*stellata*	Star-flowered false solomon's seal
	Smilacina	*trifloia*	Three-leaved false solomon's seal
	Solidago	*canadensis*	Canada goldenrod
	Sparganium	*eurycarpum*	Giant bur-reed
	Sparganium	*sp.*	Bur-reed
	Stachys	*palustris*	Marsh hedge-nettle
	Stellaria	*sp.*	Chickweed
	Taraxacum	*officinale*	Common dandelion
	Thalictrum	*dasycarpum*	Tall meadow rue
	Thalictrum	*venulosum*	Veiny meadow rue
	Thlaspi	*arvese*	Pennycress
	Trientalis	*borealis*	Starflower
	Trillium	*cernuum*	Nodding trillium
	Typha	*latifolia*	Common cattail
	Urtica	*dioica*	Stinging nettle
	Utricularia	*intermedia*	Flat-leaved bladderwort
	Utricularia	*vulgaris*	Common bladderwort
	Veronica	*americana*	American brooklime
	Vicia	*americana*	Wild vetch
	Viola	*canadensis*	Canada violet
	Viola	*sp.*	Violet
	Zizia	*aurea*	Golden alexander
Graminoids	*Alopecurus*	*aequalis*	Short-awned foxtail
	Beckmannia	*syzigachne*	Slough grass
	Bromus	*ciliatus*	Fringed brome
	Calamagrostis	*canadensis*	Bluejoint/ Marsh reed grass
	Carex	*aquatilis*	Water sedge
	Carex	*atheroides*	Awned sedge
	Carex	*bebbii*	Bebb's sedge
	Carex	*crinita*	Fringed sedge
	Carex	*lacustris*	Lakebank sedge

	Carex	*sp.*	Sedge species
	Carex	*utriculata*	Beaked sedge
	Carex	*viridula*	Green sedge
	Cinna	*latifolia*	Drooping wood-reed
	Eleocharis	*palustris*	Creeping spike-rush
	Glyceria	*borealis*	Northern manna grass
	Glyceria	*grandis*	Tall manna grass
	Glyceria	*striata*	Fowl manna grass
	Oryzopsis	*asperifolia*	Rough-leaved rice grass
	Phalaris	*arundinacea*	Reed canary grass
	Poa	*palustris*	Fowl bluegrass
	Poa	*pratensis*	Kentucky blue grass
	Scirpus	*cyperinus*	Wool-grass
	Scirpus	*lacustris*	Common great bulrush
Ferns and Allies	*Athyrium*	*filix-femina*	Lady fern
	Botrychium	*virginianum*	Rattlesnake fern
	Equisetum	*arvense*	Common horsetail
	Equisetum	*fluviatile*	Swamp horsetail
	Equisetum	*hyemale*	Common scouring rush
	Equisetum	*pratense*	Meadow horsetail
	Equisetum	*scirpoides*	Dwarf scouring rush
	Equisetum	*sylvaticum*	Woodland horsetail
	Matteuccia	*struthiopteris*	Ostrich fern
	Lycopodium	*annotinum*	Stiff club-moss
	Lycopodium	*complanatum*	Ground cedar
Bryophytes	*Aulacomnium*	*palustre*	Tufted moss/Glow moss
	Climacium	*dendroides*	Common tree moss
	Dicranum	*sp.*	Wavy mosses
	Hylocomium	*splendens*	Stair-step moss
	Mnium	*sp.*	Haircap mosses
	Pleurozium	*schreberi*	Big red-stem moss
	Ptilium	*crista-castrensis*	Knights-plume moss
	Sphagnum	*sp.*	Sphagnum moss

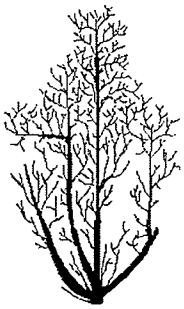
Bur Oak
Quercus macrocarpa



Balsam Poplar
Populus balsamifera



Trembling Aspen
Populus tremuloides



White Birch
Betula papyrifera

White Spruce
Picea glauca

Beaked Hazelnut
Corylus cornuta

Cherry
Prunus sp.

Mountain Maple
Acer spicatum

Appendix 3. Symbols used in the description of the successional trajectories: see figures 3.2, 3.3, 3.9 and 3.10.